EXPERIMENTS WITH ENTOMOLOGICAL ECOTOURISM MODELS AND THE EFFECTS OF ECOTOURISM ON THE OVERWINTERING MONARCH BUTTERFLY (*DANAUS PLEXIPPUS*)

By

JOHN COURTLAND WHelan

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2012
To my mom
ACKNOWLEDGMENTS

I could not have completed this dissertation without the help of many influential people in my life. From an academic standpoint, my committee, consisting of Drs. Jacqueline Y. Miller, John L. Capinera, and David W. Steadman, have provided countless hours of guidance and advice throughout my graduate studies at the University of Florida. Their support and dedication to my education has afforded me numerous opportunities to learn from them, making me a candidate throughout the process. My co-chair, Dr. Jaret C. Daniels, has been an excellent advisor and furnished me with a solid foundation on how to properly design and execute detailed experiments. Setting the bar high for how much an individual can handle, in terms of work load, his ethic was an ideal one to model after. My chair and major advisor, Dr. Thomas C. Emmel, has been perhaps the most influential person in my life throughout my graduate career. An excellent teacher, mentor, and friend, his generosity in sharing his wisdom, experience, and guidance was instrumental in shaping this dissertation, as well as my education in general. Neither would have been possible without him. His patience and ability to turn nearly any opportunity into a teaching moment has made him an extraordinary person to be associated with throughout my many years of higher level education.

In my life outside of graduate school, there were also a great many people that helped in both the completion of this dissertation, and contributed to my overall education. First and foremost, I’d like to thank my Mom, to whom this dissertation is dedicated. It was a shared dream for both of us that I would one day successfully complete a doctoral degree. Without her constant support and guidance throughout my life, this simply wouldn’t have been possible. She’s not only a wonderful teacher and
mother, but a great friend as well. Dedicating this dissertation to her is only a small token of appreciation for the role she has had in my life. I’d also like to thank my wife, Katie, who is a constant companion and has been a spectacular cheerleader throughout my studies. Without her love and encouragement, this would have been a much more difficult path. Her moral support and advice along the way were priceless.

Although there are numerous other people that very much deserve a personal acknowledgement in this dissertation, this section would continue on for several pages. They know who they are and I want them to know that whether they are a dear friend, a colleague, or a family member, this dissertation embodies their belief in me and their dedicated advocacy for my ambitions.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>4</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>11</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>13</td>
</tr>
<tr>
<td>LIST OF ABBREVIATIONS</td>
<td>19</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>20</td>
</tr>
<tr>
<td><strong>1 INTRODUCTION: HISTORY OF TOURISM AND ECOTOURISM</strong></td>
<td>23</td>
</tr>
<tr>
<td>History of Tourism</td>
<td>23</td>
</tr>
<tr>
<td>The Beginnings of Tourism</td>
<td>23</td>
</tr>
<tr>
<td>Tourism in the ancient world</td>
<td>23</td>
</tr>
<tr>
<td>Travel in ancient Egypt</td>
<td>26</td>
</tr>
<tr>
<td>Beyond Egypt</td>
<td>29</td>
</tr>
<tr>
<td>Return of the Greeks</td>
<td>31</td>
</tr>
<tr>
<td>Travel and Tourism in the Roman Empire</td>
<td>38</td>
</tr>
<tr>
<td>A new age in tourism</td>
<td>40</td>
</tr>
<tr>
<td>Motivations of early travel</td>
<td>42</td>
</tr>
<tr>
<td>The agenda of the ancient tourist</td>
<td>45</td>
</tr>
<tr>
<td>Holy Travel</td>
<td>47</td>
</tr>
<tr>
<td>The Grand Tour</td>
<td>50</td>
</tr>
<tr>
<td>The Evolution of Ecotourism</td>
<td>55</td>
</tr>
<tr>
<td>Pioneers of Ecotourism</td>
<td>56</td>
</tr>
<tr>
<td>Charles Darwin</td>
<td>56</td>
</tr>
<tr>
<td>Alexander von Humboldt</td>
<td>59</td>
</tr>
<tr>
<td>Alfred Russel Wallace</td>
<td>62</td>
</tr>
<tr>
<td>The Rise of Ecotourism</td>
<td>68</td>
</tr>
<tr>
<td>Defining tourism</td>
<td>69</td>
</tr>
<tr>
<td>Defining ecotourism</td>
<td>70</td>
</tr>
<tr>
<td>Popular ecotourism</td>
<td>78</td>
</tr>
<tr>
<td>The Rise of Entomological Ecotourism</td>
<td>81</td>
</tr>
<tr>
<td>The Early Stages</td>
<td>81</td>
</tr>
<tr>
<td>Early Field Clubs</td>
<td>85</td>
</tr>
<tr>
<td>The Benefits of Entomological Ecotourism</td>
<td>88</td>
</tr>
<tr>
<td>The Next Steps for Entomological Ecotourism</td>
<td>90</td>
</tr>
<tr>
<td><strong>2 INSECTS IN THE ECOTOUR</strong></td>
<td>102</td>
</tr>
<tr>
<td>Butterfly Farming and Ranching</td>
<td>102</td>
</tr>
<tr>
<td>Butterfly Ranching in the Solomon Islands</td>
<td>109</td>
</tr>
<tr>
<td>Butterfly Farming in Florida and Costa Rica</td>
<td>115</td>
</tr>
</tbody>
</table>
Chapter Conclusion ........................................................................................................... 215

3 GUIDING FOR ENTOMOLOGICAL ECOTOURISM ............................................... 233

Integrating Insects in the General Ecotour ................................................................. 235
Entomological Guide Training .................................................................................... 236
  Guide Training Framework ....................................................................................... 237
  Roles of Guides .......................................................................................................... 238
  Insect Exhibits ............................................................................................................ 242
Approaching the Topic of Entomology ....................................................................... 245
  Individual Accounts of Insects .................................................................................. 246
  Insect Ambassadors .................................................................................................... 248
Additional Entomological Ecotour Topics .................................................................. 325
  Insect Herbivory ......................................................................................................... 325
  Pollination .................................................................................................................. 329
  Nutrient Cycling and Decomposition ........................................................................ 330
Chapter Conclusions .................................................................................................... 333

4 EFFECTS OF ECOTOURISM ON WILDLIFE AND INSECTS ......................... 373

Effects of Ecotourism on Wildlife .............................................................................. 373
  Disturbance to Wildlife .............................................................................................. 374
  Encroachment as a Disturbance to Wildlife ............................................................... 375
    Effects on habitat choice ......................................................................................... 377
    Effects on mating ...................................................................................................... 378
    Effects on parental investment .................................................................................. 378
    Habituation of wildlife to ecotourism ...................................................................... 379
    Effects on migration .................................................................................................. 380
  Effects of Artificial Light on Wildlife ........................................................................ 382
    Lighting effects on Sea Turtles ............................................................................... 382
    Lighting effects on animal navigation ...................................................................... 384
    Lighting and insects .................................................................................................. 386
    Lighting in ecotourism areas ..................................................................................... 390
  Other Examples of the Effects of Ecotourism on Wildlife ........................................ 391
    Chimpanzees affected by ecotourism ....................................................................... 392
    Asian Rhinos affected by ecotourism ....................................................................... 394
    Waterbirds affected by ecotourism ......................................................................... 395
Effects of Noise and Flash Photography on Wildlife .................................................. 397
  Effects of Noise on Wildlife ...................................................................................... 397
  Effects of Flash Photography on Wildlife .................................................................. 398
Effects of Ecotourism on Insects ............................................................................... 400
  Ecotourism and the Monarch Butterfly ................................................................. 400
    Monarch butterfly navigation techniques .................................................................. 404
    Ecotourism at the Monarch overwintering sites ...................................................... 407
    Effects of ecotourism in the Monarch reserves ....................................................... 411
  Hearing in Butterflies ............................................................................................... 411
  Vision in Butterflies .................................................................................................... 415
5 CONCLUSIONS ................................................................................................................................................. 538
Future Research ........................................................................................................ 543
The Future of Entomological Ecotourism ................................................................. 544
Poised for Growth ..................................................................................................... 544
Future Initiatives ....................................................................................................... 546
Importance of Entomological Ecotourism ............................................................... 547

LIST OF REFERENCES ............................................................................................... 550

BIOGRAPHICAL SKETCH ......................................................................................... 591
<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-1</td>
<td>Ecotourism is not a discrete list of activities, but rather a philosophy on travel</td>
<td>101</td>
</tr>
<tr>
<td>2-1</td>
<td>Components necessary in pre-trip information packets sent to registered participants</td>
<td>227</td>
</tr>
<tr>
<td>2-2</td>
<td>Summary of localities and group sizes for Research Associate entomological ecotourism case studies from 2007-2011</td>
<td>230</td>
</tr>
<tr>
<td>2-3</td>
<td>Average daily costs for each of the tour models outlined, the One Species/One Phenomenon, Paired-Interests, and Research Associate models</td>
<td>231</td>
</tr>
<tr>
<td>2-4</td>
<td>Typical components of an entomological ecotourism trip brochure and the individual contents for each section</td>
<td>232</td>
</tr>
<tr>
<td>3-1</td>
<td>Advantages and disadvantages to each type of guide found in the ecotourism field</td>
<td>337</td>
</tr>
<tr>
<td>4-1</td>
<td>List of ecotourism activities and their impacts on wildlife based on a review of previous studies</td>
<td>493</td>
</tr>
<tr>
<td>4-2</td>
<td>Detailed descriptions of reaction behaviors exhibited by each categorical response</td>
<td>501</td>
</tr>
<tr>
<td>4-3</td>
<td>Mean longevities (days) for each flash treatment, with 95% confidence intervals, and median longevity</td>
<td>511</td>
</tr>
<tr>
<td>4-4</td>
<td>Mean longevities (days) across all flash treatments (30, 60, 90, and 120), with 95% confidence intervals</td>
<td>512</td>
</tr>
<tr>
<td>4-5</td>
<td>Mean longevities (days) between flash treatments for freshly emerged Monarchs, with 95% confidence intervals</td>
<td>512</td>
</tr>
<tr>
<td>4-6</td>
<td>Mean longevities (days) across all ages between combined treatment groups</td>
<td>512</td>
</tr>
<tr>
<td>4-7</td>
<td>Mean percentage of each response to flash by Monarch butterflies across all flash treatments (30, 60, 90, and 120 flashes), as determined by age</td>
<td>513</td>
</tr>
<tr>
<td>4-8</td>
<td>Mean percentage of reactions, as determined by increasing age categories</td>
<td>513</td>
</tr>
<tr>
<td>4-9</td>
<td>Mean percentage of each response to flash by Monarch butterflies across all age groups, as determined by flash treatment</td>
<td>514</td>
</tr>
<tr>
<td>4-10</td>
<td>The percentage of positive reactions based on flash treatment levels</td>
<td>515</td>
</tr>
</tbody>
</table>
4-11 Mean percentage of reactions across all treatments and age groups, as determined by sex of the Monarch butterflies. .......................................................... 515

4-12 Mean percentage of reactions, across all age groups, as determined by flash 516

4-13 Mean percentage of reactions by grouping all reaction categories into one, denoted by Positive Response. ................................................................. 516

4-14 Mean minutes per day that Monarchs spent in each subcage with 95% confidence intervals that the population mean is within the value of the sample mean. ................................................................. 524

4-15 Monarch antennae exhibit different structures on their club and filament. ............ 534

4-16 Queen antennae exhibit different structures on their club and filament. ............ 537

4-17 Light attenuation chart. As the distance between the light emitting device and the subject increases, light attenuates, or decreases in intensity dramatically. 537
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-1</td>
<td>A timeline of tourism’s history from 3,000 B.C. to 1,000 B.C.</td>
<td>92</td>
</tr>
<tr>
<td>1-2</td>
<td>A timeline of tourism’s history from 1,000 B.C. to year 0</td>
<td>93</td>
</tr>
<tr>
<td>1-3</td>
<td>A timeline of tourism’s history from 0 to the 1980s, when the establishment of ecotourism was solidified</td>
<td>94</td>
</tr>
<tr>
<td>1-4</td>
<td>The Grand Tour Era saw a shift in the role of travel and tourism</td>
<td>95</td>
</tr>
<tr>
<td>1-5</td>
<td>Average length of the Grand Tour 1547-1840</td>
<td>95</td>
</tr>
<tr>
<td>1-6</td>
<td>Average age of Grand Tour participants 1547-1840</td>
<td>96</td>
</tr>
<tr>
<td>1-7</td>
<td>Percentage of Grand Tour participants who attended a University from 1547-1840</td>
<td>96</td>
</tr>
<tr>
<td>1-8</td>
<td>International tourist arrivals by region (million)</td>
<td>97</td>
</tr>
<tr>
<td>1-9</td>
<td>Inbound tourism by mode of transport in 2010</td>
<td>97</td>
</tr>
<tr>
<td>1-10</td>
<td>Purposes of visit for inbound tourists in 2010</td>
<td>98</td>
</tr>
<tr>
<td>1-11</td>
<td>Examples of tourism concentric circles</td>
<td>99</td>
</tr>
<tr>
<td>1-12</td>
<td>The ecotourism spectrum exhibits two poles</td>
<td>100</td>
</tr>
<tr>
<td>1-13</td>
<td>According to a 2007 publication of the National Survey of Recreation and the Environment, bird watching is not only a common activity amongst U.S. citizens, but is growing from year to year</td>
<td>101</td>
</tr>
<tr>
<td>2-1</td>
<td>Percentage of butterflies sold in each life stage at Shady Oaks Butterfly Farm per month</td>
<td>217</td>
</tr>
<tr>
<td>2-2</td>
<td>Examples of various types of breeding cages used at butterfly farming operations</td>
<td>218</td>
</tr>
<tr>
<td>2-3</td>
<td>Larval feeding boxes are organized and filled with clippings of host plants for larvae to feed upon</td>
<td>219</td>
</tr>
<tr>
<td>2-4</td>
<td>Pupal eclosion chambers are found at both farms and exhibits, allowing butterflies to emerge as fully mature adults in a controlled setting</td>
<td>220</td>
</tr>
<tr>
<td>2-5</td>
<td>Butterfly larvae are often allowed to feed on naturally occurring or planted host plants with the hybrid EBN model</td>
<td>221</td>
</tr>
</tbody>
</table>
2-6 Total number of ecotourists joining the OS/OP entomological ecotour model during the five-year study period. ................................................................. 222

2-7 Levels of trip participation between two Mexico Monarch trips in 2011. ... 222

2-8 Levels of trip participation on three P-I model trips to Costa Rica. ............. 223

2-9 There is a negative correlation between the need for modern conveniences at ecolodges and the number or quality of wildlife experiences. ................. 223

2-10 Overall visitor satisfaction is at a maximum between two thresholds of quality 224

2-11 The Resplendent Quetzal (Pharomachrus mocinno) is perhaps the most sought-after bird by birdwatchers on an ecotour to Costa Rica. ....................... 224

2-12 Light sheets may be hung in any environment to attract nocturnal insects. 225

2-13 There is a negative correlation between the length and variety of daytime activities and the appropriate length and detail of nightly lectures while on the P-I ecotour. ......................................................................................... 226

2-14 There is a positive feedback loop between field interpretation and group cohesiveness .................................................................................. 227

2-15 A butterfly bait trap is set along a road in Panama. ...................................... 228

2-16 An ecotourist admires the variety of nocturnal insects attracted to a single light bulb in Pico Bonito National Park, Honduras. ....................................... 229

2-17 The flow of information in the Research Associate model is wide and varied. 231

3-1 Each circle denotes the set of responsibilities each type of guide must assume. ........................................................................................................ 338

3-2 Three pages of potential guide training information for entomological ecotourism guides. .................................................................................. 339

3-3 The trophic pyramid. Situated at a key position in the trophic pyramid, insects interact directly with most life forms. .................................................. 342

3-4 Living insect exhibits are excellent ways to integrate insects in the ecotour...... 343

3-5 Insect collections represent a unique way for ecotourists to view, photograph, and appreciate insect diversity. ......................................................... 344

3-6 Leaf-cutter Ants. ....................................................................................... 345

3-7 Arboreal Termites. .................................................................................. 346
3-8  Dung Beetles.................................................................347
3-9  Mopane Worm...............................................................348
3-10 Giraffe-necked Weevil......................................................349
3-11 Blue Morpho Butterfly......................................................350
3-12 Jungle Nymph Stick Insect...............................................351
3-13 Balfour (1915) reports that indigenous tribes in Papua New Guinea use the femur of certain stick insects as fishhooks. ..................................................352
3-14 Urania Moth........................................................................353
3-15 Cracker Butterfly...............................................................353
3-16 Stingless Bees.................................................................354
3-17 Migratory Locusts may come in several different shapes, sizes, and colors, largely dependent on whether they are in their migratory phase or not...........355
3-18 A Helicopter Damselfly is displayed in a man’s palm, exhibiting its large size.. 355
3-19 Glowworms........................................................................356
3-20 Clearwing Butterflies..........................................................357
3-21 Bullet Ant...........................................................................357
3-22 Charaxes Butterflies............................................................358
3-23 Goliath Beetles.................................................................359
3-24 Bogong Moths.................................................................360
3-25 Palm Grubs..........................................................................361
3-26 Army Ants..........................................................................362
3-27 Human Bot Fly.....................................................................363
3-28 Mound-building Termites......................................................364
3-29 African Driver Ants..............................................................365
3-30 Birdwing Butterflies.............................................................366
3-31 Monarch Butterflies..............................................................367
Acacia Ants............................................................................................................................. 368
Dynastes Beetle..................................................................................................................... 369
Hercules Moth and other Silk Moths.................................................................................... 370
Homerus Swallowtail Butterfly............................................................................................ 371
Peanut-head Lantern Fly....................................................................................................... 372
A moth light trap in the Chiriqui Highlands, Panama, attracts thousands of moths, beetles, and other insects at night. ................................................................. 492
Infrastructure at the El Rosario Monarch sanctuary and colony site.............................. 495
Infrastructure at Sierra Chincua Monarch sanctuary and colony site............................ 496
Examples of Monarch behavior and sights within the Monarch sanctuaries................. 497
Map showing known overwintering colonies of Monarch butterflies in the Transvolcanic mountain range of southern Mexico ......................................................... 498
Various stakeholders of the Monarch overwintering phenomenon............................... 499
Stakeholders in Monarch ecotourism are also located in adjacent towns and benefit from the sale of goods and services. ................................................................. 500
Materials used for sound studies....................................................................................... 501
Greenhouses and sprinkler system used in sound and flash studies............................. 502
Monarchs were separated into four holding cages during the punctuated sound experiments. ......................................................................................................................... 502
Audio materials used in sound study................................................................................ 503
Data sheet showing various treatment combinations between the frequency and decibel levels that were used in the low frequency punctuated sound study................................. 504
Screen graphic of Subwoofer Bass Tester application (Alkek Instruments) used to generate low frequency sounds at set decibels in the low frequency punctuated sound study. ........................................................................................................ 505
Schematic of sustained sound study.................................................................................... 505
Sustained sound study experimental setup........................................................................ 506
Data sheet for sustained sound study................................................................................ 507
Monarch longevity increased significantly when Monarchs were exposed to flash treatments. As the age of the Monarch progressed from 24-48 hour to 12-14 days old, the total incidence of reactions increased.

Percentage of positive reactions for each flash treatment level when combining 24-48 hour and 12 to 14-day ages. As the total number of flashes increase from 0 to 120 per treatment, the frequency of reactions increased.

Mean percentages of reactions when combining all flash treatments at all ages. When subjected to flash, Monarch butterflies physically reacted nearly one out of every three times. Although the Morpho is a larger butterfly, the size of the thorax is not drastically different between the Monarch and Morpho.


Mean number of minutes per hour that Monarchs spent in all subcages during the sustained sound study. Mean total minutes per day spent in each of the four subcages of the experiment.

Mean number of minutes per hour that Monarchs spent in cage one, where the speaker was located.
4-37 Mean number of minutes per hour that Monarchs spent in cage three (third loudest cage).......................................................................................................................... 526

4-38 Comparing cage one and cage three, it is evident that the mean number of minutes per hour decreases for cage one, while increasing for cage three...... 527

4-39 Mean number of minutes per hour that Monarchs spent in cage two. ............. 527

4-40 Mean number of minutes per hour that Monarchs spent in cage four............. 528

4-41 Examples of public exhibits displaying freshly emerged butterflies.. ............. 529

4-42 Monarchs “cascading” from their roosts in the El Rosario Monarch Sanctuary in Mexico.. .................................................................................................................. 530

4-43 Monarch antennae are differentially pigmented with the base of the filament or flagellum darker than the bulb or club (Guerra et al. 2012). ......................... 530

4-44 Scanning Electron Microscope (SEM) photos of the Monarch butterfly antennal club. ..................................................................................................................... 531

4-45 Side and above views of the coeloconic sensilla described in Hallberg (1981). .......................................................................................................................... 532

4-46 Scanning Electron Microscope (SEM) photos of the Monarch butterfly antennal filament.. ................................................................................................. 533

4-47 Scanning Electron Microscope (SEM) photos of the Queen butterfly antennal club.................................................................................................................... 535

4-48 Scanning Electron Microscope (SEM) photos of the Queen butterfly antennal filament............................................................................................................ 536
# LIST OF ABBREVIATIONS

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>JH</td>
<td>Juvenile Hormone</td>
</tr>
<tr>
<td>OS/OP Model</td>
<td>One species/one phenomenon model of entomological ecotourism</td>
</tr>
<tr>
<td>P-I Model</td>
<td>Paired-interest model of entomological ecotourism</td>
</tr>
<tr>
<td>RA Model</td>
<td>Research associate model of entomological ecotourism</td>
</tr>
<tr>
<td>S-I Model</td>
<td>Single-interest model of entomological ecotourism</td>
</tr>
</tbody>
</table>
Our present-day concept of ecotourism has evolved from over five thousand years of tourism’s history. The early Egyptians, Greeks, and Romans were the first to travel for the sake of pleasure, ultimately forming the foundation of tourism culture. However, it was not until the most recent centuries that nature began to take a commanding role in the motivations for travel. The Grand Tour era marked a pronounced transition in travel, as young naturalists emerged to become the pioneers of ecotourism, exploring the wilderness for the sake of pleasure and education. Today, ecotourism is expanding at unprecedented rates and new ecotourism niches are arising.

Nature-based tourism that incorporates insects, termed entomological ecotourism, promotes the values of ecotourism in new ways through several discrete models developed within this dissertation. Whether an entomological ecotour focuses on a single phenomenon, is paired with another ecotour focus, or is primarily research-based, entomological ecotourism has earned a place in the ecotourism industry. In order for insects to be accepted into general ecotourism, interpretation and guide
training should focus on the most charismatic insects in the world to capture the interests of more than just dedicated entomological ecotourists.

Ecotourism functions in many positive ways, not least of which is its ability to create value for natural areas. Ecotourists are more willing to pay for areas that are more naturally beautiful and rich in flora and fauna. However, studies indicate that in some cases ecotourism can have negative side effects by disturbing the same wildlife that ecotourism is designed to protect. In this dissertation, research was conducted on the effects of noise and flash photography on Monarch butterflies to further investigate such impacts on wildlife. Each year, millions of Monarch butterflies aggregate in overwintering colonies in Mexico and are highly visited by ecotourists, making it an ideal system in which to conduct one of the first studies on ecotourism’s impacts on insects.

It was hypothesized that noise and flash photography, both common byproducts of ecotourism, would elicit disturbance reactions, function to repel the butterflies, and, in some cases, decrease longevity. Results from these experiments did not support the hypotheses and, in fact, yielded surprising outcomes. Exposure to punctuated sound in frequencies standard of human crowd noise (200 – 9,000 Hz) as well as very low frequencies (100 – 200 Hz) yielded no response on part of the Monarchs. However, Monarchs spent significantly less time in areas of experimental cages where sustained noise levels were the highest. Flash photography was found to be disruptive to butterfly behavior, causing Monarch test subjects to display a variety of disturbance reactions when exposed to camera flashes. However, flash seemed to have a positive effect on longevity, with butterflies that were exposed to flash exhibiting a 70% longer lifespan when compared to those that were not exposed. Ultimately, these data suggest that
noise and flash photography are not of critical concern to the health of Monarch butterflies and the migration event in general, but should be limited wherever possible in the Monarch overwintering grounds. Future studies are needed to test for additional effects of ecotourism on the Monarch butterfly, such as effects of ecotourism on soil erosion and forest quality within Monarch colony sites.
CHAPTER 1
INTRODUCTION: HISTORY OF TOURISM AND ECOTOURISM

History of Tourism

The incredible advances in the way humans move about the surface of the earth over the past several centuries gives the impression that today’s concept of tourism has only really been possible since the advent of modern modes of transportation. In reality, humans have engaged in tourism for over five thousand years, and our present-day forms of tourism are remarkably similar to those that started it all. Nevertheless, throughout the past several millennia, the motivations, styles, and general ease of travel have indeed evolved significantly. In the following sections, we will trace this progression of travel and tourism throughout the ages. Although tourism has likely existed in a raw form before the most notable civilizations, we are confounded by the written histories of such, and as a result, we will hereby focus on the earliest records of tourism with the Egyptians, Greeks, and Romans, as tourists in the ancient world.

The Beginnings of Tourism

Tourism in the ancient world

As civilizations built up around the Nile in the ancient world, there became a great need to commute between the various city centers, which began to line the riverbanks. Ships were the logical vehicles to facilitate such movement, starting as simple vessels constructed out of woven papyrus reeds. Within only decades, however, 40-ship flotillas composed of sturdy wooden vessels were recorded as sailing down the Nile by 2,700 B.C. (Casson 1971). One of the greatest attributes of the Nile for water-based transportation was that Egyptians were able to sail in both directions – downstream due to the current and upstream due to prevailing winds from the north. When possible,
water-based transportation was dominant. It was quick, reliable, and direct. However, where rivers did not exist, transit took a much simpler form, and travelers resorted to walking, or in some cases using donkeys as primary modes of transportation. The world would not see the first terrestrial vehicle appear until around 2,500 B.C., when the Sumarians of Northern Mesopotamia developed wagons with heavy wheels that were drawn by oxen or wild asses (Casson 1994).

A major advancement began to take shape with the introduction of the horse, originally as a working animal in roughly 2,300 B.C. The presence of trained horses, used over several centuries as a draught animal to pull simple wheeled carts, gave rise to the chariot, the choice vehicle of Kings and Nobles. With the chariot gaining elite status soon after its inception around 1,600 B.C., money was no object when considering the materials and design of such prized vehicles. The wealthy members of society employed the most skilled laborers and purchased the most expensive materials in order to fine-tune and engineer these vehicles (Crowther 2007). As the chariot became lighter and faster, it was not long before it was adopted as a tool of war (Moorey 1986). Firmly fixed in society at the time, the chariot was constantly being improved upon for speed and agility. This was a time of great advances in technology, perhaps attributed to desires by the wealthy elite to refine their chariot design for greater speed, maneuverability, and comfort. New innovations would soon allow carpenters to heat and bend wood to make spokes, furthering the abilities of the chariot, which also served to make it a more desirable symbol of social status. Only a few centuries later, we see the chariot spread northward to northern Europe and Greece, and eastward to India and China (Littauer and Crouwell 1979).
The chariot’s rise in popularity across Europe and Asia was primarily due to its use in war and hunting. Nevertheless, the chariot was also used as a vehicle for tourism, as seen in early Mycenaean culture where paintings in the town center of Tiryns depicted the chariot driver with a pair of ladies touring the countryside (Casson 1994). Although the lack of roads limited the growth of chariot-drawn transportation at the time, there is evidence that roadways did exist. The rise and spread of such roads likely contributed to the popularity of what some historians term “chariot tours”. Although paved roads were unheard of in 2,000 B.C., the packed earth roads that were referenced in countless letters, stories, and hymns, could sustain travel at rates up to 3½ miles per hour. Seemingly sluggish by today’s standards, this pace matched that of mule-drawn carts on prized Roman roads that existed two millennia later (Casson 1994) (Figure 1-1 and Figure 1-2).

While terrestrial tourism may have been relatively insignificant up until the advent of the chariot, ships provided the necessary transportation for travelers and tourists for many centuries prior. As seen throughout the history of early civilizations, travel to religious and cultural festivals was perhaps one of the earliest forms of tourism. Historians like Herodotus detailed events of ancient festivals with great specificity. At a particular festival in Herodotus' writings, known as Bubastis, men and women would crowd into boats and sail on the Nile river passing from town to town, playing music, yelling, laughing, dancing, making fun of townspeople, and exposing themselves. Continuing like this until reaching the city of Bubastis, this celebration is marked with great sacrifices. Herodotus wrote that more wine is consumed at this one festival than during the entire year (Marincola and De Selincourt 1996). This sounds remarkably
similar to today’s Mardi Gras festivals that take place each February. However popular these festivals were, and they indeed were with some attracting upwards of 700,000 attendees, other forms of tourism continued to evolve during this period and shape the way we view modern day tourism.

**Travel in ancient Egypt**

Starting in and around 1,500 B.C., Egypt entered into a time where tourism began to flourish. At this time, some of Egypt’s most spectacular and renowned remnants of great civilizations were already a thousand years old and objects of considerable affection and intrigue. The Sphinx and three pyramids at Giza, the pyramid complex at Abusir, and the step pyramid of Djoser at Sakkararah were among the many great structures that literally surrounded Egyptian society (Yoyette 1960). At this same time, we see the emergence and soon-to-be prominence of two characteristic behaviors of ancient tourists. One is the desire to leave a mark, regarded today as graffiti, and two is the need to return home with souvenirs. This is a poignant evolutionary step towards modern-day tourism. Fortunately, only a small fraction of society could write at this point in history and those that could were often educated and skilled at their craft. Nevertheless, unapproved etchings on the pyramids, tombs, and sanctuaries were widespread, many of which were illegible and disdained by the guardians of such monuments, as well as fellow scribes. These feelings are encapsulated by writings of the Egyptian scribes Pennewet and Wia on a wall of the chapel at Djoser’s Complex: “I say: Explain to me these words. My heart is sick when I see the work of their hands…It is like the work of a woman who has no mind; would that we had someone who could have denounced them before they entered the temple” (Casson 1994).
Coupled with this desire to make it known that you visited a place by writing on the attraction itself was the desire to show those to whom the traveler returns (i.e., family, friends, business partners) the various sites one visited during the course of the trip. From small mementos and replicas of monuments, to rare jewelry, returning with a souvenir was as important as the visit itself to the ancient tourist. Some ancient tourists even went as far as to return with human souvenirs, as was the case when once the Pharaoh’s envoy returned from Sudan with a “pygmy trained in native dance” (Casson 2001, MacDonald and Rice 2003). This importance can extend beyond the traveler and to their family and friends, as can be seen in the following letter: “I have never before written to you for something precious I wanted. But if you want to be like a father to me get me a fine string of beads, to be worn around the head. Seal it with your seal and give it to the carrier of this tablet so that he can bring it to me. If you have none at hand, dig it out of the ground wherever such objects are found and send it to me. I want it very much; do not withhold it from me. In this I will see whether you love me as a real father does” (Oppenheim 1967). The fervor with which the sender writes is indicative of not only the intense desire by the individual, but also of potential motives for travel among tourists of the day.

Travel during the last several millennia B.C. saw a shift from being exclusively for government officials on official business to the common man. Along major transit routes, the need for rest stops and provisioning posts gave rise to some of the first lodges. At first, these were government-run and to be used only by government officials (Casson 1994). With many of these officials serving as couriers, transporting documents from city to city, these outposts began to take the form of an early postal
system (James et al. 1995). In traditional fashion, non-confidential mail would be passed off at these lodges to whomever would be passing through and going to the intended address. More secure documents were rightly the sole responsibility of the courier. While these early lodges were exclusively for government personnel at first, the model began to be replicated to serve the common people of society. Although these early inns were not exactly wholesome establishments, they began to satisfy the primitive needs of common travelers whom before the existence of such would descend upon a town or festival with no formal facilities to satisfy their requirements of food or lodging. Resembling today’s music festivals, ancient tourists were expected to arrange their own camps, bring their own provisions, and essentially fend for themselves. Thus, early taverns and bars served a significant need of society at this time and increased in popularity, despite their seedy nature. As an indication of their quality, a document recovered dating back to the first half of the second millennium B.C. states that while in an early inn: “If a man should urinate in the presence of his wife, he will not prosper…He should sprinkle his urine to the left and right of the door jambs of the tavern and he will prosper” (Gelb et al. 1958). Throughout the next millennia, we see a gradual improvement in public lodging.

Sea travel was long regarded as the most comfortable way to travel in the ancient world, and as new technologies arose to make it more efficient and safe, the seas were no longer exclusively for traders, explorers, navies, and pirates. With the steady increase in sea travel came a relatively well-mapped world. Combined with the fact that most major tourist attractions were either on major water ways or at least proximal to them, ship-based tourism was the choice method of travel during the turn of the last
millennia B.C. (Finley 1970, Casson 1994). However, the new advances in seamanship also brought an increase in naval warfare, due in part to the transition from the Bronze to Iron Age, as well. Egypt was one country that saw both the upside and downside of the seas and the enemies that used it for war. Known mysteriously as the “Sea People” by historians, wave after wave of naval invaders flooded the Nile region and sent Egypt into a remission of living in the past around 1,200 B.C. Their now archaic civilization became prime for tourism, as decades of warfare had in effect fossilized a great deal of the landscape, including the wonders of the world found in Egypt (Casson 1994). With great destruction brought a novel economic opportunity – tourism.

**Beyond Egypt**

At the turn of the last millennia B.C. (i.e., 1,000 B.C.), the older naval superpowers (i.e., the Minoans, Mycenaeans, and Egyptians) were replaced by the Phoenicians. Their largely trade-based society perpetuated their affluence in maritime activities and the world saw them as the rulers of the sea for the next several centuries (Casson 1991). Concomitant with this prevalence of sea travel was a lessening commitment to land-based travel infrastructure. With a clear gap in infrastructure, the next major advancement in tourism was a push for roadway construction and expansion during the Assyrian empire from around 900-600 B.C. With a mighty military force of great discipline and organization, roads were constructed to facilitate the movement of their army. These new roads had to be of utmost quality: durable enough to accommodate large Assyrian chariots and the “tanks” of the ancient world – the battering rams (Oded 1970). In addition to supreme durability, these roads were outfitted with guard posts every six miles, each post having the ability to communicate with the next via fire signals. Much like the outposts of the early Greeks, these were vital for communication.
Excavations of the area found early written travel-guides giving names of places along each route, as well as distances from one another (Casson 1994).

Another major advancement during the eminence of the Assyrian empire was the ability for men to ride horses. While the horse had found its place in society many centuries prior, it was the Assyrians that adopted it not simply as a draught animal, but a vehicle for combat (McMiken 1990). Just as other military technologies migrated from the battlefield to everyday life, so too did the horse as a vehicle.

After the Assyrians were conquered in 612 B.C., the vast, expansive, and successful Persian Empire arose from the ashes. The main secret to their success in creating order, as well as in warfare, was their well-developed and swift system of communication between the capital and distant city centers. At the heart of this system was the 1,600 mile “royal road”, which was constructed and maintained primarily for government couriers, but open to all (Marincola and De Selincourt 1996). Spaced every 10-15 miles were rest houses and inns to facilitate travel, not only for the valued couriers, but also for royal members of the empire (Casson 1994). As a result, we see a somewhat punctuated rise in quality of highway accommodations at this point in history (Figure 1-2). Here, we also see a unique trait of the courier system that also gave rise to a distinguished class of travelers. Written by Herodotus, the following describes the Persian courier system: “Men and horses are stationed a day’s travel apart, a man and a horse for each of the days needed to cover the journey. These men neither snow nor rain nor gloom of night stay from the swiftest possible completion of their appointed stage. The first man, having covered this, hands the dispatches to the second, the second to the third, and so on, the dispatches going from one to the other
through the whole line” (Marincola and De Selincourt 1996). With the courier’s station ever-changing, a traveling class was born, exposed to a variety of landscapes and built for the hardships of the open road.

Much like those of the Assyrians, the roads in the Persian Empire were well built to the standard of being able to handle more than just men and horses. Although pioneered by the early Greeks, a class of chariot-wagon began a long tenure for not only transporting government officials, but also groups and harems of the wealthy non-governmental upper class in Persian society (Casson 1994). With the strong organization and control offered by the Persian Government, travel for the sake of travel became more feasible with a reduced risk of robbery and ill-fated encounters with desert marauders. In addition, key city centers began to be linked by these carriage roads, some equipped with bridges, road signs, way stations, and guard posts. While road paving had yet to become practical or affordable, the packed earth roads were in good enough condition to permit wheeled carts, such as wagons, chariots, and carriages, as well as animals, such as camels, donkeys, and horses (Casson 1994). On major routes, there also existed inns, taverns, and even what we would today consider “interstate-towns”. By 500 B.C., the synergy of the Persian Empire and its roadway system led to a previously unseen feasibility and practicality in travel – in walks the tourist.

**Return of the Greeks**

The defeat of Persia in 479 B.C. saw Greece emerge as a major world power once more, becoming an epicenter for trade and new technologies. Regaining their prominence on the world stage, they sought to broaden their empire, which required new advancements in trade, communication, and military technology – all things that
would eventually benefit the travel and tourism industry as well. During this time, we see the construction of large 100-foot ships with interior quarters and massive crews able to transport up to 500 tons of cargo across open seas. These vessels were largely the choice modes of transportation by traders and travelers, offering relatively comfortable accommodations during transit. Greek roads, on the other hand, were poorly constructed and unpredictable. Although the word “Greece” has its place in history, there were in fact several fiercely independent city-states that comprised the whole of Greece (i.e., Athens, Sparta, Corinth, Thebes, Syracuse, etc.). As a result, overland travelers were very wary to begin a journey with any sort of overland-vehicle for fear that the road would not connect to the various other states and regions of the greater Greece. Of those roads that were reliable, they were often established on precipitous cliffs. As written by the historian Pausanias: “For six miles it ran along a narrow, crumbling ledge half-way up the face of an almost sheer cliff…So narrow was the path that only a single sure-footed beast could make its way with tolerable security along it. In stormy or gusty weather, it was dangerous; a single slip or stumble would have been fatal” (Frazer 1913). Despite these harrowing conditions on most paths and roads throughout Greece, great care was taken constructing and maintaining those roads leading to sacred places, particularly when they were the sites of the great festivals (Connor 1987). Roads of this variety could accommodate a wagon large enough to fit and sleep an entire family. However, many such roads were still known as “rut roads”. In an effort to save time and money, ruts were carved into the earth in place of leveling the entire roadway for the traffic to drive upon. The advantage that these rut roads had over conventional ones was that once they were carved, they remained
virtually weather and wear-proof for many years. The disadvantage was that inevitably at some point on the rut road, the path would be narrowed into just one pair of ruts, causing vehicles headed in opposite directions to have difficulties. Often one vehicle would have to back up a very long distance until reaching a bypass in order to allow the other vehicle to continue. Mirrored by such notorious roads in today’s world, like the Careterra de la Muerte or Road of Death in Bolivia, these highways soon became infamous in the ancient world. In fact, one of the most famous murders in literature likely occurred because of these rut roads. In the tale of Oedipus Rex, when he and his father came together unknowingly at one of these rut roads, it was here that Oedipus killed his father because of his father’s insolent offense by running Oedipus off the road with his horse-drawn cart. Tourism and travel remain arduous at this time.

Unlike the Royal Road of Persia, Greek roads had very little in terms of amenities. There were few shade trees (important when walking or traveling for days in an open chariot) and virtually no road markers (Dillon 1987). Apart from general discomforts, there were real risks for travelers during this time. War was constant and water travel risked capture by enemies or pirates (Casson 1991). Land travel had similar risks with highwaymen eager to plunder and steal from travelers (Casson 1994). While each city-state had police and offered sufficient protection within the city walls, the countryside was a no-man’s land. One’s servants and slaves were the only real protection offered. The only recourse was to be minimal in the number of goods and valuables brought along with the traveler. This, however, presents another problem of what to do with one’s valuables that were left behind. With no real vaults or safe deposit boxes in existence, travelers often resorted to bringing all things of value along with them on
extended trips. As this became more and more of a problem due to theft and highway robbery, ancient travelers began to use religious temples as a sort of treasury. By depositing valuables at the “foot of the Gods”, petty thievery was much less of an issue, with the valuables remaining there to be picked up once the owner had returned from abroad. Amassing fascinating collections, these temples resembled modern day museums (Casson 1994). Regardless, some form of money had to be taken along with the traveler to pay for items on the road or at the festivals they were destined to reach. Altogether considered Greece, the many city-states were effectively independent and in fact most had their own currency. For this, money-changers were ubiquitous and essential. Although gold and silver were the standard, money-changers would not only convert the currency into usable tender, but they also served to verify currencies (Orsinger 1967).

Perhaps the most notable surge in tourism paralleled the rise of the early PanHellenic religious festivals in the last millennia B.C. With the Olympic, Pythian, Isthmian, and Nemean games being the most revered and well known of all the Greek festivals, each was intended to honor a certain god through acts of prayer and sacrifice. Above all, they honored superlative athletic and artistic performances. Honoring Zeus at Olympia, the well-known Olympic games were the oldest and most important of the Greek religious festivals, still honored today in the modern World Olympic Games every four years (Swaddling 1999).

The motivations for travel among Greek citizens was universal – it was the powerful feeling of being a part of something special at the grandest stage and before their gods. In addition, it was an opportunity to wander amongst works of art,
monuments, and buildings of great historical significance and beauty (Casson 1994). Despite the relatively distant location of the Olympic games in relation to the rest of the empire, the predictably scorching weather during summers, and the lack of proper provisioning (including drinking water), tens of thousands of spectators were present (Swaddling 1999). In part, popularity of the four major PanHellenic festivals was due to the “sacred truce” called for the month when the games were going on. As a testament to the reverence that Greek culture had for their religious festivals, all wars (of which there were many at any given time) were put on hold while citizens of each city-state would converge as athletes, artists, and tourists (Conner 1987).

The Pythian games were somewhat of a stark contrast to the highly athletics-based festival held at Olympia. Dedicated to Apollo and located near his oracle at Delphi, the Pythian games can be compared to modern-day international music and film festivals. Focusing primarily on contests in choral dancing, singing, and the Pythian melody, which was an instrumental music program dedicated to describing the mythical struggle between Apollo and a dragon, the Pythian games were much more about creative performances. In addition, artwork was a key part of the games, with special programs that exhibited sculptures and paintings (Casson 1994, Golden 2008). Despite the large attendance at these festivals, accommodations were still relatively limited, with early hotels being little more than ephemerally transformed sanctuaries and temples. Additionally, these were mainly reserved for higher officials such as priests, statesmen, and generals, with the common townspeople left to find shelter where possible.

With the resurgence of Greece in the last several centuries B.C., individual city-states also began to emerge as tourist destinations, but as year-round attractions
instead of temporary booms for certain festivals (Figure 1-2). For example, Athens, with its exciting new buildings crowning an already impressive city, began to rank as an international tourism destination on par with Egypt, to which many Greek tourists traveled by this time. As was evident with the exclusivity of lodgings during festivals, tourism was still for the upper echelon of society during the fifth century B.C. For the common people, they tended to rely on housing by family members or friends when visiting an area for any substantial period of time. Although inns did exist at this point, they were largely intended for use by transient travelers and remained somewhat disreputable. The paucity of amenities and general sleazy condition of the rooms were not fit for anything but to provide a roof over one’s head for a few nighttime hours to rest before continuing on the next day. A testament to their poor condition is the opening scene of Aristophanes’ *Frogs* in which Dionysus makes the urgent request to Heracles to make a list of ‘landladies with the fewest bedbugs” (Henderson 2008). Nevertheless, those travelers with no private residence open to them were obligated to stay at these inns during their travels. A traditional inn would have few or no windows, no bathroom, and no place to eat. Bathhouses and restaurants were separate establishments found elsewhere in town (Casson 1994). As tourism continued to rise from the fifth to fourth century B.C., inns and taverns became more frequent in busy centers and ports, particularly at the port of Corinth. Although travelers to festivals likely found themselves jammed into seedy inns, sleeping on temple porches, or wherever they could find space out in the open, there seemed to be a growing number of finer establishments setting up a standard for the tourism industry by the fourth century B.C. (Figure 1-2).
With travel and tourism firmly established in Greek city-state society, there arose the need for foreign consuls in order to handle problems for travelers while abroad. Today, we call them embassies and consulates, but in the Greek civilization, accredited representatives from one state living in another were termed Proxenos (Wallace 1970). Their prime duty was to aid and assist compatriots however possible, with secondary duties resembling somewhat of a modern-day concierge. Ranging from securing admission to meetings of the assembly to purchasing tickets to the theatre, Greek Proxenos were of infinite value to the general traveler, but especially to dignitaries and fellow nobility (Wallace 1970). Although the position of proxenos was an unpaid one, it granted certain privileges, facilitated tremendous networking (i.e., for business, trade, etc.), and was highly honorable (Casson 1994).

Early Greek tourism was still far from the relaxing vacation many imagine when thinking of modern-day tourism. Whether by land or by sea, the risk of inclement weather, malicious pirates, or simply the routine difficulties associated with uncomfortable living conditions in an era not quite ready for the service industry, travel continued to be difficult. Although there were those who traveled for the sake of traveling, the majority had a set goal or destination in mind, such as facilitating trade, seeking remedy for illness, or making their way to a PanHellenic festival. Nevertheless, travel and tourism continued to grow in popularity throughout the fifth and fourth centuries B.C. What the world needed at this time was the organization and control of the Persians combined with the wealth and pleasure-seeking mentality of the Greek. Enter the Romans.
Travel and Tourism in the Roman Empire

The expansive conquests of Alexander the Great were leading up to something spectacular and although he did not survive to see the eventual culmination of his efforts into a unified state, his dreams and those of his successors were personified by the Roman Empire. Stretching from Spain to Syria, one could go from the shores of the Euphrates to the border between Scotland and England, all while staying within the bounds of one's own government's jurisdiction (Casson 1994). This freedom, along with a well-built network of roads, ample control over barbarians and other pirates, and a unified currency, provided for a golden age of travel. Just as in the past, new technologies enabled greater exploration of the seas, and monsoon cycles were better understood and harnessed to expedite ocean travel between the Middle East and India (Thomson 1948). In addition, motives for trade and travel increased with knowledge of Chinese silk, cinnamon-leaf, camphor, and jade. Conversely, the demand for Graeco-Roman statuettes, jewelry, and pottery by India and China moved trade ships and overland caravans both ways (Thorley 1969). With Roman society growing in wealth and stature, the demand for luxurious goods increased, so traders would push the boundaries to find ivory, spices, silks, cinnamon, cotton, and pepper (Miller 1969).

The demand for luxurious goods was not the extent of the purchases made by the wealthy during the prosperous Roman times of the ultimate two centuries B.C. Holiday villas began to become the playgrounds for the wealthy. Two sorts of villas existed during the Roman Empire – along the shore of the Bay of Naples for the cool and pleasant days of spring and in the hills for the summertime, when the Mediterranean sun made the shore unbearable. Those of wealth and stature would maintain several villas at each location to avoid the monotony of always moving to the other residence,
season after season and year after year (D’Arms 1970). In a style known as “portico-house”, these villas consisted of a long porch overlooking the sea with a series of small rooms behind it, adjoined side by side in order to minimize the hot sunlight from getting in. Sounds rather like a hotel, does it not? The highlights of holidays spent at the villas were the evening dinner parties at which the host would entertain guests with elaborate presentations of seaside delights, often including rare delicacies such as oysters and saltwater eels (D’Arms 1970).

Private villas were not the only destination for those on vacation at the Bay of Naples. Beachside resorts, hot springs, and raucous yacht parties were hedonistic indulgences heavily popularized in Roman culture (D’Arms 1970). The attitude and ambiance was quite the opposite in the hills, where travelers would go for peace and quiet. While travel has historically been only truly comfortable and luxurious for the wealthy upper class, the prosperity of the Roman Empire yielded for the first time a new class of traveler. Although not quite yet possible for the lower classes of society, elegant villas, country retreats, and beachside resort holidays were becoming feasible for a greater percentage of society, particularly an emerging middle class (Casson 1994).

Tourism and travel during the age of the Greek city-states was based on five motivations: 1) Business, 2) Health, 3) Pilgrimage, 4) Festivals, and 5) To see the world (rarely). The Romans added the sixth reason, the Holiday, which was their annual departure from town for the shore or mountains and back (Casson 1994). However, it was not merely the new genre of travel that the Romans contributed to the tourism world, but perhaps even more significantly, it was the volume and scale of travel. Never
before had travelers ventured in so many directions and in such numbers. As we shall see, there were many contributing factors that elevated tourism throughout the Roman Empire.

**A new age in tourism**

Roman roads have long since been revered as one of the most significant engineering feats in the ancient world (Margary 1955, Sitwell 1981). Having learned to make sewers, aqueducts, bridges, and properly drained roads from the Etruscans, the Romans had a solid foundation in hydraulic engineering (Boethius et al. 1992, Casson 1994). However, the Roman’s took road building one step further and inaugurated the use of pavement for extensive portions of major highways – a first in the ancient world. Although road paving did not necessarily originate with the Romans, it was they who opted to use it for such great distances. This allowed for the development of larger vehicles that were capable of handling heavier loads. Stretching for incredible distances (often 20-30 miles, through forests and over hills), and being remarkably straight and level, the technology employed by Roman road engineers is believed to have been unsurpassed until the nineteenth century A.D. (McAdam 1863).

The massive advances in road building throughout the Roman Empire shifted the emphasis away from ship-based travel. Unlike ocean travel, travel by land, over the reliable Roman highways, could occur at any time of the year, not just when monsoon winds were favorable. Paying careful attention to hydraulic dynamics and materials, Roman engineers took great efforts to ensure that roads would not be damaged from what was historically the bane of the roadway – water, in the form of snow, ice, and rain.

While maritime technologies also enjoyed advances during the height of the Roman Empire, ship-based tourism did not appear to make the same leaps and bounds
as did land-based tourism. Although sea travelers could embark on a journey without the necessary costs of obtaining a vehicle, draught animals to power it, and travel companions to aid in their protection, the conditions aboard most trading vessels were meager at best (Casson 1991).

The benefits of land-based travel were therefore appealing. First, favorable weather was not a matter of life and death. Second, travel could begin at virtually any time of year. Even precipitous mountain passes were only considered off-limits during the most serious winter storms. They remained open and functioning for much of the year. However, overland travel required more baggage. Extra clothes for variable weather conditions, kitchen equipment for preparing and eating meals on the road, and of course, many servants to assist with all of this, were required. As tourism gained popularity, the existence of inns and restaurants once again turned the tables further in the direction of land-based travel.

At this time in history, with the last few centuries B.C. seeing the meteoric rise of the Roman Empire, inns and restaurants were still used primarily by the middle and lower classes, with the upper class opting to stay with and be fed by wealthy friends and family (Casson 1994, 1999). Some even owned villas and other residences at strategic points along travel routes so that they could overnight in their own house while traveling (D’Arms 1970). This did not mean, however, that this stifled the development of inns, lodges, and restaurants during the height of the Roman Empire. It was the rising demand by the middle and lower classes that truly fueled tourism development during this point in history. Nevertheless, travelers resorting to inns and lodges had much lower expectations than today. Bedbugs, for example, were so common and routine a
sight that they were referred to as “summertime creatures of the inn,” according the Pliny the Elder (Healy1991).

Restaurants became very popular under Roman rule, with some popular streets having as many as 30 in one half-mile (D'Arms 1970). Just as today, there were many variations on restaurants, ranging from street vendors to fine dining. The more formal establishments also served the purpose of entertaining. At these Roman versions of night clubs, food was only part of the scene. Often, people would go to a “restaurant” and remain there the entire night, gambling, eating, drinking, and meeting women (Casson 1999).

**Motivations of early travel**

A certain amount of travel during the days of Roman rule was done for the sake of traveling – to experience new cities with new restaurants, new bars, and new women. However, a more significant proportion was done with a specific goal or destination in mind. Most early travel was to behold key points of history. Temples, such as the Acropolis, famous cities, such as Corinth and Athens, famous graves, such as Oedipus, Achilles, Helen and Alexander, and artwork, such as Praxiteles' Aphrodite or Myron’s Cow, were on nearly every traveler’s “bucket list” of the day. Similar to today’s art enthusiasts, those of ancient Rome were particularly intrigued and attracted to the “old masters”. Works of art from past centuries would draw travelers from all directions, who would hop from temple to temple to view these masterpieces (Becatti, 1968). These temples, which housed the majority of art in this day, outside of privately held collections, became like modern-day museums and art galleries (Casson 1994). Such temples began to display not only works of art, but also the remains of heroes, much like the Catholic Church does of saints today. While sculptures, paintings, and carvings
were some of the first displays housed in these temples-turned-museums, articles of clothing from famous battles, swords, armor, inscribing, and other historical memorabilia began to appear as well (Casson 1994). With warring city-states constantly in the throes of things, the spoils of war began to include pieces of fine art, such as statues, goblets, and more, which were then dedicated to the prevailing state. Soon, nearly all public buildings were adorned with art.

In parallel with a culture of mythological curiosity, some temples claimed to have the bones and bodies of monsters and other relics from ancient mythology. While these often ended up being the bones of unearthed mammoths and other creatures with alternate explanations, it gave rise to a widened sense of curiosity about the natural world. Chimpanzee skins from Africa, meteorites from China, ostrich eggs, Indian nuts, Indian reeds as big as tree trunks, and perhaps the most impressive Indian curiosity of all, the horns of giant Gold-digging Ants began to captivate the traveler (Healy 1991). While these temple exhibits were filled with a somewhat radical melange of worldly artifacts, they represented the origin of the natural history museum.

Although these museums appealed to an intrinsic allure towards nature and natural things, many had to do more with feeling the divine hand of a god when visiting them or the natural place from which they came. Not that this is necessarily contrasting to some of today’s nature-tourists, but the emphasis was certainly more on the religious component of the landscape, river, mountain peak, or remarkable animal. Possibly due to the regularity with which such past generations of humans were able to gaze upon unobstructed natural beauty, nature tourism did not seem to excite them. Nevertheless, we do see that during Roman rule, several destinations on the typical tourist’s agenda
did involve nature for its own spectacle. Perhaps the most well known was the Channel of Euripus. This narrow channel between the mainland of Greece and the island of Eurboea had a fierce and unpredictable current that supposedly switched directions at random. Written about by Paulus, one of the great travel writers in ancient Rome, it was he who popularized this natural phenomenon. There was also Mount Etna, where tourists could walk right up to the edge of this volcano’s exposed crater. The Hotsprings at Hierapolis also drew crowds, where a fissure in the ground would periodically emit a noxious gas so strong that it killed birds that flew through it or oxen that were led too close (Casson 1994). It appears that innate human curiosity drove the earliest forms of nature-based tourism, but not without the proper marketing, of which early travel writers played a significant role.

A further testament to the anthropocentric tourism that existed during the Roman Empire was the creation of a list of the Seven Wonders of the World. All wonders being constructed by humans, the list included the Pyramids of Giza, the Hanging Gardens at Babylon, Phidias’ statue of Zeus at Olympia, the Temple of Artemis at Ephesus, the Colossus of Rhodes and the Lighthouse at Alexandria (Clayton 1990). While there is an omnipresent parallel between the tourist of today and the tourist during the time of the Roman Empire, one clear distinction presents itself, which is how they interpreted what they were actually seeing. Ancient tourists did not distinguish between the mythological and historical past. Mythology, in most cases, was history for the ancient societies (Casson 1994). These statues and memorials of legendary figures were as close to historical fact as anything else at the time. This certainly helped to create a virtually
endless number of interesting and important places to visit for the traveler in ancient Rome.

**The agenda of the ancient tourist**

Tourists in ancient Rome were drawn to three main areas of the world – Greece, Egypt, and Asia. Although destinations in Africa and India were known at the time and saw a somewhat steady interchange of goods, this extensive travel was largely reserved for businessmen and traders. Although the mode of transportation has changed over the past several millennia, the actions and general itinerary of the traveler have undergone relatively little alteration. Upon arrival, the tourist would likely embark on a stroll around the city, with evening strolls being common. In areas with heavy tourist foot traffic, vehicles would be banned during daytime hours to permit more leisurely walking. The itinerary of the tourist would likely be planned with reference to a guide book: Pausinias’ *Guidebook of Greece* being the standard of the day (Frazer 1913).

When at a destination, the tourist had to be careful not only for the thieves and shysters, but also for the prolific salesmen of souvenirs, charcoal sketchers, and miniaturists that would all compete for attention and money (Frazer 1913, Casson 1994). So, too, did the tourist need to be wary of the eager assemblages of guides that would accompany the interested traveler around monuments, temples, museums, and exhibits. Although helpful in some situations, they were viewed primarily as a nuisance to tourists in the ancient world, as explicated by a popular satirist of the day saying, “Zeus, protect me from your guides at Olympia, and you, Athena, from yours at Athens” (Casson 1994). Perhaps it was their forward nature in approaching tourists that was so disdainful, because their commonplace behavior of embellishing and fabricating
information about the sites was actually met with great interest. Although somewhat obscure, early travelers seemingly preferred to be told lies about what they were seeing, especially in cases where the truth would have been less colorful. As quoted by the Roman travel writer, Lucian, “Abolish fabulous tales from Greece and the guides there would all die of starvation, since no tourist wants to hear the true facts, even for nothing” (Perrottet 2003). Even today, accredited guides in Greece have hardly updated their methods (Perrottet 2003).

Just as we do today, tourists of the ancient world enjoyed the diversions and performances offered in a typical itinerary. Street performers and sidewalk artists offered a change of pace that the tourist enjoyed. One of the more popular diversions/stunts was a must-see part of any Egypt itinerary. It involved men from the nearby village of Busiris climbing the slopes of the famous Pyramids of Giza from the very bottom to the top (Healy 1991). With the pyramids relatively intact during that era, one can understand the incredible difficulty of scaling the walls with nearly perfectly smooth slopes. Another example was further up the Nile. Sacred crocodiles, hand-fed for years, were trained to come on command, open their jaws, and allow their teeth to be cleaned and wiped dry with cloths (Langhorne and Langhorne 1830). There was also an early version of extreme sports, with local boatsmen of Aswan working their way upstream and then turning around and “shooting the rapids” at great risk of life and limb (Jones 1932). The most celebrated performance was one not by man, but by a creation of man, of sorts. At Thebes in Egypt, tourists would flock from all over the Roman Empire to witness the “talking” of two gigantic stone statues. At daybreak, starting around 27 B.C., people began to hear a mysterious cracking noise resembling the
snapping of a string instrument coming from the statues (Jones 1932). Although it is now believed that the noise came from trapped air in the porous stone, heated by the first rays of the rising sun, the stone phenomenon was highly popularized and heavily visited during its time (Casson 1994).

Towards the end of the typical tour during the Roman times, two things were likely to happen, as was seen previously. First, and the more perplexing of the two, was that the tourists would scratch their names into the monument or point of interest (Casson 1994). The second was to purchase souvenirs. Not all that different from tourist memorabilia of today, souvenirs of the past were typically some type of replica of the main attraction. In addition, certain areas had signature items. For instance, the Bay of Naples offered small glass vials with tiny pictures inserted inside depicting major tourist sites, complete with location label and date (Casson 1994). However, souvenirs were not just restricted to miniature replicas and ancient snow globes. The wealthy would often purchase full-size replicas to return with and display at their villas. Another similarity with today’s travel and that of the ancient world was the Customs process upon returning home. Everything except personal items was dutiable, with typical taxes levied at 2-5% of the purchase price. However, duties for larger goods (not coincidentally those that were often purchased by the wealthy) incurred luxury taxes of 25% (de Laet 1949, Casson 1994).

**Holy Travel**

Travel under Roman rule saw tremendous advances which laid the foundation for the next millennia of tourism. With the advent of Christianity, a great cause and purpose for travel was born, and tourism escalated without precedent (Casson 1994). However, travel was not the only thing that was altered and restructured with the
adoption of Christianity as the religion in Rome under emperor Constantine. The new religion formed a parallel bureaucracy with which to run the government. With this, travel by clergy such as bishops and clerics was not only approved, but also funded heavily, just as travel had been previously for only the highest of government statesmen (Casson 1994).

Travel to the Holy Lands of Jerusalem and surrounding areas was popular not only with officials, statesmen, clerics, and bishops, but with the religious scholar of the time and even the common man. It was stated by Jerome, “Everywhere in the world we venerate the tombs of martyrs…how can anyone think we should neglect the tomb in which they placed our Lord.” Many agreed with Jerome that travel to the Holy Land was not only justified, but necessary. Just as the Greeks and Romans had laid the tracks for visiting “Homer Country,” the new trend was to visit “Bible Country” (Casson 1994).

By the end of the fourth century A.D., travel to the holy land was in full swing, and guidebooks emerged as early as year 333 (Wilkinson 1971). However, with the Roman Empire no longer having the omnipotent and vast army and navy, danger lurked around every corner, especially at sea (Starr 1975). Much like the early Greek and Roman travelers, Christian pilgrims found it best to stay with friends, family, or business partners while traveling to the Holy Lands. However, there was a growing trend for clergymen to stay at churches when traveling. Provided with a bed, food, shelter, and prayer, these accommodations were not luxurious, but were welcome to the weary traveler. Also like travel in the preceding centuries, the typical inns were often very basic and unfit for all but the most rugged of tourists (Casson 1994).
Travel to the Holy Lands was really just an extension of early Roman travel, so it is not surprising that many of the same traditions were observed during this era of travel, too. The Christian pilgrim could not help himself or herself when visiting a sacred tomb or monument and would covertly indulge in scribbling his or her name somewhere nearby to prove to future visitors that they were indeed there (Geyer 1898). To show those back home that the traveler was successful in their oftentimes 100-plus day journey to reach the Holy Lands, there were numerous souvenirs and mementos to choose from and carry home. However, unlike their Greek or Roman ancestors, the gimmicky snow globes of their day were no longer objects of desire (Casson 1994). Instead, things such as pinches of dirt, or blades of grass from areas mentioned in the Bible, were considered of much more worth to the traveler (Cabrol-Leclercq 1907). Some even went as far as to take a splinter off of the True Cross. This being only possible on Good Fridays, when visitors were able to kiss the cross, a daring individual would bite off a mouthful to take home (Wilkinson 1971). Needless to say, watchful deacons prevented this from happening without recourse, but this did not stop others from selling fake splinters to travelers, claiming that they were indeed true fragments of the cross. Fake souvenirs were commonplace, with other examples being dirt drenched in the blood of Christ, or particles of plaster from where the angel announced the death of Jesus to the Virgin Mary (Cabrol-Leclercq 1907). However, the most prized souvenir was a small case that enclosed several drops of oil that burned in the tombs of famous martyrs or saints (Wilkinson 1971).

The Roman era of travel did not necessarily come to an end, but rather transformed with shifting priorities and motives among tourists. With the early Greeks
and Romans laying the literal and metaphorical foundation for travel and tourism in the ancient world, the new era of holy travel became dominant. From here, it would be seen as the most popular motive for travel and tourism until many centuries later when an academic revolution took hold.

**The Grand Tour**

A major milestone in the evolution of tourism, the Grand Tour marked a distinct shift in the motives for travel. Still today the exact definition is debated, but the general consensus, and as well as this author, view the Grand Tour as “a tour of certain cities and places in western Europe undertaken primarily, but not exclusively, for education and pleasure” (Towner 1985). The term was first used in the early 17\(^{th}\) century and was largely considered to be a critical step in the education of privileged young men (Brodsky-Porges 1981) (Figure 3). Routinely lasting up to three years, the Grand Tour is thought of as both a concept (i.e., an educational tour), as well as a particular itinerary, which centered on France, Italy, Germany, and Switzerland (Mead 1914, Towner 1985). It was primarily Europeans that engaged in the Grand Tour, until the 19\(^{th}\) century when Americans initiated a similar circuit of Europe for both education and pleasure (Baker 1964, Friedlander 1876, Towner 1985).

The era of the Grand Tour marks perhaps the first point in history where travel became a key benefit to the tourist in the way of advancing one’s level of knowledge and skill, rather than purely for pleasure, as was the case in the earliest days of tourism seen during the Greek and Roman times. Although the underlying psychological motivations for engaging in the Grand Tour are impossible to be known, the empirical reasons can be categorized into several distinct classes. The merits of the Grand Tour were many, including assisting in one’s career, overall education, cultural affluence,
literacy, health, scientific understanding, and business (Towner 1985). Converging these categories into even broader ones, we see that education, social status, health, and wealth were the primary motives. While business has always been a key motivating factor for travel by traders and other executives, as was health, seen in specific examples of spas and temples being tourism destinations throughout history, it is at this point that we see a shift in social perception. The benefits of travel and tourism to individuals was changing. Previously in history, travel was more of a perk to those of elite social status and prominent careers, such as statesmen, ambassadors, and the educated upper class. Once in an elite class, it was your privilege to engage in such gratuitous travel. However, with the advent of the Grand Tour, travel became a method for propelling oneself into a desirable career, or a more elite and privileged circle of society. Never before was travel used widely as a tool. Seemingly, the cause and effect were beginning to switch, with travel functioning as a status-building mechanism due to its educational and experience-building utility (Figure 1-4).

In the centuries that saw the Grand Tour come and go, a transformation was exhibited from a Classical to Romantic approach that shifted the emphasis of the tour near the start of the 19th century. At its start in the early 17th century, the concentration of the Grand Tour was largely on social education, with itineraries focusing on cultural hotspots for arts and fashion. With time, though, the natural beauty that abounded in Europe came into the spotlight and was realized for its true potential in education.

The Classical Grand Tour heavily emphasized the value of Italian culture, concentrating on the northern towns of Turin, Milan, Verona, Vicenza, Venice, Florence, and Rome. Second only to Italy were the virtues of France and its rich tradition and
history. The classical treasures of the lower Rhone Valley, such as Vienne, Orange, Arles, Nimes and the Pont du Gard were one set among the primary nuclei at this time. In addition, travel to Paris was obligatory, as it provided essential gentlemanly education in a time where manners and fashions largely originated in this epicenter for culture and the arts. During the second half of the 17th century, Versailles was created and became a pillar of the Grand Tour for its grandeur and symbolism of French dominance (Towner 1985).

Regardless of the exact cities visited on the itinerary of a young Grand Tourist, the general route had them originating in Dover, England, then crossing the English Channel into France, continuing southeasterly through Switzerland and towards Italy. With Italy being the focal point for many Grand Tourists, the entire country was traversed before heading north through Germany and then west through the Low Countries (i.e., present day Belgium, Netherlands, and Luxembourg) (Brodsky-Porges 1981). As with travel in ancient times, the conduits for travel dictated much, and water travel continued to be a logical choice for the traveler. The Rhine, Po, Rhone, Loire, and Danube rivers greatly influenced the choice of routes, being both less expensive and quicker than land routes (Brodsky-Porges 1981, Towner 1985). However, the seas and waterways were teeming with pirates, as usual, so overland travel had its advantages in safety, even though highway thieves were present, too. An interest in landscapes and nature was very much limited during the classical tour, with any scenery showcased being mostly that of fertile humanized landscapes (Towner 1985).

The shift that occurred from the Classical to the Romantic Grand Tour, as the 18th century drew to a close and the 19th century was just beginning, marked a distinct
change in attitudes and behaviors among tourists with regard to nature. Although the actual itinerary of the tour remained relatively the same, the emphasis shifted to be more centered on nature and landscapes that satisfied the desire for picturesque scenery. Major city points were still key attractions, as fashion, culture, and language were still objectives of the tour, but waypoints and countryside between them became highlights during this phase of the Grand Tour (Towner 1985). Landscapes such as rural villages, battlefields, and ruins that were once revered for their historical significance during the classical phase were now viewed as picturesque displays of wild nature. This shift in emphasis meant that those cities and countries unable to offer the nature that these travelers craved underwent a period of decline, falling out of trend and consequently off of the itinerary. While places like Florence exhibited medieval and Renaissance buildings, a fashionable society, and romantic scenery, the Low Countries, such as Belgium and Luxembourg, possessed only prosperous towns and productive humanized countryside. Unable to cope, the Low Countries soon went out of fashion in the late eighteenth century. As the Romantic period of the Grand Tour continued to evolve, places that offered a diversity of features, including those made popular during the Classical period, were most successful and remained on the Grand Tourist’s itinerary. As stated elegantly by Towner (1985) in reference to why some areas were able to remain popular through the shift from the Classical to Romantic Tour, “an analogy with ecology indicates some of the main features…the stability of an ecosystem is a function of its species diversity: the greater the diversity, the more stable the system. Some centers on the Grand Tour had long-term stability because they possessed several facets and were thus able to cater to the changing tastes and
fashions of the tourists.” Charles Darwin would have been proud of Towner’s (1985) insight.

Just as the motives and specific attractions shifted, as the Grand Tour era progressed, so too did those participating. Throughout this era, a strong middle class began to emerge and subscribe to the Grand Tour concept (Towner 1985). While still far from the poverty class, this new class had limited time and money in which to engage in the lengthy three-year tours typical of more wealthy early Grand Tourists. While the itinerary remained relatively congruent throughout the centuries, in terms of the various destinations visited, it was the length of stay in each destination that changed the most (Figure 1-5). In an effort to save time at a point in history when transit time was unchangeable, Grand Tourists would choose to stay for less time in each respective destination. The shift in class was coupled with a shift in demographics among tourists. By the 1830s, this middle class would spend as little as one tenth of the original time allotted to the Grand Tour and be composed of an older and less educated cohort (Figure 1-6 and Figure 1-7) (Towner 1985). It is at this time that society departed from the Grand Tour model and a more industrialized tourism era was born. Nature would remain as a focal point for certain tourists in the coming century, with the Grand Tour representing what this author believes to be the foundation for modern day ecotourism (Towner 1985, 1991).

This transition from Classicalism to Romanticism in the Grand Tour marks a key point in the evolution of nature-based tourism. As descendents of these Romantics, our society today still craves this balance of cultural authenticity and natural beauty. However, before we go into detail on ecotourism in the present day, it is worthwhile to
look at the evolution of this somewhat modern concept and some of the early pioneers in this unique form of nature travel.

The Evolution of Ecotourism

Ecotourism is a still-evolving term that is relatively modern in origin. As a result, it may be considered a new concept altogether, although in its broadest sense, it has been in practice for centuries. While travel in the ancient world (i.e., throughout the Greek and Roman times) saw relatively little emphasis on nature or wilderness, with culture and festivals seeing most of the tourism traffic, there were indeed written accounts of tourism to natural areas for interested individuals to witness the power, rarity, and mysteries of nature (Casson 1994). Today, this alone would not meet the relatively exact requirements of what constitutes true ecotourism, but keep in mind that ecotourism has evolved into what it is today from these basic origins. The pilgrimages and holy travel that prevailed from the end of the Roman Empire and through the Dark Ages and Medieval times did involve nature, but largely due to the allure of biblical acts taking place in such areas (i.e., not necessarily for the sole purpose of nature tourism) (Casson 1994). It was not until the middle of the second millennia A.D. that we began to see a distinct revolution in the motivations and style of tourism (Towner 1985). The Grand Tour was a unique approach to both education and travel, combining the two in an irreversible pairing that would see a new brand of tourism emerge and persist through to the present day. It was during the Grand Tour era that we see ecotourism’s pioneers emerge and lay the foundation for what it was to become.
Pioneers of Ecotourism

Charles Darwin

Perhaps no figure in science stands out as much as Charles Darwin in regards to scientific discoveries made during travel. However, Darwin was distinctly unassertive when it came to his ambitions early on in life. After abandoning his career in medicine, much to the disgust of his father, Darwin decided to change educational paths and studied instead to become a clergyman in the Church. However, it was his insatiable appetite for collecting insects that sparked a proficient interest in natural history. Through relationships fostered at Cambridge, particularly with the likes of Professor John S. Henslow, an opportunity was presented to young Darwin that would forever change his life, as well as history in general.

Still relatively disenchanted by structured education, the opportunity to join a five-year voyage on the H.M.S. Beagle granted Darwin a unique opportunity for freedom that he eagerly sought after years of formalized education fraught with expectations from his family. With the prospect of collecting fascinating insects while serving as the ship naturalist, a newfound spirit encouraged Darwin in a way that previous vocations had not (Remington and Remington 1961). However, despite his enthusiasm, his family failed to share in his confidence and willingness to embark on a lengthy journey around the world. With his characteristic apathy and posture of subordination still present when confronting his family with new ideas, he pleaded with family members to view his voyage favorably. Even amidst his vigor to join Captain Fitz-Roy on this iconic journey, he still appeared unconvinced of his own desire, as he wrote to his family: “But pray do not consider that I am so bent on going, that I would for one single moment hesitate if you thought that after a short period you should continue uncomfortable [about me
going]” (Barlow 1933). Despite Darwin’s apologetic attitude about embarking on his Grand Tour, he was indeed motivated and set sail with some semblance of blessings from this family. It is probable, though, that it was, in fact, these regretful feelings that instigated Darwin to write such detailed letters to his family throughout the voyage, which eventually formed his comprehensive diary about the voyage (Barlow 1933). It was this diary by which Darwin made his first great contribution to literature and science. Although parts were initially published in separate volumes, with such lengthy titles as *Journal of Researches into the Geology and Natural History of the various countries visited by the H.M.S. Beagle under the command of Captain Fitz Roy, R.N. 1832-1836*, it was his extensive diary that ultimately would become one of Darwin’s most famous works, *The Voyage of the Beagle*. While people today hardly regard this publication as his most famous, it was very much a “best-seller” of the time and had a pronounced impact on motivations for travel during the Post-Grand Tour 19th century (Tallmadge 1980). It is still today an iconic piece of travel literature.

Travel books were extremely popular at the time of Darwin’s voyage and appealed to mass audiences (Tallmadge 1980). Darwin himself indulged in reading travel books during long periods at sea, according to a letter that he wrote his sister in 1832 stating that, “If there is any sea up, I am either sick or contrive to read some voyage or travels” (Barlow 1946). It was perhaps this constant exposure to travel literature that gave Darwin such a solid base in the art of travel writing, for he was indeed gifted. However, travel literature underwent a clear change, in terms of what was accepted and popular between the 18th and 19th centuries. In the 18th century, an ideal travel book had to be a perfect balance between both practical, matter-of-fact information and personal feelings
and reflections by the author. Too much in one direction was met with disinterest for being either too dry, or too egotistical (Batten 1978). However, at the same time that history saw the shift from Classical to Romantic styles of the Grand Tour, so too did history see the transition from a classical to romantic style of travel writing. In the beginning of the 19th century, travel literature was split into two distinct genres. Those books with more factual information were demoted to guidebook status, whereas those that centered on the traveler and his or her personal feelings, impressions, and interactions with foreign landscapes and cultures were promoted as true literary works of art. It was this new style that very much came into fashion, just as travel was opening up as a possibility for new classes of society (Tallmadge 1980, Towner 1985). Because of the emphasis on the personal experience by the author, the personality of the travel writer became irrevocably important. Although best known for his revolutionary scientific conclusions and reasoning, perhaps Charles Darwin’s most direct contribution to society at the time was his ability to convey the pleasures and excitement of adventures, largely in the Romantic Grand Tour era. Darwin excelled in his ability to transform a raw account of his voyage into a much different, highly entertaining, literary piece. His goal in writing was not necessarily to recount the voyage step by step, which was the job of Captain Fitz-Roy in his official report, but instead to transform the experience as a lively story that captivated the reader. Darwin did so through his own ingenuity. By rearranging the chronology of his trip, abridging much of his diary to create a single story line, and establishing a consistent point of view, he fashioned a narrative character that was not only entertaining, but highly respectable (Tallmadge 1980). The ensuing book held a message critical to the
evolution of nature-based travel and ecotourism – scientific discovery can be a responsible and respectable form of adventure. People in the mid 19th century bought into this concept and followed in Darwin’s footsteps to create a new genre of tourism. This new genre combined the authenticity that motivated travel in the ancient world, the education and experiential learning emphasized in the Grand Tour era, and now a deliberate search for natural beauty and the wonders of personal discovery in wilderness. This is starting to sound a lot like ecotourism.

Alexander von Humboldt

Known as the “re-discoverer of the Americas,” Alexander von Humboldt (1769-1859) made a brave and directed effort to explore, describe, and interpret the world as had not been done previously in history (Sachs 2003). A cosmopolitan thinker, Humboldt was regarded, particularly in the Americas, as the founder of a new science that created a web of interdependence between all things in the world and, “to recognize unity in the vast diversity of phenomena” (Goetzman 1986). Later regarded as a founding father of ecology, Humboldt’s achievements were rooted in travel (Sachs 2003). Being a life-long tourist, in effect, his adventures in the natural world were a direct result of the sentiment held by European society at the time to learn through travel, bolstered by the Grant Tour era. In a Post-Colonial world, Humboldt reported and published not only new scientific findings, but also key critiques on the social conditions of the colonies in the new world. He seemed to bridge a gap between two disparate sides of European society and stood out for doing so. In a time when, as William Goetzmann wrote, “the explorer was a symbol of . . . a kind of superhuman Odyssean vision, and ultimately mankind’s biblical urge to ‘dominate the earth’,” Humboldt unwound this conventional view with his intentions, “to depict the
contemplation of natural objects, as a means of exciting a pure love of nature” (Helferich 2004). In short, Humboldt made a poignant connection between nature and culture (Sachs 2003). As we shall see, this connection is a critical tenant to the principles of present day ecotourism. The truly miraculous thing is that he critiqued the wrongdoings of colonialism (i.e., exploitation of cultural and environmental resources) at a time when he was already revered as a hero in Europe's imperialistic mindset. What was a hero doing by going against the long-standing tenants of society?

What differentiated Humboldt from previous naturalists was his understanding of this link between society and nature. As he wrote in the introduction to the Personal Narrative of his Latin-American expedition, “The discovery of an unknown genus seemed to me far less interesting than an observation on . . . the eternal ties which link the phenomena of life, and those of inanimate nature” (Humboldt and Bonpland 1818). By traveling as much as possible, and by interacting and interviewing other travelers, Humboldt used this information to form theories (most of which have been proven perfectly true by today’s technology), such as how ocean currents affected mean temperatures across the world. He also aimed to figure out how geological formations (i.e., mountains, coastlines, etc.) affected vegetation patterns, and even how deforestation and agricultural monoculture affected the health of ecosystems. His revelations came from asking questions and creating connections in the chaos of nature, rather than by forming discreet conclusions about the organization of species, in contrast to those such as Linnaeus, Darwin and others (Humboldt and Bonpland 1818, Sachs 2003).
Through Humboldt’s reports on the effects of colonialism on the human and natural environment, he did what many of today’s conservationists intend to do, which is to educate people on the effects that they and their society have on the world, both near to home and far away in lesser-known places (Sachs 2003). This was a constant theme throughout his many publications, which also targeted major social issues, such as inequalities in land distribution, the tragedy of the commons, violence against indigenous groups, and unjust work environments. He repeatedly would write of the unsustainable nature of mining and foreign exchange in the Americas. As stated in Humboldt’s *Political Essays*, he believed that, “The only capital of which the value increases with time consists in the produce of agriculture…nominal wealth becomes illusory whenever a nation does not possess those raw materials which serve for the subsistence of man or as employment for his industry” (Dunn 1988).

Parallel to his observations and reports of social injustices were those on environmental conservation. Throughout his travels, Humboldt would posit massive questions, such as why in Venezuela the Lake of Valencia’s water level had dropped over time. Again through questioning, observations, and travel, he was able to ascertain that it was in fact deforestation and the cultivation of indigo in the surrounding areas that caused this pronounced environmental change. Although it was a popular thought at the time that there must have been an underground outlet from which the water would flow over time, Humboldt realized the truth. He correctly ascertained that without the massive stands of trees with roots that aided in the soil’s water retention, the water would drain too quickly to replenish the spring that ultimately fed the lake (Sachs 2003). While traveling through South America, Humboldt wrote that, “By felling the
trees which cover the tops and sides of mountains, men in every climate prepare at once two calamities for future generations: want of fuel and scarcity of water” (Humboldt and Bonpland 1818). At present, when both are major issues in our world, his forethought regarding environmental conservation was as unique as it was ominous.

Humboldt was truly an interdisciplinary figure, engaging society in many issues that he felt were interconnected, particularly with regard to the natural world. However, this interconnection cannot be mistaken for a belief in similarity throughout the world. Humboldt realized that it was in fact the diversity of ecosystems that lead to their proper functioning. The word biodiversity had not yet been coined at the time of Humboldt’s travels, but had it been, it would likely have appeared as a recurrent theme throughout his publications. As a traveler, geographer, biologist, ecologist, anthropologist, climatologist, and geologist, he was a jack of many trades. For his education and empirical approach to both conservation and travel, we can add ecotourist to this list as well.

**Alfred Russel Wallace**

Being so apt to go against both traditional theories and practices of naturalists at the time, it is unusual for such a man to be literally adored by everyone with whom he interacted (Durant 1979). Although technically regarded as the co-author of the theory of natural selection by modern-day perspective, Alfred Russel Wallace was never truly credited with this honor at the time of his discovery. Having the opportunity to in fact publish his own theory of natural selection before Charles Darwin did, Wallace was a most gracious colleague when Darwin did indeed publish his account first, and thus gain the majority of the credit for an idea that both Darwin and Wallace shared (Wallace 1916, Durant 1979). In fact, Wallace was Darwin’s biggest supporter. He never ceased
to give Darwin the credit for this discovery, even though many to this day believe that it was a shared endeavor. In 1864, six years after publishing the *Origin of Species by Natural Selection*, Darwin wrote Wallace saying, “you ought not to speak of the theory as mine; it is just as much yours as mine. One correspondent has already noticed to me your “high-minded” conduct on this head.” Wallace, as intently as ever, replied, “As to the theory of natural selection itself, I shall always maintain it to be yours and yours only” (Wallace 1916). If there is one man to blame for Wallace’s lack of credit, it is Wallace himself.

Despite this famous controversy, Wallace contributed a great deal to science for which he did indeed receive credit. In addition to being one of the most vocal defenders for Darwin’s theory of natural selection at a time when it was largely considered blasphemous and nonsensical, he also wrote on the first important application of the theory of natural selection to mankind, traveled extensively throughout South America and Southeast Asia, and from 1860 to 1870 alone published over 40 scientific papers on his research and exploration in the Malay Archipelago (Durant 1979). Like Humboldt, Wallace became more and more interested in the connection that man had with nature. However, this obsession would eventually cast him out of reverence within most scientific circles (Schwartz 1984). Ultimately favoring a spiritual hypothesis of life’s origin, in place of his earlier support of natural selection, Wallace’s tremendous skill for empirical observations and scientific discovery was left isolated in the travels of his younger years, from 1848 to 1862 (Camerini 1996).

Alfred Russel Wallace’s rise to scientific prominence was similar to that of many great biologists throughout history. Primarily, the correlation stands out that both their
education and research involved extensive travel and exploration. What truly set Wallace apart during this late phase of the Grand Tour and expanding colonialism was that he was not a gentleman naturalist, a sophisticate, an empowered colonialist, a high Victorian, or an artisan. He could not be categorized by any of the traditional ‘labels’ assigned to most explorers and naturalists in the mid-19th century (Camerini 1996).

Wallace’s beginnings were in fact similar to those of Darwin, in that neither stood out as a distinguished pupil (Durant 1979). They were not necessarily destined for greatness. However, where the two differed was that Wallace did not have access to the funding with which Darwin’s father provided him to attend higher education institutions like Cambridge and Edinburgh. While a young Darwin found himself learning geology from detailed lectures by Adam Sedgwick and botany from long walks with John Henslow, young Wallace was forced to direct his own education through working, reading, and apprenticing with his brother in the land surveying business throughout Britain (Wallace 1916, Camerini 1996). Not only did this expose Wallace to an outdoors ethic early on, but also to a new and emerging class of society in 19th century Europe. This ‘middle’ class was manifesting itself into a thinking class with an ethos that searched for improvement in society. While Darwin was at Cambridge reading Herschel’s *Introduction to the Study of Natural Philosophy* and Paley’s *Natural Theology*, Wallace was in working men’s clubs reading Thomas Paine’s *Age of Reason* and Combe’s *The Constitution of Man*. The mood of these and similar publications that Wallace poured over were anti-authoritarian and spoke of rationalism and skepticism. They called for individual improvement through educational and egalitarian reform (Paine 1794, Combe
1850). Soon, Wallace began to form his own natural religion that embodied a faith in nature, as well as a commitment to social reform. These values traveled with him well.

Natural history was becoming increasingly more popular in Britain in the 1840’s, much to the credit of famous travel and science writers at the time. Although not as popular as the study of medicine or religion, natural history was the interest of many subsets of society, from pub culture to the wealthy elite (Barber 1980, Merrill 1989, Camerini 1996). The most intimate way to study and enjoy natural history was in the art of collecting (Findlen 1994). With a rich history and tradition, collecting served two purposes for the collector. First was for monetary gain. With the rare and beautiful specimens collected on exotic journeys, one could sell specimens (i.e., pelts, bird skins, insects, feathers, shells, fossils, etc.) to wealthy collectors to fund travel and make a living (Wallace 1916, Belk 1995, Camerini 1996, Hollerbach 1996). Second was for enjoyment and discovery, which so often go hand in hand with naturalists and scientists. Not only is the hunt for spectacular organisms thrilling and enjoyable, but the ensuing scientific value of the collection provides lasting rewards to both the individual and science in general. It was these prospects that united Wallace with another key historical figure in 1845, Henry Walter Bates. Throughout the next several years, they would exchange correspondence and discuss insect collecting, natural history books, and each other’s growing fascination over such figures as Humboldt and Darwin (Wallace 1905). Encouraged by early travel writings such as Charles Darwin’s *Voyage of the Beagle* and William Henry Edward’s *A Voyage up the Amazon* (1847), as well as the reassurance from British entomologist Edward Doubleday that the trip would be well-funded by the sale of collected specimens, the two set out on an iconic journey into
the Brazilian Amazon. Although fate would have it that the majority of Wallace’s Brazil
collection would be tragically lost due to a ship fire during his return across the Atlantic,
his years of experience working with his brother in the surveying industry would provide
the knowledge and skills needed to map extensive areas of the Brazilian Amazon, the
products of which were shipped back to England prior to his return. Perhaps more
importantly, though, those four years gave him significant practice and experience in
coordinating the difficult logistical tasks inherent to fieldwork in total wilderness (Wallace
1905). Skills ranged from using letters of introduction to find lodgings and collection
localities, to working around the routine (and not so routine, at times) issues of locating,
collecting, and shipping specimens back to England, to simply managing the dangerous
threats to life in isolated wilderness (Camerini 1996). This experience would prove vital
for what Wallace termed his most ‘central and controlling’ incident in his life, his 11-year
collecting expedition in the Malay Archipelago (Wallace 1905).

Arguably the most important work that Wallace was credited with was The Malay
Archipelago (1869). However, from this single expedition, he also produced over 40
other scientific publications. He introduced topics that are still ardently researched
today, including biogeography, natural selection, and conservation biology. His work on
Papilionidae (Lepidoptera) produced what became a landmark paper for adaptive
radiation that Darwin himself acknowledged as one of the greatest papers supporting
their co-founded theory of evolution, stating that it “will do more for spreading our views
on the modification of species than any separate treatises on the single subject itself”
(Wallace, 1916, Schwartz 1984, Mallet 2009). It was also on his Malay expedition that
he suffered his most significant bouts of malaria, which he widely acknowledged as
providing the “downtime” of quiet contemplations needed to form his theory of natural selection (Wallace 1905, 1916).

Without delving into great detail about the specific itinerary, or individual species recorded, what is the value of Wallace and his Malay expedition? His accomplishments are tremendous to the body of scientific literature, with his papers being some of the very first written records of the world’s most spectacular wildlife, as well as detailed accounts of mysterious cultures found throughout present-day Malaysia and Indonesia. However, from a tourism standpoint he helped to pioneer a new type of travel. This travel was a search for the authentic, the rare, and the beautiful. It was heavily engraigned in the natural landscape and centered on the search for remarkable wildlife and cultures. Just as Alexander von Humboldt did several decades prior to Wallace’s expeditions, observations made during these scientific expeditions altered the way that people viewed the world. Their contributions were immediate and long lasting, with still today expedition itineraries retracing their routes for the sake of tourism and conservation science. The detailed accounts of Wallace, so eloquently presented in his many publications, are so thorough that modern-day conservation biologists use The Malay Archipelago (1869) and Island Life (1880) in which to compare present-day surveys of existing biodiversity throughout Southeast Asia. At a time when mass tourism was just beginning, with the first organized tours of Europe led by Thomas Cook in the 1850s, it was not only an appetite for travel that motivated these early patrons of ecotourism, for their tourism options were expanding back home in Europe. It was instead an insatiable hunger for discovery, authenticity, and novelty that took Wallace and others to such lonesome wilderness. It was a passion for understanding and
ameliorating mankind’s effects on nature that caused them to comb the globe in search of answers and unconventional experiences. Interactions with cultures provided insight on man’s connection with nature, and intensified this relationship. These same tenets are still embodied in some of today's modern travel adventures, but one has to know where to look. They are not found in mass tours of European countryside, or on cruises to nowhere. They remain in the wilderness, with itineraries rooted in exploration, novelty, and the ever-present search for the authentic.

In the coming sections, we shall see these similarities to modern day ecotourists emphasized. While these previous examples represent the earliest pioneers in ecotourism, it is inevitable that the style, aim, and ruggedness of the ecotour will change over time. However, the activities in which these early explorers engaged are remarkably similar to those of today, to a different threshold of hardship, of course. Nevertheless, there are common themes, which will be steadily addressed throughout the remainder of this dissertation.

The Rise of Ecotourism

As seen from examples stretching back through the past several millennia forward to the present, the evolution of ecotourism, and even tourism in general, was one with a slow and ill-defined beginning. Thousands of years had passed without any record of travel and tourism incorporating nature for the sake of education and conservation. Although this summary of ecotourism’s rise may regrettably omit key periods of exploration that produced individuals equally as important to the history of ecotourism as Humboldt, Darwin, or Wallace, the written record of such is limited, if not all together absent. Nevertheless, the importance and influence that these early pioneers had on the world cannot be overstated. In an effort to further understand
ecotourism, and what makes it different from more conventional leisure activities, we must first look at tourism in general.

**Defining tourism**

Throughout the centuries, tourism has developed into a major worldwide industry of great economic importance. In the past 60 years, tourism has skyrocketed to nearly one billion world-wide tourists annually (Figure 1-8). This large group spends a considerable amount of money – three billion USD a day, to be exact. Today, tourism accounts for 30% of the world’s exports of commercial services. As an export category, tourism ranks fourth in the world, behind fuels, chemicals, and automotive products. In terms of growth, it is the world’s fastest growing industry, even in times of recession, as has been seen from 2008-2010. By 2020, tourism is projected to increase by over 50% of its current levels, with 1.56 billion tourists traveling annually (UNWTO 2010).

With the overall increase in discretionary income throughout the years, as well as technological advances in how we travel (Figure 1-9), tourism is one of the most popular and identifiable forms of leisure behaviors in the world today (Kelly and Godbey 1992). It also now represents the major motive for travel, with business, health, and religious travel subordinate to leisure and recreation (Figure 1-10).

To no surprise, there is no universal definition of tourism. Tourism may simply refer to an activity where travel is involved, or it may be defined by specific activities while traveling, such as sightseeing, educational trips, shopping, attending special events, or relaxation (Kelly and Godbey 1992). Other definitions may specify that tourism must involve a minimum travel distance from one’s home, or that it requires at least one overnight stay to be considered true tourism. In the present work, however, we will look at tourism as being simply travel for the sake of travel. Buck (1978) and
Graburn (1977) stated that sociologically, tourism is a form of play. When looking back at travel in the ancient world, there was a defining transition when travel was engaged in for no other reason than because it was enjoyable. This could mean a ride through the countryside or a trek across mountain paths. It could also mean a cruise to nowhere, or a shopping trip to New York.

Tourism is the largest in a series of concentric circles in which all other forms of tourism are encased (Figure 1-11). Ecotourism, agri-tourism, mass tourism, volun-tourism, and other varieties of tourism are derivatives of this basic overall concept. They are complementary in nature, and all housed within the tourism framework, yet each has a separate set of values that are quite different from one another. While they are all founded in the concept of travel for the sake of travel, each involves significantly different motivations and key characteristics that translate into even more diverging subgenres. For the remainder of this dissertation, we will concentrate on the ecotourism genre, with specific emphasis on the deviations and subgenres that fall within this dynamic industry.

**Defining ecotourism**

The line in the sand between tourism and ecotourism is a set of principles and values relatively unique among the various tourism genres. Often coined as “Green Tourism,” “Responsible Tourism,” “Sustainable Tourism,” or “Alternative Tourism,” ecotourism exhibits a clear emphasis on sustainability. However, there is much more to it. Just as the definition of tourism can take many forms, ecotourism, being a newer and less studied area of leisure, is perhaps even more debated in terms of its interpretation. Tenets such as sustainability, responsibility, cultural awareness, environmental
sensitivity, and education are frequently used to define ecotourism (Western 1993, Honey 2008).

There is no shortage of official definitions for ecotourism. The word was first coined by Mexican architect Hector Ceballos-Lascurain in 1983. As founding President of PRONATURA, an influential Mexican conservationist NGO, he first used the word in a presentation made in Mexico City to petition for the conservation of key wetlands in the Yucatan Peninsula of Mexico. In his address, Ceballos-Lascurain stated that “Ecotourism is that tourism that involves traveling to relatively undisturbed natural areas with the specific object of studying, admiring, and enjoying the scenery and its wild plants and animals, as well as any existing cultural aspects found in these areas. Ecotourism implies a scientific, esthetic, or philosophical approach, although the ‘ecotourist’ is not required to be a professional scientist, artist, or philosopher. The main point is that the person who practices ecotourism has the opportunity of immersing him or herself in nature in a way that most people cannot enjoy in their routine, urban existences. This person will eventually acquire a consciousness and knowledge of the natural environment, together with its cultural aspects, that will convert him into somebody keenly involved in conservation issues” (Ceballos-Lascurain 1987). For the first try at defining ecotourism, it was impressive. However, this introduction into a new terminology and philosophy was not static. It quickly became a widely supported concept and was met with much deliberation. A new era of tourism and scholarly pursuit was born.

Although the term ecotourism was not officially accepted by the IUCN until 1996, this did not mean that others avoided taking their own approach to defining this new
form of nature tourism after Ceballos-Lascurain’s 1983 definition. Early scholars of ecotourism, Ballantine and Eagles (1994) note that ecotourism differs from other forms of tourism, in that ecotourism combines specific social (travel to learn about nature) and attraction (visiting wilderness) motives, and requires a specific time commitment (33% of ones time must be spent in the field). Wight (1996) defined ecotourism as an enlightening nature travel experience that contributes to the conservation of ecosystems, while promoting the integrity of host communities. Because ecotourism encompasses an activity, a philosophy, and a development model, it is not particularly easy to summarize accurately, as was epitomized by Hector Ceballos-Lascurain’s lengthy explanation of the word in his inaugural definition. It is not the intention of this paper to analyze the many definitions, as they can vary greatly in both their content, as well as how readily they are accepted. Ecotourism is best understood through analysis, which will continue throughout this paper. Nevertheless, it is best to proceed with a clear definition that acts as a foundation to the overall concept. Today, the most widely embraced definition, by both the industry and academia, is that ecotourism is responsible travel to natural areas that conserves the environment and promotes the welfare of local people (TIES 1990). True ecotourism must be a responsible form of travel to natural areas that functions to conserve the environment and the livelihood of local people in areas visited.

It is these underlying values of ecotourism that has driven it to become one of the world’s most promising ways to conserve natural areas, as well as the flora, fauna, and landscapes within. As Western (1993) writes, ecotourism is a way of paying for nature conservation and increasing the value of land left natural. Land protected only for the
sake of protection has fewer advocates for its safety and long-term preservation than land with a community of stakeholders that profit from the protection of land. These stakeholders come in a variety of forms, ranging from local communities, governments, non-governmental organizations, tourists, and other philanthropists, but largely consist of those in the host country. The many forms of profit include intangibles like instilling a sense of community and national pride, or the promotion of cultural tradition. There is also indirect profit from the promise of future use of natural resources (i.e., sustainable farming, hunting, fishing, botanicals, etc.) due to protection and conservation of an ecotourism area. However, the most popular form of ecotourism profit is monetary profit.

Ecotourists pay for a variety of services when traveling. Payments are made to transportation services, hotels, lodges, restaurants, food suppliers, national parks, guides, airports, and more. The vast majority of ecotourism attractions (e.g., natural areas, preserves, river boat rides, etc.) charge admission for entrance. These fees will do many things on a local level, like create jobs, pay salaries, and help improve community infrastructure like roads and trails. Parks and communities also charge indirect fees through souvenirs and other memorabilia offered to the tourist. In contrast to travelers in ancient times, modern-day tourists are forbidden from inscribing one’s name on the places they visit. However, one tradition that has held the test of time is the ritual of returning home with souvenirs and gifts. While t-shirts and postcards certainly abound in souvenir shops, authentic hand-made crafts, such as jewelry, woodwork, and tapestries allow local communities to profit from goods made directly by the people that inhabit them. In many developing countries, the sale of these goods
accounts for a significant portion of total tourism revenues by local communities (Lindberg and Enriquez 1994, Wunder 2000).

There is indeed a variety of ways for host countries and communities to profit from visitation by ecotourists. As a result, host countries readily appreciate the value of such natural attractions that promote visitation by ecotourists. Regardless of a country’s own affinity to maintaining a pristine and beautiful landscape, the monetary incentive that follows in the wake of ecotourism is often enough to create an entire culture of sustainability. Ecotourism is quickly becoming a solution in today’s environmental conservation battle by minimizing exploitative behaviors on the environment, such as slash and burn agriculture, overhunting, overfishing, poaching, and the pet trade (Western 1993, Honey 2008). People around the world are realizing that pristine wilderness is worth much more in the long run by preserving it and its beauty, rather than converting it into short-term profits through deleterious processes like unsustainable forestry or agriculture.

In the previous Tourism section, the size and growth potential for the tourism industry were detailed as a summation of the various tourism genres. While this is impressive and noteworthy, it pales in comparison to the growth seen in the ecotourism genre from the time that studies were initiated in 1990. Since then, ecotourism has been expanding steadily at 20% – 34% a year, with some years seeing ecotourism growing nearly 300% as fast as the overall tourism industry (Mastney 2001, World Tourism Organization 2004). Experts predict that within only several years’ time, ecotourism will likely expand to cover 25% of the world travel market, exhibiting an
annual value that approaches 500 billion USD (The International Ecotourism Society 2006).

These dollar figures are indeed impressive, but it is what is possible as a result of these dollar figures that is at the heart of ecotourism. From biodiversity conservation to elementary school education, tourism dollars spent via ecotourism initiatives are reinvested into local areas at rates up to 95%, which is in stark contrast to more general tourism, which may see outside interests (i.e., foreign businesses) retain up to 80% of the money paid by tourists (Honey 2004). By keeping money local, communities are the first to benefit from ecotourism enterprises. This creates a strong support structure for the lodge, or park, or whatever the ecotourism enterprise may be, which in turn shows the community that strong ecotourism values will enable profitability by all.

So far, ecotourism has been presented as a holistic term that is elemental, in that it cannot be broken down into smaller forms. In fact, ecotourism is still a greater concept, in which further derivations lie. The motives and objectives of an ecotourist are not perfectly generalizable. Although ecotourism may be a search for the "authentic," as MacCannell (1976) postulated as a goal of all tourists, the intention of the ecotourist can take many directions. Some ecotours may concentrate on the role and diversity of cultures in the environment, while others may be designed specifically for bird watching or photography. Others may prioritize the search for spectacular landscapes, minimizing wildlife observation. Still others may emphasize large mammal viewing or great migrations, as in the case of the typical African safari. There is relatively no limit to the potential foci of ecotourism. However, these choices and
decisions are largely governed by the motivations and comfort levels acceptable to ecotourists well before embarking on an ecotour.

In the realm of ecotourism, there is a sliding scale, with novelty, authenticity, and remoteness at one end, and comfort, coziness, and general ease of travel, at the other end. However, it is seldom this straight-forward. A more preferred continuum is often referred to in the literature as the hard/soft ecotourism spectrum, with varying degrees of compromise between the two poles (Figure 1-12) (Laarman and Durst 1987, Lindberg 1991, Chapman 1995, Palacio and McCool 1997, Weaver 1998, Weaver and Lawton 2002, Weaver 2005). Hard ecotourism is typically more novel and less developed. Having less structure, this derivative of ecotourism is more adventurous and appropriate for a select clientele. The experience often proves to be more authentic and personal. On the other side, soft ecotourism is typified by more established ecotourism products or activities. Because they often come with a higher degree of infrastructure and are able to provide ecotourists with a higher level of comfort, soft ecotourism experiences appeal to a larger subset of the tourism population and thus are more popular, generally speaking. Consequently, novelty and authenticity are reduced, along with the intensity of the personal experience typical of hard ecotourism. This cost does come with benefits, though. Soft ecotourism places more emphasis on education and interpretation, while allowing for shorter, more efficient ecotours (Figure 1-9).

Hard ecotourism should not be considered greater, better, or more influential than soft ecotourism, as each has its place in the greater ecotourism arena. Certain ecotourism destinations, products, and activities lend themselves better to one side of the spectrum, and everyone benefits because of this. While it is logical to believe that
hard ecotourism, with a greater level of interaction with nature, is preferable for the host community, environment visited, and world in general, the difficulty of travel and other obstacles inherent to hard ecotourism minimizes the overall positive impact from ecotourism, due to small participant numbers. Although the level of interaction and connection with nature on softer ecotours is less, it can be argued that the worldwide impact is as great if not greater because of the larger audience. Because this is indeed a spectrum, very few ecotourism products abut perfectly to one end or the other. It is much more common for specific components of an ecotour to be nearer to one end, with others being closer to the opposite end (Figure 1-9). For example, the U.S. National Park system is a classic example of soft ecotourism because it facilitates (1) shorter trips, (2) larger groups, (3) multi-purpose visits, and (4) emphasizes interpretation through informational signs and ranger-led discussions. However, certain items in the spectrum like (5) amount of physical activity, (6) level of comfort, (7) expectation of services, (8) degree to which one interacts with nature, and (9) individual reliance on tour operators or travel agents, are completely subjective and are very different across the population of visitors. While generally speaking, ecotourism in U.S. National Parks would see that things like amount of physical activity and expectation of services weighted more towards the soft end of ecotourism, some ecotourists may visit with few expectations of services and be very physically active. Destinations rarely have prescribed positions for all qualities listed in the ecotourism spectrum.

Antarctica is a classic example of hard ecotourism, for it facilitates (1) longer trips, (2) specialized visits, (3) fewer expected services, and (4) a deep interaction with nature. However, it has subjective elements as well. Things like (5) group size, (6)
amount of physical activity, and (7) level of environmental commitment, depend largely on the ecotourist’s own motives and decisions when planning the ecotour. Depending on these decisions, such elements could in fact switch sides of the spectrum, even if the overall trip averages out to be closer to one side. Most ecotours will indeed be ranked closer to one end of the spectrum, but this does not mean that each individual element needs to be on the same side for something to be considered hard or soft ecotourism (Weaver 2005).

The juxtaposition of hard and soft ecotourism is a framework that houses all varieties and subgenres of ecotourism. There still is a focus or theme to most ecotours that transcends the hard/soft spectrum. A birdwatching tour, although more commonly fitting the soft ecotourism model, may fit the hard ecotourism model if designed in such a way. Ecotours are designed and marketed based on these foci, not on whether they are hard or soft. For instance, one would be hard-pressed to find a brochure for a lodge in Costa Rica whose motto was “Hard-ecotourism at its Finest!” Instead, this lodge would emphasize the strong interaction with nature, or the types of learning experiences to be enjoyed by visitors. Nor would you find a luxury trip to Antarctica boasting that they provide “the softest form of hard ecotourism imaginable!” Instead, they would highlight the quality of amenities on board, or the level of nature interpretation during excursions. For these reasons, we shall depart from the concept of hard and soft ecotourism here and concentrate more on the qualities, components, and foci of the tour.

**Popular ecotourism**

Ecotourism today continues to evolve with new concepts, tour models, and attractions appearing continuously throughout the world. The basic tenets of
ecotourism have been laid out in the previous section, but from a scholarly viewpoint. From the practical stance, it is still a bit vague as to what ecotourism really is. To be considered ecotourism, the core components of the definition must be met first. The ecotourist must be visiting a natural area, and as a result of visiting, they must be aiding in environmental conservation and improving the welfare of local communities. In some regards, ecotourism is not so much of a category of activity as it is a philosophy. From mountain trekking to stargazing, there is virtually no end to the variety and combinations of activities that one may engage in while on an ecotour. Table 1 provides a short list of typical and not-so-typical activities in which ecotourists engage while on an ecotour.

Among the various examples of ecotourism activities, nature observation stands out as the most common activity on an ecotour. Focusing on the observation of landscapes and wildlife, simply put, it is enjoying nature for nature’s sake. Continuing with the concentric circle theme from earlier, wildlife watching is still a greater circle that contains specific niches. This may be tiger-watching atop an Indian Elephant, or watching birds feed at fruit stations from a jungle lodge veranda. There is an almost limitless range of nature observation activities one can do across the globe. Listing all of them would extend this Chapter for hundreds of pages. We shall avoid that for now.

Traditionally, bird watching is regarded as being at the top of the list in terms of niche forms of wildlife watching and nature observation (Ceballos-Lascurain 1996, Cordell and Herbert 2002). In fact, surveys conducted by the National Survey on Recreation and the Environment (NSRE), the U.S. Department of Agriculture (USDA) Forest Service, and the Universities of Georgia and Tennessee estimate that in 1995, about 54 million people participated in bird watching in the United States alone (NSRE
In just over a decade, follow-up surveys showed that this number had jumped to over 80 million. With about one out of every three people in the U.S. participating in birding, this population spent over 8.2 billion days birding between the years of 2004 and 2006. Not only does this mean that there are a lot of people interested in birds in the U.S., but it also suggests that this is not merely a casual interest. In fact, of these 80 million birders, the mean annual number of days each person spent birding was 101.1 (Figure 1-13) (NSRE 2007). This transcends the level of mere hobbyist or interest and suggests that birding is a true life passion of the average birder.

Over thirty years ago, the first study on the habits of birdwatchers was conducted and calculated that over 20 billion dollars was spent by birdwatchers each year in the U.S. alone (U.S. Department of Interior 1982). A decade later, an economic analysis of a subset of the birding population found that collectively, the 43,000 birders who participated in the Audubon Christmas Bird Count in 1983 spent over 80 million dollars that year on bird-related activities (Wiedner and Kerlinger 1990). If these numbers sound impressive, it is because they are. Birds certainly are charismatic organisms with ornate markings and plumage, elaborate mating behaviors, and fascinating parental care, but the alluring qualities that draw many into the birding world are not entirely unique to birds. In fact, a great deal of flora and fauna exhibit similar patterns. It is the belief of this author that the principal reason for the impressive size of the birding industry is the support structure available for birdwatchers, or “birders”.

The first use of the word “bird” as a verb, leading to the now common use of the word “birding,” was in 1918, but it was during the Victorian era in Europe when bird watching and bird trapping started being conducted so extensively (Steinheimer 2004).
After several hundred years of tradition and passion, today an entire industry is centered around birding. There are birding lodges, with fruit stands and liquid feeders set up at verandas to aid in viewing. There are birding tour operators that plan entire ecotour itineraries around seeing charismatic birdlife in exotic locations, and there are thousands of detailed field guides for helping identify and spot birds from Argentina to Zimbabwe and everything in between. If only these had existed in the days of Darwin, Humboldt, and Wallace! Actually, the story would have been quite different if this were the case. Without them, the current enthusiasm for and knowledge of the world’s birds would probably be far less.

These early pioneers were natural history renaissance men. They had interests and expertise in many natural sciences, including geology, botany, zoology, entomology, and ornithology. However, the preponderance of ornithological research conducted by these early forefathers of natural history is followed closely by another key interest. To any reader that explores the writings of Darwin and Wallace, a unique trait is shared between the two – a passion and love for insects (Wallace 1916). On their respective expeditions they paid almost as much attention, if not more, to the entomological wonders of each locality they visited, as those of the botanical, geologic, and ornithological worlds. Their resulting publications were vast and contributed much to the scientific community, as well as to museum collections. In a way, you could say that they were some of the first to engage in entomological ecotourism.

The Rise of Entomological Ecotourism

The Early Stages

This is the first mention of the term entomological ecotourism in this dissertation, and much like tourism and ecotourism, there is no universally accepted definition for it.
However, this is not because of any conflicting viewpoints or a saturation of related definitions in the literature. There, in fact, is little-to-no reference to entomological ecotourism in scientific or historical publications. This is simply because the term has never really been documented as a separate entity before. A lack of precedence for the term’s use does not mean that the concept is novel, though. In fact, just as ecotourism’s pioneers would scour the earth in search of adventure and discovery, entomological ecotourists would explore the world for its diverse and spectacular insect fauna. Serendipitously, the very same pioneers of ecotourism were also the pioneers of entomological ecotourism. Just as ecotourism evolved from an ancestral concept to a modern-day definition, so too has entomological ecotourism. From origins of collecting insects for museums, entomological ecotourism has grown into a multidimensional ideology. Today, it is defined as nature-based tourism that incorporates insect education as a means to improve environmental and community welfare.

The roots of entomological ecotourism are entangled in the lives of some of the most well known naturalists like Charles Darwin and Alfred Russel Wallace. Their travels allowed them to collect, study, and appreciate insects and their diversity from all over the world. Having lived in an “age of natural history,” their passion ignited societal interest in the natural world, and their education provoked an intense passion for entomology. Darwin’s fascination with beetles has been well documented, as he sought to collect and observe them wherever possible during his travels. Reflecting on collecting beetles during his undergraduate career, he wrote in his autobiography, “No pursuit at Cambridge was followed with nearly so much eagerness, or gave me so much pleasure.” The intensity with which Darwin studied insects, both while at home and
abroad, was summarized perfectly by Darwin himself: “I give a proof of my zeal: one day, on tearing off some old bark, I saw two rare beetles, and seized one in each hand; then I saw a third and new kind, which I could not bear to lose, so that I popped the one which I held in my right hand into my mouth. Alas! It ejected some intensely acrid fluid, which burnt my tongue so that I was forced to spit the beetle out, which was lost, as was the third one” (Darwin 1887). Not only were there inherent risks in the exploratory-style of travel that these early ecotourists engaged in, but there were added risks in the style of collecting as well.

In some cases, the insects were more indirect in eliciting physical harm to their potential captors. Take Alfred Russel Wallace, for example, as he recollected his first encounter with the birdwing butterfly, Ornithoptera croesus, during his Malay expedition: “My heart began to beat violently, the blood rushed to my head, and I felt much more like fainting than I have done when in apprehension of immediate death. I had a headache for the rest of the day” (Wallace 1869). This passion was not limited to only these two historical icons. In fact, the fervency which figures like Darwin and Wallace displayed towards entomology extends back to the mid 1600s, with individuals like Thomas Moffet and Ulysse Aldrovandi producing two of the first comprehensive books on insects, Insectorum Theatum (1634) and De Animalibus Insectis (1638), respectively. It is difficult to attribute the birth of entomological ecotourism to either Moffet or Aldrovandi, though, as most of their study material (i.e., specimens) came to them via traders, rather than either of them acting as the actual ecotourist. Nevertheless, they played a key role in the birth of entomology as a discipline. Moffet,
although a doctor of medicine by trade, became regarded as the “Prince of Entomologists” by contemporaries (Salmon 2000).

The movement to form a society intrigued by entomology and natural history in general was not solely due to individuals like Moffet, but rather was the result of a collective effort and a long history of great entomologists. With the standard of living rising in parts of society from decade to decade in the 16th-19th centuries, concomitant with a lessening fear and superstition about nature, this new age was one of curiosity: curiosity about the natural world and science. Embodying a growing sentiment and reverence for the natural world, the Royal Society was founded in Great Britain in 1662, which was shortly thereafter mirrored by other learned societies, as more and more lab scientists and field naturalists were established throughout Britain and Europe (Salmon 2000). With figures such as Isaac Newton and Francis Bacon revolutionizing the way people would think about our relationship with the natural world, this curiosity was only amplified, making nature irresistibly exciting.

Leading up to icons like Darwin and Wallace was an equally impressive, but lesser known cohort of entomologists and naturalists. By the early 1700s, entomology and insect collecting became regarded as fashionable. It was even popular enough to be satirized by the poet Alexander Pope in 1712 in The Rape of the Lock (Salmon 2000). Perhaps surprising due to the exclusively-male nature of early entomological and natural history societies, women were in fact the earliest insect collectors during this new wave of high society naturalists (Salmon 2000). Helping to promulgate this new social activity, dignified females like Lady Margaret Cavendish, Madam Merian, and Mary Somerset contributed much to the popularity of collecting insects, especially
among informally trained amateurs – a very important group in the evolution of ecotourism entomology. In fact, the vast majority of contributors to insect collections worldwide today are still amateur entomologists (T. Emmel and A. Warren, pers. comm.).

The first entomological society was formed somewhere between the years 1720 to 1742. Calling themselves the Society of Aurelians, after the aureolus (Latin for golden) coloring of some butterfly chrysalids, the vague origin of the society is largely due to the informal nature and inexact transition from coffee house get together to scientific society. However, except for those members living in proximity to London, where these social meetings would routinely take place, entomologists, both professional and amateur, likely worked in relative isolation in the mid 18th century. At the dawn of the Victorian Era in the early 19th century, collecting became increasingly more inclusive and social, as roads improved, and rail networks were constructed into previously inaccessible wild places (Salmon 2000). Here we see the birth of the field club.

**Early Field Clubs**

The first field club for entomologists and other pursuers of Natural History was established in 1831 and was known as the Berwickshire Naturalists’ Club. The main purpose of the organization was to arrange field excursions for the collection and observation of insects by its members. However, the club also served as a clearinghouse for local information on natural history, particularly of entomology. Members would contribute their data and findings to then be integrated, assembled, and distributed to other members by way of scientific publications. In a way, these field clubs were early databases of information. Although the Berwickshire Naturalists’ Club remained small in size, throughout the next several decades, this club model was
replicated across Britain. Similar organizations appeared widely throughout
Manchester, Liverpool, Birmingham, Tyneside, and Yorkshire (Salmon 2000). In
addition to attracting some of the top naturalists in this time period, such as John
Henslow, Darwin’s mentor, Professor Sedgwick, and C. C. Babington, these societies
produced highly influential journals, such as The Naturalist, which is still an important
reference to scientists around the world today. By 1873, there were no less than 169
locally based scientific societies in Britain alone, with at least 104 of these being
dedicated field clubs (Allen 1994). Although these societies had broad-ranging
interests, including the collection of fossils and plants and a general appreciation of the
beauty in nature, the collection and observation of butterflies was always the most
popular activity during field outings (Salmon 2000).

The activities enjoyed by members of these clubs were not limited to outings in
nature, though. A great deal of attention was also paid to the social aspect of things –
particularly with regards to food and drink. Members would routinely dine lavishly at the
homes of their colleagues and be treated to a “well-spread table, furnished with fruits
from his Lordship’s garden, and wines from his cellar, which formed no inappropriate or
unwelcome termination to the day’s ramble” (Salmon 2000). Elaborate shows would be
put on to demonstrate scientific technique or to exhibit collections. While many of these
dinners and exhibitions were intimate and small, some elicited quite a response. For
instance, the first “Grand National Entomological Exhibition,” put on by the South
London Entomological Society in 1878, drew a crowd of over 70,000 guests (Salmon
2000). Although these numbers were not replicated each year, these clubs certainly
had a growing following. Throughout the Victorian Era, these societies had a lasting
impact on society. By the end of Queen Victoria’s reign, most of the era’s great names were no more, but their tradition and legacy lived on in their life’s work and in the culture they helped to create.

Field clubs represented some of the earliest forms of structured entomological ecotourism. Including both professional and amateur entomologists, these clubs hosted outings not solely for the purpose of rigorous scientific research and insect education, but for the simple pleasures of searching for and finding insects in the context of adventure and exploration. We have seen that days in the field were often balanced by lively nighttime discussions and social gatherings. Whether these gatherings take place in jungle lodge dining rooms, as today’s entomological ecotours do, or in the houses of contemporaries in the Victorian Era, there is a straightforward resemblance between historic field club tours and those of today.

From the 16th century until present, key individuals are responsible for our present-day concept of entomology, as a science as well as a passion. However, those responsible were not only the forefathers (and foremothers) of entomology, but of ecotourism, too. It is striking how analogous the evolution of both ecotourism and entomology are. While each of these realms has their own pioneers, originally having little to do with the other, there is in fact an uncanny occurrence of overlap in the interests of early pioneers of ecotourism and entomology. In many cases, it was the obsession with entomology and natural history that instigated key figures to roam the globe in search of discovery.

One cannot help but notice a change in entomology’s fashion in today’s society. While it remains a highly respectable science that serves nearly all sectors of industry,
agriculture, and health, entomology as a motivation for travel and exploration seems to have changed from what we can glean from the history books’ interpretation of entomology in the 17th, 18th, and 19th centuries. While ecotourism is surging, there seems to no longer be that solid connection between ecotourism and entomology, as was so apparent in the rise of each. In fact, the lines barely cross anymore.

At this point, we must pose the question as to why insect ecotourism barely exists, while other forms of ecotourism, like birdwatching ecotourism, flourish? There is clearly a history of amateur and professional entomologists traveling for the sake of observing insects, but why is this confined to the past? If entomological ecotourism were to share in only a slice of the 80 million followers that the birding industry boasts in the U.S. alone, insect education would increase dramatically. However, before continuing, we must ask why it is important to promote entomological ecotourism?

The Benefits of Entomological Ecotourism

The promotion of entomological ecotourism serves many purposes. The first is perhaps the most straightforward. Simply, when people participate in entomological ecotourism, they gain a better understanding of insects. This understanding is multidimensional. Depending on the context of the ecotour, one may learn about insects’ connections with other wildlife, or the plants that they depend upon. They may leave the tour having a better understanding of a particular insect’s role in nutrient recycling or pollination. Ideally, an ecotourist will learn about several important roles that insects play and be able to witness these roles as they occur in the wild.

Other than the inherent value of knowledge, why is an understanding of insects important? This leads us to the second purpose of promoting entomological ecotourism. Insects provide a foundation for understanding the entirety of our natural
world. They function at all trophic levels. They form the food base for countless other organisms. They pollinate and/or feed upon virtually all species of flowering plants. In a word, they are indispensable. Edward O. Wilson said it best when he stated that, “if all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos.” By understanding insects as a major kingpin in the environment, one may have a more complete understanding of all life.

This brings us to our third purpose for promoting entomological ecotourism. You cannot save what you do not know. A mantra in conservation biology, this unambiguous phrase has been integrated into so many speeches, mission statements, and publications that its origins are lost. Today we face the grave reality that our world is in crisis. Biodiversity is vanishing at an alarming rate, with habitat destruction being the principal cause. Entomological ecotourism serves to conserve habitat through the traditional principles of ecotourism (i.e., creating value for natural areas through the economics of tourism), as well as through the knowledge gained from insect education. More informed ecotourists will return home with a greater awareness of the delicate balance found in nature and hopefully be more cognizant of their own role and potential in conservation efforts. Being one of the most speciose groups of animals on earth, insects provide a perfect example of the rapid disappearance of the world’s biodiversity. Also being keystone taxa, meaning that they collectively play a greater role in the functioning of healthy ecosystems than other taxa, their critical position in the web of life is a valuable lesson. The knowledge gained while on entomological ecotours serves to promote conservation. This may be directly, when an interested ecotourist returns
home to then contribute to rainforest restoration projects, or indirectly, as they share conservation messages with friends or by using social media. The more people who understand and care about conservation, the more likely our entire society will adapt to the changes we must make in the way we conserve natural areas.

The fourth purpose for promoting entomological ecotourism is to create new ecotourism opportunities. We have seen the value of ecotourism from examples presented earlier in this Chapter. Increasing the overall scope and number of additional opportunities serves to expand ecotourism into new areas and to new levels of influence. Creating niche markets for ecotourism does not necessarily compete with existing niches, but rather attempts to recruit new followers to the world of ecotourism. By increasing the overall number of opportunities, it is reasonable to think that the overall number of ecotourists in the world will increase as well.

These four factors are not a finite limit. As ecotourism continues to grow, new purposes and new benefits are likely to emerge for why insects should be integrated into the ecotour.

**The Next Steps for Entomological Ecotourism**

With the proper support structure, I believe that insect tourism has just as much potential as bird watching or any other ecotourism niche, as an industry, activity, and lifestyle. Some support does currently exist, by way of expertly constructed entomological field guides, international organizations, and an extensive scientific knowledge base. However, there is tremendous room for growth, and opportunities should exist to put these tools in the hands of ecotourists. In order for insects to reach the front stage of public international attention, insects should be integrated into what is now the fastest growing sector of the travel industry – ecotourism. Supported by
centuries of precedence, entomological ecotourism is at a prime position to take hold as an established subgenre of ecotourism. The following Chapter 2 will detail opportunities for growth, with specific attention to ways for insects to be integrated into the modern ecotour.
Figure 1-1. A timeline of tourism’s history from 3,000 B.C. to 1,000 B.C.
Figure 1-2. A timeline of tourism's history from 1,000 B.C. to year 0
Figure 1-3. A timeline of tourism’s history from 0 to the 1980s, when the establishment of ecotourism was solidified
Figure 1-4. The Grand Tour Era saw a shift in the role of travel and tourism. Prior to the Grand Tour, travel and tourism were mainly privileges of those with elevated social status. However, the Grand Tour era initiated an additional role of travel and tourism – to promote a rise in social status.

Figure 1-5. Average length of the Grand Tour 1547-1840. The overall length of the Grand Tour decreased throughout the era due to changing tour attitudes and goals, as well as the limited time and money of the emerging middle class (Towner 1985).
Figure 1-6. Average age of Grand Tour participants 1547-1840 (Towner 1985)

Figure 1-7. Percentage of Grand Tour participants who attended a University from 1547-1840. (Towner 1985)
Figure 1-8. International tourist arrivals by region (million). International tourist arrivals have grown exponentially in the past 60 years. Presently, worldwide tourism numbers are approaching one billion annually (UNWTO 2010).

Figure 1-9. Inbound tourism by mode of transport in 2010. Modes of transportation have greatly changed throughout the centuries. Whereas water traditionally represented a major share in modes of transit, it is now in the shadow of both air and road transportation (UNWTO 2010).
Figure 1-10. Purposes of visit for inbound tourists in 2010. The majority of tourists now travel for the sake of leisure and recreation, when compared to the other main purposes of travel, including business, health, and religion (UNWTO 2010).
Figure 1-11. Examples of tourism concentric circles. Tourism has many derivatives, which are all housed in the tourism framework, but also have their own derivatives.
Figure 1-12. The ecotourism spectrum exhibits two poles. Hard ecotourism is typical of new ecotourism products or activities with limited infrastructure, whereas soft ecotourism is typical of existing products or activities that are capable of providing more comfort for larger groups of ecotourists (Weaver 2005).

<table>
<thead>
<tr>
<th>HARD</th>
<th>SOFT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strong environmental commitment</td>
<td>Superficial environmental commitment</td>
</tr>
<tr>
<td>Specialized visits</td>
<td>Multi-purpose visits</td>
</tr>
<tr>
<td>Long trips</td>
<td>Short trips</td>
</tr>
<tr>
<td>Small groups</td>
<td>Larger groups</td>
</tr>
<tr>
<td>Physically active</td>
<td>Physically passive</td>
</tr>
<tr>
<td>Physical challenge</td>
<td>Physical comfort</td>
</tr>
<tr>
<td>Few if any services expected</td>
<td>Services expected</td>
</tr>
<tr>
<td>Deep interaction with nature</td>
<td>Shallow interaction with nature</td>
</tr>
<tr>
<td>Emphasis on personal experience</td>
<td>Emphasis on interpretation</td>
</tr>
<tr>
<td>Make own travel arrangements</td>
<td>Rely on travel agents &amp; tour operators</td>
</tr>
</tbody>
</table>
Table 1-1. Ecotourism is not a discrete list of activities, but rather a philosophy on travel. Activities that involve nature tourism and also promote environmental and community wellbeing are considered ecotourism by today’s standards.

Examples of Ecotourism Activities

- Wildlife Watching
- Hiking
- Mountain Trekking
- Photographic Safari
- Plant Observation
- Fossil Observation
- Star Gazing
- Floral and Faunal Rescue
- Whitewater Rafting
- Rock Climbing
- Road Biking
- Off-road Biking
- Running/Marathon
- Snorkel/Scuba
- Scientific Research
- Zip-lining
- Arial Tours
  (balloon, helicopter, plane)

Figure 1-13. According to a 2007 publication of the National Survey of Recreation and the Environment, bird watching is not only a common activity amongst U.S. citizens, but is growing from year to year.

<table>
<thead>
<tr>
<th>Years</th>
<th>Percent Participating</th>
<th>Sample Size</th>
<th>Mean Annual Birding Days</th>
<th>Sample Size Birding Days</th>
<th>Number of Birding Participants (1,000s)</th>
<th>Total Number of Annual Birding Days (millions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994-1995</td>
<td>27.0</td>
<td>17,216</td>
<td>87.7</td>
<td>3,626</td>
<td>54,416.0</td>
<td>4,774.9</td>
</tr>
<tr>
<td>1999-2000</td>
<td>33.2</td>
<td>28,327</td>
<td>81.9</td>
<td>8,602</td>
<td>70,993.6</td>
<td>5,811.0</td>
</tr>
<tr>
<td>2001-2003</td>
<td>31.6</td>
<td>41,822</td>
<td>92.9</td>
<td>11,423</td>
<td>69,652.2</td>
<td>6,469.8</td>
</tr>
<tr>
<td>2004-2006</td>
<td>36.3</td>
<td>14,969</td>
<td>101.1</td>
<td>3,894</td>
<td>81,470.8</td>
<td>8,238.2</td>
</tr>
</tbody>
</table>
CHAPTER 2
INSECTS IN THE ECOTOUR

The rapid growth in ecotourism over the past several decades has given concomitant rise to numerous new subcategories of ecotourism, with specific tour features highlighted in itineraries. These new genres of ecotourism may focus on specific wildlife, such as birds, while others may have a predominant service component, such as volunteer-based ecotourism, where donating services and goods to communities is a key purpose of the tour. Although there are ultimately a finite number of subcategories for specialized ecotours, it is difficult to imagine that we will see the end of ecotour experimentation anytime soon. Both day tours and multi-day tours are constantly evolving to hone in on specific components to ecosystems, industries, or projects.

Insects are not typically thought of as an emerging market in the ecotourism world, but with some investigation, it appears that insects could surface as a key attraction in many nature-based tourism enterprises. The sections of this Chapter detail the variety of ways that insects are currently integrated into ecotourism, as well as novel approaches that may further the development of entomological ecotourism.

**Butterfly Farming and Ranching**

Across the world, butterfly farms exist in order to raise butterflies for sale. The sale of these butterflies may satisfy one of several objectives. The butterflies may be sold as live organisms, largely used for butterfly exhibits, such as gardens and enclosed vivariums, but they may also be used in butterfly “releases”. An increasingly common trend is for adult butterflies to be released at events such as weddings, funerals, birthdays, and even grand openings of stores (E. Smith, pers. comm.). In addition,
Monarch butterflies (*Danaus plexippus*) are often purchased from butterfly farms to be “tagged” and released for the purpose of participating in the Monarch Watch program at the University of Kansas. New uses for live “farmed” butterflies are constantly being invented. There is also, however, a significant “dead stock” trade of farmed butterflies. This dead stock is comprised of dead butterfly specimens used for their aesthetic value in jewelry, artwork, and other displays. Rare or exceptional specimens also have scientific value and are often donated to research institutions when reared at butterfly farms to be studied.

The simplest element to the definition of a butterfly farm is the fact that they “grow” butterflies. While some farmers breed butterflies, and thus are actively involved in all stages of the butterflies’ life cycles, others only work with part of the life cycle. When working with only part of the life cycle, the farmer often collects larvae or pupae from the environment (i.e. forest, jungle, field, etc.) to then be reared to adulthood at a chosen location. The latter is typically referred to as butterfly ranching and is considered to be quite distinct from butterfly farming (Parsons 1982, 1992). The level and duration of care given to the butterflies is perhaps the most significant difference between these two “classes” of butterfly farming. It is also much more common to find butterfly ranching in remote areas and tropical countries, such as Papua New Guinea, Malaysia, Taiwan, and the Solomon Islands, where the higher level of infrastructure and expertise necessary to operate a full-scale butterfly farm is more difficult to obtain. Nevertheless, revenue generated from butterfly ranching in these countries is significant. Estimates from over 20 years ago predicted that the worldwide figure generated from these farms exceeds $100 million dollars, with $20-$30 million coming from Taiwan alone (Collins
and Morris 1985, Emmel and Hepner 1990). Mercer and Clark (1989) noted that a Manus Island (PNG) farmer specializing in two endemic species (*Papilio weymeri* Niepelt and *Graphium codrus auratus* Rothschild) was able to generate an annual income of $3,500 in 1989, comparable to the revenue of butterfly farming to that of successful small-scale coffee operations.

Another key difference between butterfly ranching and farming is the level of butterfly production, meaning the number of butterflies produced per unit time. The level of production can vary from several adult butterflies a month (more typical of ranching) to thousands each day (more typical of large-scale farming) and has an obvious effect on the level of infrastructure and time commitment from those involved (Parsons 1992). The level of production also affects the overall community impact in terms of jobs produced. In turn, the purpose of the operation is usually very different between ranchers and farmers. In conjunction with the typical remoteness of butterfly ranching operations, the relative infrequency of visitation by those interested in purchasing butterflies results in an inconsistency in production on part of the rancher (pers. obsv.). Most ranchers concentrate on producing only one or two highly prized species of butterflies to sell to dedicated Lepidopterists willing to travel far for a single butterfly or male/female pair. On the other hand, some Taiwanese ranching operations producing up to 2,000 butterflies per day from a single rancher who is patient enough to sit by a urine-baited trap near a sandy riverbank (Parsons 1992).

True butterfly farming takes an entirely different approach. As mentioned previously, the butterfly farmer is involved in the entire life cycle, with each life stage separated from the environment to manage for quality (i.e., excluding parasites and
predators, controlling humidity and sunlight, and regulating host plant use) to ultimately increase yield and consistency. Because of the control measures put into place, there is more stability in the production of butterflies, as well as a general increase in yield when comparing ranching to farming. Coupled with this predictable yield and the fact that farms are generally more accessible (i.e., a few hours or less by car or bus from an urban center) a network of buyers, distributors, and sellers has arisen, enabling the farms to sell living material to live butterfly exhibits around the world. These live butterflies are most often shipped and sold in the pupal stage due to their immobility, external toughness of the integument in the pupa, and ease with which this life stage travels, having no need to feed or drink during the transition. Exhibits wishing to display live butterflies may be housed within a botanical garden, a natural history museum, or sometimes they may be stand-alone private enterprises. The ability to deal in live butterflies widens the market significantly to the farmer (Collins and Morris 1985, Morris 1986, Parsons 1992). The relatively short lifespan of a butterfly necessitates a system of frequent distribution, which is less available with remote butterfly ranching operations. However, both institutions are able to take advantage of the deadstock demand for the “specialist” trade (low quantity/high value) and the “decorative” trade (high quantity/low value), which preceded the newer livestock trade (Pyle and Hughes 1978, Pyle 1981).

This established network of sales and distribution is common to the larger scale farms, which may have dozens of employees. The typical one or two-man operation with a hierarchical network of suppliers and distributors seen frequently in ranching is less common among butterfly farmers, but this is not to say it is absent. With farms operating as structured businesses, they often work with smaller farms to create a
supply chain, enabling individuals or families to profit from butterfly farming even if they
don’t have the expertise or resources to operate a full-scale farm. Without the central
farm’s help, distribution becomes a problem. This network may assist not only in
distribution, but also with training and even supplies. In Costa Rica alone, there are
over 50 of these smaller farms that supply to one large farm, having a tremendously
positive impact on local community welfare (E. Rodriguez, pers. comm.).

Between farms and ranches, farms are certainly the more emergent of the two
methods of butterfly “production”. A significant reason for this is the accelerating
demand for live butterflies, not only in the U.S., but across the developed world (Collins
1987). Live butterflies are used at weddings (in place of throwing rice), funerals (in
place of flowers), butterfly research programs (at universities and other higher education
institutions), and live butterfly exhibits (at botanical gardens, museums, and theme
parks) (Z. Greathouse and E. Smith, pers. comm.). With the ease of communication via
the internet and email, butterfly breeding techniques are improving continuously, and
new methods are promoted and shared with the entire world with just the click of a
button. A small-scale butterfly gardener in New Jersey may begin experimenting with
butterfly breeding and by using the media resources available to him or her, has the
opportunity to learn from experts and quickly become a profitable butterfly farmer. This
lack of expertise has always been a key problem in the promotion of butterfly ranching
and farming (Parsons 1992). The information age of today has changed that.

The scale of an individual farm (i.e., land area it covers, production levels, number
of employees, etc.) is quite variable. So, too, is the relationship between the farms and
the environment around them (Whelan 2008). It is nearly universal that these farms
occupy more natural and rural habitats, and this is the case for several reasons. First, most larger farms require an abundance of property to keep hundreds to thousands of host and nectar plants, multiple butterfly rearing rooms, oviposition cages, larval feeding centers, areas to store the butterfly stock before shipping, and very likely an office. Land this size is harder to find in more developed or urbanized areas. Second, butterfly breeding stock may be replenished on an as-needed basis from wild-caught individuals, borrowing a lesson from the butterfly rancher. When located in a more pristine and rural setting, it is much easier to capture wild butterflies, and even easier when the property is yours to manage, monitor, and conserve. This is exactly the philosophy of major farmers and ranchers in Malaysia, who have been reported to purchase large expanses of private forest in order to augment their farming operations with total value calculated to be over $350,000 (Collins 1987). Also, in areas of extremely high diversity, new species of butterflies and host plants may be integrated into the farm system on a trial basis, as they are found in the surrounding forested areas (Daniels et al. 2008, E. Rodriguez, pers. comm.). This allows for the farm and its employees to diversify themselves in the species being bred, as more resources become available. Lastly, the location of the butterfly farm has a significant impact on the rapidly developing ecotourism component, which is now ubiquitous at farms across the globe.

Today, many butterfly farming operations inherently meet the standards to be considered an ecotourism enterprise. Farm owners are rapidly realizing the potential of this growing industry and are taking steps to promote their facilities as tourism destinations. Guided tours, educational workshops, butterfly gardens, and bookshops are some examples of the tourism features found at butterfly farms that function to
promote visitation. However, another powerful tool is being used to benefit the commercial side of the operation as well – scientific research (Parsons 1982, 1983, 1992).

The use of butterflies by farmers for commercial gain depends on and supports scientific research and monitoring to the point that the operation itself and the science behind it are interwoven (Morris 1986). There is potential for the knowledge gained at butterfly farms to be used not only in benefitting the farm, but also to enhance scientific understanding of butterflies in general. Farms have made the perfection of butterfly breeding techniques their business, which is invaluable from a conservation standpoint, especially should it one day prove necessary in species rearing and reintroduction programs (Parsons 1992). From a purely scientific viewpoint (i.e., non-commercial), the integration of research into the butterfly farming programs is tremendously valuable and should become commonplace where possible. From a commercial viewpoint, scientific investigations will help promote the educational and interpretive side of farms as ecotourism destinations. Not only does the integration of scientific work help promote the farm, as ecotourists today are becoming increasingly more educationally-minded, but the data and results of various research projects could be assembled into publishable material (Parsons 1982, 1983). This could translate into bookstore and gift shop items, which would directly support the commercial side of the farm, or appear in a range of media, from scientific journals to internet news articles, helping to promote the farm through its association with education at all levels.

As tourism grows in the butterfly farming industry, everyone involved benefits, including the biodiversity and environment surrounding the farm. More employees are
hired, visitors are educated and become enthusiastic about nature and conservation, and undeveloped habitat increases in value, as it becomes a backbone for generating income. For example, one major farm in Costa Rica has pledged that all profit from the butterfly farming operation will be used for the purchase and preservation of new land in the surrounding jungle (E. Rodriguez, pers. comm.). In addition, the Wau Ecology Institute estimated that in 1989 a fully-operational butterfly farming operation in Papua New Guinea would likely see income in the range of $44,000 USD. A steady income of this sum adds incredible value to the surrounding forest and functions to strongly dissuade deforestation practices. This is a tremendous personal or family income for this region and is replicable for countries across the world.

Although areas like Costa Rica and Papua New Guinea are exceptionally suitable for butterfly farming and ranching due to the climate and wild butterfly fauna, a minimum level of expertise is needed. The following sections include several case studies of existing butterfly farms and ranches across the world, and how once this minimal level of expertise is reached, the farmer may significantly help entomological ecotourism.

**Butterfly Ranching in the Solomon Islands**

Situated off the eastern side of the New Guinea mainland, the Solomon Islands rise up out of the South Pacific waters in Tropical Melanesia. Consisting of roughly 1,000 islands, the human population of approximately 600,000 people are divided amongst nine governmental provinces across the archipelago.

Although the top industries, including agriculture, fishing, and forestry provide the majority of employment opportunities and make up a large part of the estimated GDP (1.5 billion USD), the remoteness of many islands, both big and small, necessitates more innovative and independent employment opportunities to spread employment
opportunities more evenly. Butterfly ranching, although less than common to date, provides some employment in rural villages in the scattered islands throughout the archipelago. Sourakov (2001) was the first to thoroughly describe the day-to-day practices of a typical butterfly rancher in the Solomon Islands, but numerous other papers have described butterfly ranching and farming operations from across the world (Pyle and Hughes 1978, Pyle 1981, Parsons 1982, 1983, 1992, Collins and Morris 1985, Morris 1986, Collins 1987, Mercer and Clark 1989, Emmel and Hepner 1990). Despite the seemingly limited number of iterations with regards to various methods, styles, and practices of the typical butterfly breeder, there exist almost limitless adaptations to the science and art of rearing butterflies from wild-grown populations.

Butterfly ranching takes many forms, ranging from large-scale operations with intricate supply chains, to one-man operations using his or her own home as the rearing facility, office and gift shop all in one. The later is the topic of discussion in this section, as pertains to the remote islands within the Solomon Islands archipelago – an area still seeped in great mystery and intrigue. The following represents a first-hand account by the author during a research expedition to the Solomon Islands in August of 2009.

**Description of Ranongga Island butterfly ranching.** Setting out from Fatboys Gizo, a small lodge located on Mbabanga Island, near Gizo, New Georgia, I headed with my guide and boatman on a 2.5 hour journey towards Ranongga Island. Having heard from an overzealous and a bit inebriated boatman and artifact carver the night before that there indeed existed a “butterfly farmer man” from his Island, I took a chance and set out with a high definition camcorder in hand and an adventurous spirit. I was determined to capture this rural practice on film, as a way to permanently preserve the
knowledge harnessed from presumably many years of farming butterflies in this unique way.

After the boatman called out several times to patient fishermen sitting in their dugout canoes just off of the rocky coastline of Ranongga, we pinpointed the location of Rava Village as just north of Pienuna and landed against the rocks. With just enough time between the next wave of ocean swells for me to jump out with my gear before the boat was once again slammed against the rock jetty, I made it to shore. After paying “kastoms” to the local in charge for permission to land at his village, which loosely translates to customs from Solomon Island Pidgin to English, I was escorted by a gang of mesmerized children to a mostly grass and straw hut where I was to meet the village butterfly farmer. After introducing myself, I found out that Nathan was the name of my new butterfly-farming friend. He learned of my interest in butterflies and proceeded to bring out two boxes of papered specimens of *Ornithoptera victoriae*. In all, there were 27 pairs of these specimens, all in perfect condition.

Nathan was a veteran of butterfly farming and had sold over 1,000 butterflies since he began this work at 30 or 35 years of age. At this visit in 2009, he was 66. Collecting around 20-30 pupae each month from his one-hectare private ranching area near his garden plot, he is careful in protecting his source of income. No one helps him and few even know the approximate location of his source of host plants on which the *Ornithoptera* feed. Returning to his ranch about once a week, he cleans up the plants in order to promote new growth and to allow ample sunlight to reach all strata of the *Aristolochia* vine, while keeping track of the movements of anywhere from five to 20 larvae. He makes careful mental notes on the growth of these larvae so that he may
return at just the right time to harvest the pupae and bring them back to his home. Once safely in his straw hut, he allows them to emerge naturally before becoming fresh papered specimens for sale.

Aware of common mortality issues affecting Lepidoptera pupae, Nathan is ready with a spray bottle of fresh water to cool them off when they become too hot or too dry from the Solomon Islands sun. He is also extremely careful in attaching the pupae to the thatched roof so that as they emerge, they may hang freely in order to let their wings harden just as they would in the wild. When the weather is cool, he will expect the pupae to emerge within three weeks; when hot, perhaps four. When the adult *Ornithopera* have fully emerged, he promptly injects the adults with methyl spirits, as he calls the purplish chemical that he purchases from time to time on visits to Gizo, which is approximately three hours away by motorboat.

Rather unique to Nathan’s operation, he has no supply chain whatsoever. There is no “broker” from a nearby area to purchase specimens for overseas shipments. He must work entirely on his own to sell his butterflies. With no internet or email, let alone electricity, it is mostly a sit-and-wait tactic. Most of his clients visit him to purchase butterflies from places like France, Japan, and Australia and are very willing to pay his asking price of SBD200, or about $25 USD per pair. His most recent clients were a man and wife from the Czech Republic who came to purchase three pairs of adult specimens. These, however, were his only sales in 2009 up until my August visit. Nevertheless, he acknowledged that this was sufficient income on which to support himself for the remainder of the year.
Knowing that I would not be able to return to the US with any of these specimens, I did the next best thing and purchased a live pupa from Nathan so that I could photograph it emerging in the coming days back on Mbabanga Island. At SBD50 (roughly $6 USD), this was a great deal and yielded some fantastic photos and video of it. Obviously, a special effort has to be made by entomological ecotourists to find and be able to observe these remote locations of individual farmers, but the experience is unique enough that it could be worked into more adventurous ecotourism itineraries.

During this visit to Rava Village, my guide and boatman left to do some reconnaissance while I was ashore in order to find out the location of another butterfly farmer nearby. After meeting back with them at the shore several hours after the initial landing at Rava village, we took a short boat ride (roughly 20 minutes) and landed at a sandy beach about 10m long. Greeted by a much younger man than before, as we walked to the center of the small village, I could already tell that his style of farming would likely differ.

The primary difference is a typical one, with the addition of a “broker” from Honiara, the capital of the Solomon Islands, playing a significant role in both production and distribution. With the addition of a supply chain, this farmer, named Rodo, was able to sell up to 60 pairs per year by harvesting from one of his three 20-square meter plots, as well as hiring local children and offering SBD20 (about USD 2.50) for each pupa found. Like Nathan, he incorporates his ranching visits with times that he tends his garden, making it an extension of his existing agricultural work.

With visits from his broker in Honiara relatively infrequent and almost always unannounced, he must anticipate a visit and be ready with stock to sell at all times. At
about SBD2000 for 20 pairs of *Ornithoptera victoriae*, he takes about a 50% pay cut versus Nathan at the first farm, but the convenience factor of selling in volume to a broker makes it worth it, according to Rodo, and I would tend to agree. However, with over 30 years of experience farming butterflies as a principal business, he remembers days when he would sell to visitors from Japan and New Zealand for SBD3 per specimen.

Clearly, the flora and fauna have been able to support this small-scale industry for many decades, but legal and political barriers prevent normal development of an export business. The Solomon Islands government would support development of a butterfly farming industry but hastily and carelessly made regulations by foreign governments prevent this. In 1991, a U.S. CITES delegation attempted at a CITES conference to punish the Solomon Islands for then-lax export laws of other wildlife materials by banning the export of any Solomon Islands species to CITES signatory countries. A confusing legal situation has ensued. Contrast this situation with other nearby countries where nationally supported enterprises have solidly benefited both the people and butterflies. Programs like the nationally-run Insect Farming and Trading Agency (IFTA) in Papua New Guinea brought to light the real possibility of regulating insect trade in a responsible and sustainable manner, yielding significant profits (Parsons 1992). Nevertheless, the practice of butterfly farming in the Solomon Islands for small-scale export by travelling collectors or dealers persists and offers economic incentive to remote villages that have very few other ways to earn money.

With both ranching scenarios examined in the Solomon Islands, there is a definite feeling of informality. The steps taken for production, rearing, and maintenance fit well
into the daily tasks of life. However, profitability is greatly restricted, as production and distribution are irregular and relatively unpredictable. In order to promote predictable distribution, whether it is via a broker or selling directly to clients, a higher level of predictability in production must come first. This is where one must make the transition from butterfly ranching to butterfly farming.

As already detailed in the previous section, butterfly farming can take many forms, but ultimately sees the farmer rearing butterflies from the egg stage, all the way to the pupal and adult stages. With one adult female butterfly of most species yielding dozens to hundreds of eggs over the course of her life, the potential for dealing with significantly greater numbers of butterflies and greater profit in the farming scenario is clear. However, with these greater numbers come a greater investment of time, resources, and knowledge on part of the farmer. The following section details characteristics of two large-scale butterfly farms in Costa Rica and in Florida.

**Butterfly Farming in Florida and Costa Rica**

Around the world, there are numerous examples of the variations and different techniques that farmers apply to butterfly farming operations, but the two farms detailed in the following examples from Florida and Costa Rica represent two of the largest in the world. They also exhibit very different modes of operation and degrees of potential exposure to entomological ecotourism.

**Butterfly farming in Florida**

Florida is very well suited to butterfly farming, due primarily to the mild winter temperatures that allow for nearly year-round growth of plants and butterflies, especially when the operation is enclosed properly in greenhouses. In addition, over 180 native species of butterflies have been recorded in Florida, with roughly half of them being
relatively common (Daniels 2003). This provides evidence of not only the terrific conditions available to wild butterflies, but also represents a good stock of butterflies with which to replenish captive-reared populations at farming operations. The following account describes the largest butterfly farm in Florida and one of the largest in the world in terms of production levels (E. Smith, pers. comm.).

Shady Oaks Butterfly Farm, located in Brooker, Florida, encompasses a total of 170 acres, with the farm operational structures occupying five acres in total. This author would classify the farm as a large-scale self-contained butterfly farm in that it regularly sells over 5,000 butterflies (combined pupae and adult butterflies) each month during the high season (March-October). The reason for assigning it a “self-contained” status is that all of the rearing and production of butterflies is done on site. This contrasts with other farms, which have smaller off-site locations that they use in their production methods. More details on this process will be presented in the following section on the Costa Rica example.

Because virtually all of their business comes from the U.S., Shady Oaks is able to deal in all life stages of butterflies. Although shipping the soft-bodied larvae from Malaysia to butterfly exhibits or classrooms in Europe or North America would be nearly impossible, Shady Oaks is able to supply butterfly caterpillars to locations across the country due largely to the rapid delivery of parcels in nearly all parts of the U.S. Their years of experience and innovation with packaging these juvenile Lepidoptera also is key to their success. In addition to larvae, Shady Oaks ships eggs, pupae and adults. During their high season from March to October each year, in one month they ship an average of 2,000 eggs (varies from 1,000-3,000), 1,200 larvae (but varies from 400-
8,000), 1,600 pupae, and 2,800 adults to clients across the U.S. (Figure 2-1). The remainder of butterflies produced at the farm that are not sold to customers are used as breeding stock, with roughly 900 adult butterflies on site during the March-October time period. Come October, butterfly numbers are maintained at lower numbers and largely for the purpose of maintaining genetic integrity before full-scale production resumes in March of the following year (E. Smith, pers. comm.).

Clearly, there is a sharp contrast to the butterfly ranching operation upon examining the difference in production rates. However, further differences are seen in the style of production. The previous reference to breeding stock alludes to the fact that butterflies are indeed bred at this and all true farming operations. While wild-caught butterflies are sometimes mixed in with populations to integrate new individuals into the gene pool of breeding butterflies, nearly all butterflies sold are the direct result of the mating and reproduction by captive butterflies at the farm. Beginning with the egg stage, each butterfly is directly nurtured until reaching the particular life stage at which it is sold and shipped to the customer. This nurturing begins with the collection of the eggs from dedicated breeding cages (Figure 2-2). Then, eggs are washed in a 5% bleach solution for exactly 60 seconds in order to sterilize the chorion of the egg from bacterial diseases, viruses, and any minute parasitoids that may have encountered the egg prior to it being collected. Once removed from the bleach solution, eggs are places in specialized larval feeding boxes loaded with host plant cuttings (Figure 2-3). As the larvae hatch and mature, they consume copious amounts of host plants, necessitating near daily additions of host plants, in addition to frequent changes of boxes to minimize the potential of disease transmission with the build up of frass (i.e., feces). Larvae are
allowed to pupae in the same container as used for larval feeding, but are promptly removed as soon as the pupal case is hardened and matured. In order to more properly anticipate emergence time so as to match purchase requests, pupae may be stored in temperature-controlled environments as a way of delaying eclosion. For those butterflies that are required to fully mature before shipment, pupae are glued to hang in their natural position in dedicated emerging chambers and allowed to emerge from the pupal case and dry before being removed and prepared for shipping (Figure 2-4).

Because of the highly regulated nature of production at this farm, the success rate is very high for each egg produced, allowing for such high numbers of production. In addition to the physical exclusion of each life stage from the environment, all steps are conducted in thoroughly maintained laboratories that are routinely cleaned with bleach to prevent the introduction of disease, bacteria, or viruses, not to mention animal predators, parasites, and parasitoids. This is another contrasting element to butterfly ranching, which likely loses a significant percentage of yield. Because all life stages of butterflies are constantly subjected to natural environmental conditions in the butterfly ranching model, they are susceptible to stochastic events in nature, as well as predation, parasitism, and disease agents that occur in these natural settings.

There is a cost to this high level of control found at most butterfly farms. Although there are no reported operational cost figures, the five acres of farming operations, including multiple rearing houses, greenhouses, breeding houses, and sterilization rooms, adds to the cost of production. In addition, Shady Oaks employs approximately a dozen workers during the high season, and half as many during the low season. Although they are capable of producing thousands of butterflies per month, there is a
constant investment in infrastructure and personnel to make the farming operation work as well as it does.

**Butterfly farming in Costa Rica**

The third example of butterfly farming operations presented in this sector describes a butterfly farm in Costa Rica that is a hybrid between the previous two examples, demonstrating the vast plasticity in this industry. Selling over 20,000 butterflies per month, El Bosque Nuevo, located in Guanacaste Province, Costa Rica, is considered by many to be the largest butterfly farm in the world in terms of production levels. Spanning over 180 acres (40 of them being used for farming operations and 140 used in forest conservation and research), this may also one of the largest farms in the world in terms of acreage, too. What makes El Bosque Nuevo (EBN) function at this level is its unique model of combining small-scale farming with its large-scale central operation. Throughout the country, EBN has over 50 “satellite” farms that each specialize in rearing a small variety of butterfly species, but all together create a spectacular diversity of butterflies able to be sold and shipped across the world. Oftentimes comprised of only a single individual or family operating out of their home, these satellite farms are scattered throughout Costa Rica and located in a diversity of areas and provinces, capitalizing on the range of altitudes, topography, and climates that are found in all areas of this small tropical nation. Each individual satellite is taught by EBN on how and what butterflies to rear, which in itself is another example of the hybrid nature of the farm. To take advantage of the plethora of wild host plants, butterflies are often reared outside on either naturally occurring or planted host plants (Figure 2-5). By maintaining breeding stock in a more enclosed and controlled...
environment, eggs laid will hatch into first instar larvae and later transferred to the more substantial outdoor plants.

With any butterfly farming operation, parasites, parasitoids, and predators present a key problem in rearing butterflies (Boender 1995, Whelan 2008). They are often barely visible, making them difficult to detect, not to mention easily capable of slipping through small openings in screens and doors. To combat this problem, EBN and its satellites use a technique of bagging the larvae while on the host plant (Figures 2-5). This serves several purposes. First, it prevents the larva from wandering off of the host plant, which would result in a loss of an individual for production purposes. It would be nearly impossible to find a larva on another plant in the dense secondary and primary growth of natural areas in Costa Rica. The second purpose is to exclude parasites, parasitoids, and predators from contacting and ultimately killing the larvae (or at the very least reducing the fitness of the organism to an unacceptable level). The third purpose is more one of practicality. With the ample supply of rain, soil nutrients, and sun in the tropics, there is little need for host plants to be contained in pots, reared in greenhouses, or otherwise removed from the environment. In addition, keeping plants outdoors minimizes cost by requiring fewer permanent structures in which to contain the plants. This method is also a terrific conservation tool. By reducing development and forest clearing, which would be needed in order to construct new greenhouses, shade houses, and rearing labs, this technique of outdoor bagging keeps the environment more natural, more heterogenous, and ultimately healthier. This method is practiced at the satellite farms, as well as the main farm, resulting in the impressive yield of over 5,000 butterflies per week.
The practices of El Bosque Nuevo represent an interesting hybrid in the industry. By working with small-scale farmers, EBN functions to complete a supply chain that enables individuals or even families to make money by devoting relatively little time and money to producing butterflies. In remote areas of Costa Rica, this extra money (on the scale of $20-$100 a week) can make a great difference. EBN also functions as an educator to teach families how to farm butterflies who would otherwise have no exposure to the enterprise. Because of the unique method of utilizing outdoor grown and planted host plants in the rearing process, EBN is actively promoting conservation by using natural landscape features in the operation.

When examining the evolution and popularization of insect-related tourism, the role of butterfly farms cannot be overemphasized. Not only do they provide the basis for many attractions across the world, such as butterfly houses, gardens, museums, and other exhibits, but they themselves are becoming ecotourism attractions. For example, Shady Oaks routinely sees 50 visitors a week during the high season, and EBN often hosts roughly 50 visitors in the school-age range weekly, as well. From individual tourists stopping in for a look to organized student field trips, there is evidence that butterfly farms are not only capable of supplying educational and aesthetic organisms to exhibits around the world, but are also capable of being tourist attractions, further propagating scientific literacy and conservation biology.

Experiments with Entomological Ecotourism Models

When asking a typical tourist the role that insects play in his/her vacation, he/she will typically respond with some allusion to bug spray, how much they hate spiders, or the annoying flying roaches they encounter in Florida during trips to Disney World. However, when you ask a typical ecotourist about the role insects play in his/her tour,
he/she is more likely to comment on the spectacular butterflies they saw in Central America, the massive termite mounds in Africa, or the giant walking sticks of Malaysia. It is difficult to pinpoint the reason why there is a difference in attitudes of those participating in mass tourism versus ecotourism, but the critical thing to note is that there is a certain awareness and appreciation of all nature by those people choosing to participate in an ecotour. While the promotion of insect education is important for all of society, in order to advance conservation and general scientific and environmental literacy, ecotourists are a practical target on which to focus educational efforts.

However, this is not the only reason that entomological ecotourism is quickly emerging as a new and dynamic genre in today’s spectrum of the nature-based tourism industry. The fact is people are interested in and signing up for insect-related ecotours at an escalating rate.

The following case studies detail insect-focused ecotours that exist in today’s ecotourism realm. These studies were real ecotours with real clients that were organized, marketed, and led by this author as the definitive way to understand the many facets of the entomological ecotour. These studies represent five years of field work investigating the major components of these tours. Each section details a specific entomological ecotour model, as well as the specific elements involved in trip planning, marketing, and ultimate execution of the tour.

At the start of my graduate studies in ecotourism entomology, I began experimenting with the various components of insect-related ecotours in planning and leading entomological ecotourism expeditions. Over five years of trials experimenting with the variations on what an insect-focused ecotour could be, I have developed
several discrete models, which are listed here and detailed extensively in the following sections. These are the One Species/One Phenomenon Model, the Paired Interest Model, and the Research Associate Model. In the following pages, I will go through each model to explain the various components, with specific emphasis on the results of various planning techniques, marketing strategies, and ultimate execution for each trip model. I then continue by detailing how each of these models sets up the ecotourism entomology industry for additional growth and expansion, citing specific examples where future growth is the most needed and most likely to succeed.

**One Species/One Phenomenon Model**

The one species/one phenomenon model, from here on abbreviated as OS/OP, was investigated using one particular species and phenomenon for the sake of this case study, but as we will see later, it can be replicated with other species, and in other localities across the globe. The species used for this study was the Monarch butterfly (*Danaus plexippus*), with the phenomenon being the annual migration of the Monarch to the overwintering colonies in Southern Mexico.

Each year, approximately two billion Monarchs migrate from the eastern United States, flying over 2,000 miles before reaching a series of overwintering sites in Southern Mexico where they will spend the winter (Urquart and Urquart 1976, 1978). Divided in recent years into 12 separate colonies, these overwintering Monarchs cluster by the millions on Oyamel Fir Trees (*Abies religiosa*) in relatively predictable areas throughout the apex region of the transvolcanic range, where the Sierra Madres Occidendales and Orientales meet. From November to March of each year, these butterflies attempt to remain relatively quiescent, leaving their tree roosts as little as possible to drink water occasionally from nearby mountain streams, and even more
infrequently, a bit of nectar from flowering plants (the genera *Senecio, Lupinus, Salvia,* and *Verbesina* being most common sources) (Brower et al. 1977). However, as mid-day temperatures warm throughout the season to the 60s and lower 70s degrees Fahrenheit, butterflies exposed to sunlight will leave their roosts by the tens and hundreds of thousands, flying through the air for brief periods of time in order to thermoregulate before resettling and again joining the colony clusters in shaded areas (Brower et al. 1977, Calvert and Brower 1986). In the larger colonies, which number over 100 million in an average year (Brower et al. 1977, Brower 1995), one may witness millions of dormant butterflies lining the tree trunks and branches, while millions also fly in the air against clear blue mountain skies. Combined with the ever-picturesque backdrop of mountain scenery, the Monarch overwintering colonies are very appealing if not irresistible to ecotourists.

When discussing the topic of ecotourism entomology, there is perhaps no better example in the world than an ecotour designed around witnessing the migration of the Monarch butterfly. The following section will detail the components of the tour model used in this study.

**Monarch Migration Ecotourism**

In the OS/OP approach to entomological ecotourism, the model is based on one key component to the ecotour – the particular species of insect and the phenomenon that makes it so charismatic, as to merit an entire tour based around it. In the case of the Monarch migration tour, the goal is to expose the entire group of ecotourists to the Monarch overwintering event that takes place in Southern Mexico. As mentioned above, there are numerous characteristics to the tour and more will be detailed in this section, but the principal goal is to lead the ecotour group to the Monarch sanctuaries,
where the millions of overwintering butterflies are found. However, it is not as simple as it sounds. The tour planner and leader is responsible for much more. Inherently, this individual is in charge of the group’s general contentment and well being. Although mother nature is responsible for the principal component, which is the fantastic display of millions of Monarchs, the tour must take things into account such as the number of days spent engaging in Monarch-related activities, how long the group spends in the Monarch colonies, the format of each Monarch visit, and more. In addition, for international tours, it is up to the trip planner and leader to choose appropriate lodging complementary to the style of tour, arrange for safe dining, and equally safe and reliable transportation.

The success of an ecotourism expedition largely depends on these decisions, with the measure of success largely quantified by the level of participation year after year. With 10 separate expeditions over the five-year study period, leading eager ecotourists to witness the Monarch migration, 248 ecotourists joined this tour and participated in the one species/one phenomenon model. These numbers represent participation from 2007-2011, amidst a massive worldwide recession, further suggesting the success of this model (Figure 2-6). To theorize reasons for this success, the following subsections will analyze individual components of the tour, as well as broader scale marketing components that are important in achieving high levels of participation in the OS/OP model.

**Lodging and dining.** Because there is typically one specific attraction in the OS/OP model, proximity to the site of interest is very important when choosing lodging. In the case of this Monarch expedition, the general location of lodging is critical. The
town most ideal to the itinerary and proximal to the sites of interest gets priority. Because of the nature of the tour, the town of Angangueo represents not only a well-positioned mid-point between the two Monarch sanctuaries visited during the itinerary, but also has a history of supporting visitation to the Monarch sanctuaries, and proudly exhibits colorful murals and artwork depicting the Monarch butterfly and its journey. Although extras such as these are not imperative to the success of a lodging choice, it is an added bonus and is endearing to the ecotourists, suggesting that they are staying in the heart of “Monarch Country”.

Group size is another serious consideration. Some lodges often have limited capacity and are geared more towards families and individual travelers (i.e., FIT tours). If the intention is to host only a small group of ecotourists (i.e., less than 10), these lodging options are fine, as the lodge or hotel will likely welcome full capacity with a single small group booking. However, should expansion of group size become probable, it is much better to begin a long-term working relationship with a lodge that is capable of supporting larger groups. In the case of these Monarch expeditions discussed so far, the lodge chosen was capable of hosting up to 60 people in double occupancy in their 30 guest rooms. However, families with small children may be able to fit up to four people per room when sharing beds. This does not necessarily mean that the goal of the Monarch tour, or the OS/OP model in general, should be to reach such group sizes, but it does mean that there is a more reasonable guarantee of space, even if sharing with another sizable tour group during the same time period.

Where to eat is another critical component that is parallel with the decision of where to spend the night. Typically, these go hand in hand, as most lodges and hotels
have adjoining restaurants. This is often the preferred dining option for breakfasts and dinners, as meal times for both are often the first and last things an ecotour group does together each day. Added travel times to local restaurants is both taxing and unnecessary. In addition, meal times may be before dawn, or after dusk, making the lodge/hotel the safest choice, eliminating the need to travel in non-daytime hours.

The quality of the lodge and restaurant is paramount, but must be complementary to the overall quality of the tour. Oftentimes, the quality of the lodging and meal choices dictates the quality of the tour, so this is an important decision not to be passed over on the part of the tour leader and/or planner. In the case of the OS/OP model, the targeted nature of the planned day-time activities often allows for more eventful evenings in order to balance out the day with a diversity of activities and experiences for the ecotourist group. For example, more elaborate or longer dinners were deemed acceptable during the course of this study. In addition, the quality of the lodging should exude an inviting feel to outside areas of the grounds in order to complement daytime activities.

Ecotourism has often been believed to be a search for the authentic (Kelly and Godbey 1992). The tourist wants to find what is real, pure, or meaningful in the world (MacCannell 1976). This is satisfied extremely well with the OS/OP model, as it directly shares a natural phenomenon with the ecotourist who has deliberately sought out such an experience by joining the ecotour. For this reason, it is important that the rest of the tour match the expectations and complement the inherent authenticity of the natural phenomenon with veritable lodging and cuisine.

The unique thing about the OS/OP model is that as the rarity or magnitude of the principal attraction increases, the potential for variations in overall style of the tour
increases in concert. This is because standards of lodging and dining are more flexible (i.e., top-end accommodations are not critical) as the phenomenon is accentuated due to rarity or remarkability. While it is the belief of this author that the potential pool of participants joining a Monarch migration ecotour is best marketed to with expectations of soft adventure and modest luxury, one must keep in mind that the main attraction is the species or phenomenon in question. Ecotourists likely do not join a OS/OP tour solely with the expectation of eating gourmet food and sleeping in posh hotel rooms. This contrasts sharply with conventional mass tourism, which often places focus on quality of food and hotel comfort, largely at the sacrifice of exceptional interactions or experiences with the host country, its environment, or people.

From five years of study on ecotourists joining Monarch migration ecotours, the expectations by the participant, in terms of quality of lodging and meals, proved to be much lower than what was actually delivered on the tour. This makes for contented participants and a much more comfortable leader. I will elaborate upon this point in the marketing section, as this directly affects how future participants choose their tour.

The itinerary

With the OS/OP model, the itinerary is very unique. Unlike more general ecotours, there is a focal point to the tour that must be considered at all times. In the case of the Monarch migration tours, people have expectations ahead of time as to what their experience will be like, and it is the responsibility of the tour planner and leader to meet expectations for the entire group. Expectations are often shaped by marketing materials and descriptions of the tour in various print and online media. It is an important task to be congruent with said expectations while on the tour. Having field experience is perhaps the most useful quality of the tour planner and leader on an
OS/OP tour. This understanding and knowledge plays a critical role in exposing the group to the species or phenomenon in as near as ideal condition as possible. This includes time of year, time of day, duration of exposure, and context of the exposure.

Tours to the Monarch sanctuaries are best from the middle of January to the first week of March, but even within this “high season,” there are times that are better than others. During the five-year study, the most ideal time to visit was characterized by a combination of high numbers of butterflies in the colony sites, high numbers roosting on trees, but most importantly, a great amount of flight exhibited by the Monarchs. Because of the weighted importance of flight activity to the ecotourist, the end of the season proved to be the best choice of dates, due to the warmer temperatures that instigate the Monarchs to take flight by the millions. This is in part because of the need to thermoregulate and in part a response to environmental signals cueing them to begin their northward migration back to the U.S with the change in seasons (Brower 1995).

The amount of time scheduled in the itinerary to experience the ecotour feature is one of the more flexible components to the OS/OP ecotour model. This is a very subjective decision that must consider several things. The first consideration is the species or phenomenon in question. For example, an insect ecotour designed around witnessing the emergences of periodical cicadas may require little more than a one-day or one-night field trip for a class of students. On the other hand, the Monarch migration is likely a phenomenon that nature enthusiasts have read about since Urquhart’s *National Geographic* publication on the overwintering Monarch colonies in 1976. A trip centered around experiencing the migration and walking amongst the colonies of millions of Monarchs is likely a long-time dream for many trip participants and should
not necessarily be squeezed into only part of one day. This is especially true of international trips like the expeditions described in these sections. Conversely, excessive time spent in the colonies may cause those without a life-long intrigue to become bored, restless, and annoyed, which could cause ripple effects throughout the group.

Through repeated trials from 2007-2011, visits to two Monarch sanctuaries during the course of the trip proved to be ideal in managing expectations of all group members. When given the option of a third day (hypothetical and actual), many declined, feeling perfectly content with their experiences during the first two days. After the question of how many days to dedicate to the species and phenomenon in the OS/OP model comes the question of the daily itinerary and duration of time spent at the colony sites. With the OS/OP model, this is again a relatively simple decision, as the focus of the tour is experiencing the OS/OP, which in this case is the Monarch colonies. However, being in the colony sites from dawn to dusk would be too much for all but the most ardent admirers.

Governed somewhat by the 9:00 am – 6:00 pm schedule of the park entrance/ranger station and adjoining facilities, food stands, and souvenir shops, the Monarch tour follows a similar schedule. However, the total duration within the colony is also a consideration when planning the daily schedule. After a one-hour hike into the colony sites from the parking lot for the average reserve (in some cases these hikes are horse-supported), the typical ecotourist on these Monarch expeditions chooses to spend in the range of two to five hours in the actual colony site. Largely due to the serene nature of the Monarch sanctuaries, the colonies do not lend themselves to on-
site nature interpretation, question and answer sessions, or discussions, as do other ecotour destinations. Also, the individual goals of the ecotourist may differ greatly, from taking photos to videography, writing poems, sketching, or simply staring in awe as millions of butterflies surround the visitors in small and concentrated colony site. In addition, the network of park guides, horsemen, and information signs allows visitors to move about relatively self-guided once on the single hiking trail from the parking lot to the colonies. This allows people to move at their own pace and decide for themselves how long they would like to remain within the colony of Monarchs. Perhaps due to the allure of local food stands, hand-made souvenirs, or bathrooms, which are only present near the entrance of the reserve, the first members of this ecotour generally begin to depart the upper colony area after two hours. The majority will stay for 3.5 hours, and the last of the group will begin the hike back to the parking lot, where the food stalls and souvenir vendors await, after five hours in the colony site. This relaxed method of leadership during the full day of visitation to the sanctuary and Monarch colonies is relatively rare among most ecotours, but works perfectly with the OS/OP model. Because of the widely differing attitude and interest in the species/phenomenon by ecotourists, allowing the flexibility to explore on one’s own has proven to be the most acceptable style of leadership while in the Monarch colonies.

It should be mentioned at this point that these estimates for the duration of one’s visit are not universal among all those visiting the colonies, but solely for the groups exhibited in this case study. In fact, international ecotourists like these groups account for less than 5% of the total visitors each season (Barkin 2003). The vast majority of visitation comes from local Mexicans visiting only for the day and coming from nearby
cities such as Morelia, Guadalajara, Mexico City, Ocampo, and Toluca (Barkin 2003). Perhaps due in part to the extent of driving required to and from the site from these cities in a single day (several hours round trip, at least) the average visiting time is much less than for international tourists. The other possible explanation is that due to the expense and effort to come from international destinations, only the more serious (i.e., most interested) OS/OP ecotourists are among the group, hence the longer duration of their visit in the colony sites.

Balance is necessary with any ecotour, especially those tours in which tourists are traveling internationally and far from home. For the OS/OP ecotour, there is heavy weight on the OS/OP experience in terms of time, education, and general focus. While it is not entirely necessary to integrate other tour components during the OS/OP ecotour, it is often an added incentive for the ecotourist to experience more than just the one species and one phenomenon during the course of the ecotour. In the case of these trials on Monarch ecotourism, a last-day visit to the world-famous pyramids at San Juan Teotihuacan was found to be a successful balancing component to an already-satisfied group of OS/OP ecotourists. Keeping a similar structure as the Monarch colony visits, the groups were allowed to explore the vast archeological site on their own schedule, with specific recommendations provided prior to arrival at the entrance of the site. This includes the pyramids themselves, a museum, and many additional temples, palaces, and ancient apartments. Complementary to the Monarch tour, specific areas of Teotihuacan exhibit frescos and glyphs of butterflies and butterfly gods from the Teotihuacan Empire. This connectivity between activities is helpful in establishing a tour theme, which is sustained throughout the OS/OP tour.
Education

One of the defining characteristics of ecotourism is the emphasis on education as a tour component. As previously discussed, the quietude of the colony sites and independent exploration by group members makes on-site interpretation in the colony sites impractical. This time with the Monarchs is reserved for a peaceful reverence, not for lecturing. However, as also mentioned previously, because of the targeted nature of the day-time activities, there is a logical time-slot in the evening to engage in additional activities, such as daily reviews, lectures, or discussions.

A dominant characteristic of all experimental tours described in this section is the presence of what is known as a “study leader”. This is an individual who has extensive knowledge about the area visited, wildlife being observed, or culture that is the center attraction. In the case of the OS/OP model, this person must have a detailed understanding of the species and/or phenomenon in question. For the Monarch tour, this person is Dr. Thomas C. Emmel, the Director of the McGuire Center for Lepidoptera and Biodiversity, as well as Professor Emeritus in Zoology and Entomology. Having been one of the pioneers of Monarch ecotourism and observation, he is an ideal study leader for this tour. In addition to his more-than-fitting title, his years of lecture experience in both the University of Florida’s classrooms and in the field lends itself perfectly to holding nightly discussions about the Monarch butterfly, including such expansive topics as the biology, conservation, navigational techniques, and history of the Monarch and its overwintering phenomenon. The technique that has proven to work flawlessly on all trips during this experimental period is to begin with a nightly briefing, which prepares the group for the following day by outlining the schedule and discussing what to expect before leaving for the day’s activities, followed by an informative lecture.
by Dr. Emmel. With each trip exhibiting two full days in the colony sites, it has also proven to work best to have these lectures featured in the evening after returning from the day’s colony visit. This way, sights, sounds, and impressions are fresh experiences upon which to reflect during informative and engaging lectures.

**Interpretive style**

Interpretive styles may differ greatly, as anyone who has ever sat in a classroom can tell you. Teachers and professors today have a wide assortment of tools at their disposal, from powerpoint presentations, to instructional DVDs, to interactive computer programs. However, there is a relatively limited assortment of tools on these ecotours. In some cases, a white bedsheets hung from palm frond rafters at an ecolodge in Costa Rica doubles for a projector screen, while other lodges have full conference facilities, intended for company retreats and team building exercises. However, in the case of the Monarch tour, the best method of instruction has been provided by Dr. Emmel in the form of an organized, yet extemporaneous lecture and resulting question and answer session. The absence of projectors and powerpoints not only provides for a more casual atmosphere, appreciated by ecotourists on vacation, but also allows the scientific leader the freedom to go into more detail on specific topics, especially any remarkable occurrences during the group’s visit to the colonies that day. The informal but highly informational nature of the lecture is complemented by a discussion/question and answer session that can take nearly any direction, from conservation measures in other animal species, to personal experiences with Monarchs in one’s hometown. Mirroring a college lecture at times, a 45-minute to one-hour lecture is ideal in being able to cover a range of topics and issues over the course of two evenings on these five-day trips.
Leadership style

The style of leadership is one of the most important aspects to any group ecotour. Although people generally register for a trip based upon the destination, activities, or the focus of the tour, quality leadership combined with expert interpretation provides a clear delineation between average and exceptional tours. The highlight of this OS/OP model is the species or phenomenon, so it may be inappropriately assumed that less attention can be paid to the caliber of leadership. While tour companies may be able to get away with less experience or attention on part of the leaders, since witnessing the millions of Monarchs is so overwhelmingly positive, it is the belief of this author that it is the hands-on leadership style used in these Monarch trip trials that yielded repeated success and a total of 248 participants in five Monarch “seasons”. More specific attention to what defines an exceptional leader will be detailed in Chapter 3, but for now we will look closer at the style of leadership during the daily activities, as it is relatively unique among ecotours.

The OS/OP model is special in many ways. It often selects for a very interested participant (i.e., ecotourist), it is best served by having an expert leader to provide interpretation and education, and it has a unique “selling” power due to its rarity (we will get to this in the following marketing section). However, since the entire tour is based on a singular fascinating species or phenomenon, the trip acts like a magnet to a variety of interests and a variety of people. Some may join the tour with simple expectations and are satisfied with observing the Monarchs primarily. Others have more expressed interests, such as detailed photography or videography, which requires much more time, patience, and experimentation with angles, backgrounds, scenery, and capturing an array of Monarch behaviors throughout the day. Still others may view the trip from a
spiritual perspective and use the maximum time allotted to reflect on religion, or perhaps think about lost loved ones. These various approaches would be somewhat conflicting if it were not for a relaxed leadership style during the colony visits. As seen by these trials, as well as in other countries with other tour styles, sometimes the more spectacular a sight is, the more distraught an ecotourist becomes if they are rushed, or somehow otherwise left unsatisfied with expectations unfulfilled. In these five years of trials, the flexible nature of leadership and scheduling during the daily visits to the Monarch colonies found that allowing for flexibility by empowering individual ecotourists to dictate their own schedule, combined with scheduling an entire day for each site visit, yielded the most positive results.

**Other activities**

The trip to Mexico for U.S. citizens is not nearly as arduous as one across either ocean, but nonetheless, international travel can be costly in time and money. For reasons addressed elsewhere in this Chapter, the duration of the Monarch trip is five days. Some trip participants took the opportunity of being in Mexico to continue on to another activity after the Monarch trip. With the trip beginning and ending in Mexico City (i.e., international travel was not included in the tour itinerary), this is an option that has been encouraged throughout the past five years with the Monarch tour. Ranging from week-long bike tours in the Yucatan Peninsula to an extra day in Mexico City for shopping, post-trip excursions vary widely. In 2010, the first experimentation with an official trip extension was initiated.

**Post-trip extensions**

The connection between bird watching, general nature enthusiasm, and butterfly watching is one that is evolving strongly. This will be covered in more detail elsewhere
in this dissertation, but for now I bring this up as justification for choosing to offer a
birdwatching extension in southern Mexico, immediately following the Monarch trip.

The response after offering such extension was solid. Out of 31 participants
joining the Monarch tour, seven of them decided to stay on for our official bird
extension, led by ornithologist Dr. David Steadman, and spanning an additional four
days of exploration in the mountains of Southern Mexico. In addition to being the
scientific leader for the bird extension, Dr. Steadman joined the initial Monarch trip and
assisted in identifying birds found throughout the highly biodiverse Monarch colonies.

**OS/OP marketing**

**Proper trip planning.** Trip planning is integral in the success of the individual
expedition, as well as the propensity for word to spread about the trip, as happy
participants share stories, photos, and memories with friends and family. In addition, a
well-organized and planned expedition of any nature, not just one using the OS/OP
model, allows for more time that expedition and scientific leaders can interact with the
group, share knowledge and experiences, and fulfill much of the ecotourism mission,
rather than being tied up with mismanaged logistics throughout the trip. This section will
detail the steps taken to market and advertise these experimental trials of the OS/OP
entomological ecotourism expeditions. Equally as important as the proper pre-trip
planning and ultimate execution of the trip, the marketing of the trip represents the
middle section of the timeline of these expeditions (planning and execution being the
first and last components). Without a participant base, these other components matter
very little. Hence, a diversity of marketing strategies has taken place over the five-year
experimentation period, and results are detailed in the following sections.
**Trip cost.** Simply put, the cost of an ecotour is the single most important decision to make regarding marketing. The brochures, emails, websites, seminars, and presentations will likely be well-received and enjoyed by the intended audience, but an unreasonable, uncompetitive, or otherwise objectionable cost is a stiff barrier between a potential participant wanting to go and actually registering to go. While these trials have done little to suggest that there is a “right” price, or magic number, they have served to reveal certain considerations that need to be taken into account in order to make the price of a trip as appealing as possible.

Generally speaking, a trip price must be competitive with other similar trips. In the case of the novel OS/OP model, it may mistakenly be assumed that because there are few or no competitors at all, competitive pricing is less of an issue. This is incorrect, as OS/OP is a type of ecotourism and thus the tour itself is competing with tours in the entire ecotourism industry. Although potential participants may truly prefer the OS/OP tour being offered, it is a mistake to assume that there are no substitutes for a rewarding ecotourism trip. For this reason, cost is just as important for the OS/OP model as any other brand or subdivision of ecotourism.

The scenario that has proven to work the best is a simple one. Keep the costs as low as possible, regardless of what similar outfits are charging. The main competition on a national level is from a company known as Natural Habitat Adventures. Offering a six-day Monarch trip (including one more day at a separate, smaller colony), they charge $2,995.00 per person in double occupancy. While it would be tempting to set a price close to this, in competitive range, it was found that the trip costs for planning and leading the expedition are far less than this $3,000 range throughout this study. In fact,
by dealing directly with the purveyors in Mexico (i.e., lodging, meals, transportation, etc.) a price of $1,300.00 was possible for this five-day trip. Only one day less and less than half of what a larger company was charging, this sum still covered operational expenses and marketing, with any remaining money going to future trip development. It is the belief of this author that a smaller price tag not only encourages greater participation year after year, but it also directly fulfills the mission of ecotourism by dealing directly with local communities in Mexico, and also setting the price at a point to allow for more people to share in the education and experience provided by this trip. This comparison in itself is a powerful marketing tool, as the similarity in itineraries is reason enough to question the higher priced trip. However, the distinguished leadership on the trip, with Dr. Thomas C. Emmel as scientific leader, truly makes for an exceptional experience that is an unquestionable value.

**Duration.** Next to cost, the duration of the trip is an important decision for both trip logistics and marketing. The OS/OP model lends itself to a shorter itinerary due to the specific focus of the trip. While any trip may combine the OS/OP model with other models in order to make a longer, more diversified itinerary, the core of an OS/OP trip should be concentrated around experiencing the species or phenomenon. As detailed previously, spending two full days in the Monarch colonies proved to be the most successful duration of time spent with the Monarchs. In addition, the added visit to the pyramids provided balance to the OS/OP weighted itinerary. With the first and last day of any trip largely devoted to travel, this adds up to a five-day itinerary. While other tour operators extend this itinerary by one more day and end up with a six-day schedule, the actual days of the week that the trip covers comes into play. At the beginning of this
trial period of trips, each annual trip fell over the Martin Luther King (MLK) weekend in January, spanning from a Friday to a Tuesday. With Monday being the MLK holiday, this meant that only two week days were integrated into the tour. This proved to be highly desirable among trip participants, most of which would take annual leave from work in order to join the tour. As the program evolved, trips began to be added in late February and early March as a second or third opportunity for travel. Continuing with the Friday to Tuesday itinerary, even without the MLK holiday on Monday, this meant that three workdays were integrated into the itinerary. Compare this with Natural Habitat Adventures, which leads trips throughout the Monarch season, each being from Sunday to Friday. While this may work for individuals with more vacation time, are more independent with their work schedule, or are retired, this is an economically demanding schedule, as it encompasses five workdays. In February of 2011, an experimental trip was organized that did encompass more of the workweek. Amazingly, when offering the two itineraries side by side, one being the original Friday to Tuesday and the other Tuesday to Saturday, there was an overwhelming preference for the original Friday to a Tuesday among participants, whom had never before signed up for the Monarch trip (Figure 2-7). Although this was not a controlled trial, there does seem to be a huge incentive to limiting the number of workweek days over which the trip itinerary spans. Because of the nature of OS/OP trips, they are typically shorter in duration. The difference between three and five days taken as vacation days at work is a 66% increase in time “off” and thus is a serious consideration to make in the OS/OP model. With other models, trips may span for up to two weeks, making a one-day difference less significant in the minds of the potential traveler. However, with the
OS/OP model, the number of weekdays that the trip encompasses is a vital consideration for success, opening the trip up to as wide a demographic range as possible.

**Pre-trip information.** Not traditionally thought of as marketing, the pre-trip information used to prepare travelers for their upcoming trip is as important as any marketing material. This is the time to be wordy, give full disclosure, and ultimately set the tone and style of the tour that is to be delivered. While brochures and other print materials should be relatively brief and to the point (we will examine this later), pre-trip materials are valued for their copious amounts of highly valued “insider” information about a particular destination and how to prepare for travel. Producing hastily configured documents to inform travelers cannot only reflect poorly on the organizational skills of the trip planner, but also lead to confusion about what to bring, where to meet, and other critical things that could cause problems for everyone in the group once the tour has begun. For these reasons, and others that we will cover throughout the various pre-trip information sections for each trip model, informing participants ahead of time is one of the most important jobs of the ecotour leader and/or planner.

Regarding the OS/OP model, there is relatively little that differs in the style of pre-trip materials from other ecotour models. These materials require the same amount of information on what to pack, what the weather will be like, etc., as any expedition for any length of time. The principal thing that may differ is the level of infrastructure and the general familiarity one may have with the destination. In the case of the Monarch tour, there is a high level of infrastructure, and many U.S. citizens are familiar with
Mexico to one degree or another. However, as the OS/OP tour model expands, it is
understood that the traveler must go to the species or phenomenon, and not the other
way around. If there is a spectacular occurrence worthy of travel, this may take the tour
group to the metaphorical “ends of the earth” to witness it. Perhaps the species may
reside in deep underground caves, as with the glowworms of New Zealand. Maybe the
phenomenon occurs in the dead of the night, as with the periodical cicada emergences
in the United States. The point is that the more unusual the destination, the more
preparation that is required. Such is more common with the OS/OP phenomenon simply
due to the radical environments in which they occur. Specific components of pre-trip
materials will be detailed in a later section.

**Hands-on marketing.** Print materials are rapidly being replaced by a suite of
electronic media tools that are both more cost effective and use fewer resources than
traditional catalogues and brochures. Nevertheless, print media still have a place in
marketing, especially with international ecotourism trips, whose client base is skewed
toward older generations that are not as comfortable with electronic media as are the
youth of today. Largely based upon previous print media models, the standard
brochure design is universal in terms of the ways it can be used and transcribed into
electronic/internet form. Therefore, it is as important as ever to design and use effective
brochures in marketing ecotourism trips.

With the OS/OP model, the selling point is the species or phenomenon in
question. Less emphasis is needed on other components of the brochure, such as
exhaustive itineraries with lists of various wildlife likely to be seen, expedition routes,
etc., because the potential participant is likely drawn by the deliberate claim to
experience a particular thing (in this case, witnessing the Monarch butterfly migration). Emphasis should instead be placed on the introduction section of the brochure, which serves two purposes. One is to authenticate the experience for those already familiar with the Monarch migration, and two, to introduce the phenomenon to those who may not know of its allure and ecotourism potential. Detailing the experience as much as possible has proven critical, as people are generally familiar with the Monarch butterfly as a species and see them regularly. How will this trip differ from seeing dozens in a butterfly garden at any one time? The introduction is also the place in which to emphasize the appropriate timing or seasonality of the trip (further authenticating the expertise of the tour operator). Why are these dates being offered? Is this the best time of year to go to witness this phenomenon? Lastly, the introduction is an appropriate place to outline the educational opportunities throughout the trip, especially with nightly lectures from the scientific leader, who is in this case Dr. Thomas C. Emmel. During the trials of trip experimentation from 2007-2011, there was also a good bit of experimentation with brochure design. From early designs, it became evident that a leader section was valuable in order to provide context for the academic nature of the trip. Dedicating part of the brochure to listing the qualifications, accolades, and years of experience by the leadership team, potential participants were further assured of trip authenticity.

The presentation and layout of the day-to-day itinerary is somewhat unique in the OS/OP approach. As seen in the following sections, longer trips necessitate relatively lengthy itinerary sections that touch on every day, listing the various sites and experiences as efficiently and briefly as possible. For the shorter Monarch trip, and
likely OS/OP trips in general, there is more room to go into further detail on individual
days. Perhaps more importantly, however, the day-to-day itinerary in the OS/OP model
reveals the mood of the tour. Is this going to be a hurried trip where the participants are
rushed through as many colonies as possible in order to see all five sites open to the
public in just two days, or is there a more dedicated attitude to observation and
experiential learning (as is the case in these trials). Many people joining these Monarch
tours did not previously know a tour to the Monarch colonies was possible, and thought
such was restricted to National Geographic Society filmmakers and the like. Thus, they
have less of a preconceived notion of the composition of a Monarch tour itinerary.
Compare this to an ecotourism expedition to Costa Rica (more detail on this in the next
section), which has more of an inherent description of the tour due to the popularity of
the destination. In summary, the itinerary section of the OS/OP model brochure is
complementary to the previous two sections (i.e., introduction and leaders), but allows
the tour operator to expound upon the very nature of the tour schedule for a trip that is
largely novel to the first-time inquirer. This is one of the most useful ways to manage
expectations prior to departing for the trip.

To complete an information-packed brochure, the registration details were also
included in the single page pamphlet. While some tour brochures (not necessarily
Monarch tours, but tours in general) initiate a “call to action”, meaning the primary
intention of the brochure is to suggest that the reader do something, such as visit a
website for more information, or call a certain phone number to complete the
registration process, the brochures used in these Monarch trips are entirely self-
contained and allow the reader to register completely for the trip without doing anything
more than picking up a brochure. This means that valuable page space has been consumed by a “terms and conditions” page, as well as a “registration form” page. Nevertheless, it has been found in these trials that this technique appeals to the spontaneous and preoccupied just as much as it does to the meticulous and thorough by offering supplementary websites, Facebook pages, email addresses, and phone numbers to provide further guidance prior to booking.

Ultimately, the brochure used to promote an ecotour represents everyone involved on the tour operation side. Not only does it directly provide evidence of experience and organization on part of the trip planner, but also about the leadership and even about the experience and country itself. Brochures are used not only to summarize a trip itinerary, but also to manage expectations. For this reason, it is essential to be deliberate yet careful in describing an experience, as these expectations will be taken with the participant along with their luggage, cameras, and general attitudes.

**Marketing and brochure distribution**

**Florida Museum of Natural History and Museum Travel Programs.** Before discussing specific techniques used for brochure distribution of OS/OP trips, this is a good time to detail the need for collaboration with educational institutions in promoting educational and entomological ecotourism. At the beginning of this study period, a strategic relationship was fostered between Expedition Travel (the tour operator) and the Florida Museum of Natural History at the University of Florida (the travel program). Through dedicated service to its members by providing specialized travel programs and targeted opportunities, this relationship led to Expedition Travel being the unofficial travel provider for the Florida Museum. While this was treated tenderly, knowing that there were perhaps other Gainesville-based tour operators that would love to have that
designation, it did provide for special opportunities in marketing. These special opportunities fit within four broad concepts: 1) Brochure placement, 2) Hardcopy mailings, 3) Email announcements, and 4) Website announcements.

**Brochure placement.** Discussed in the previous section, the hardcopy brochure is still a tremendous tool in promoting ecotourism trips. Perhaps one of the most useful ways found in this study in facilitating these brochures is to physically place them in the Florida Museum of Natural History to be picked up at will by visitors passing by brochure stands. In fact, when asked at the end of trips how each participant heard about the trip initially, it was found that across all trips, at least 20% had either picked up a brochure themselves from the museum, or heard about it from a friend or family member that had picked one up. Considering that many trips exceed 20 passengers (and occasionally exceeding 30 and 40), this makes a tremendous difference in the total passenger count, the total number of people exposed to entomological ecotourism, and the overall influence in communities around the world.

**Hardcopy mailings.** At the start of this trial period, FLMNH was routinely offering subscriptions to the magazine “Natural History” as a bonus to membership. These magazines were mailed bimonthly and reached approximately 1,000 museum members with each circulation. In order to provide additional exposure to these entomological ecotourism trips, hardcopies of the brochures were “polybagged” into the magazine mailing, being accompanied with a set of additional brochures on activities, events, and publications thought to be of interest to members by the FLMNH marketing department. Although this directly put a copy of the brochure into the hands of potentially interested persons, the very nature of polybagging dilutes the information enclosed. There simply
is too much competition for a single piece of literature to stand out. Oftentimes, these brochures would be accompanied by a dozen other pamphlets and announcements. Nevertheless, this marketing strategy served its purpose in recruiting eager ecotourists, but at numbers far less than those recruited from the brochure placement and other methods. This trial period was cut short when the Natural History magazine was discontinued by the publisher and, consequently, no longer available to be offered to members. The museum adapted to this by placing significantly more emphasis on the e-note system of emailing members and thus prioritizing the electronic forms of information transmission to members.

**Emailing and e-notes.** There is no doubt that emailing is quickly becoming a preferred means to make announcements, advertise products, invite people to events, and even conduct day-to-day business. It is inexpensive, convenient, and highly progressive, with new technologies allowing the integration of high-resolution graphics and videos. The advantages of the FLMNH-Expedition Travel relationship is increasingly being seen with the use of Museum-sponsored emails announcing exciting travel opportunities offered through its travel program. Although the system is too new to report consistent participation rates throughout the entire scope of the study, those trips offered at the time of writing this dissertation have experienced at least two registrations per trip based on the email and e-note system. This may not seem like much, but when minimum participation levels are set at 10 registrations for some trips, this represents 20% of the signups necessary for the trip to be confirmed.

**FLMNH website.** The principal advantage to the FLMNH website is the visibility on search engines. Because of the size and popularity of the museum’s site in general,
most search engines will rate the site’s authenticity higher, allowing it to show up higher in search results. In addition, it provides links to the main Expedition Travel page (ExpeditionTravelOnline.com), further boosting its reputation by intelligent search engine algorithms.

The linkage between the trips described in this Chapter and the FLMNH increases visibility of the trips in a very general way. Whether people find out about the trips through picking up a brochure, or receiving an email, these are ways to disseminate information otherwise unavailable for a tour operator. However, apart from the increased visibility, the museum plays an equally critical role in the authenticity of the trips, which, as we have already discussed, is a very important motivation for travel. In return for the exposure and advertising opportunities, each museum travel program trip is accompanied by a curator, professor and/or director within the museum. Not only is this a special opportunity for the curator, professor or director to get into the field, but also for the museum to showcase its highly experienced faculty towards an eager audience. This builds vital relationships between the Florida Museum and the global community.

**Brochures and marketing**

The brochure for an OS/OP trip is critical in marketing, but parallel to the physical layout and informative components is what one does with the brochure once it is printed. As detailed in the FLMNH Section, a relationship was fostered at the beginning of this study that permitted this author to place brochures at strategic points in FLMNH to promote travel to museum visitors. This hits a target demographic that results in sign-ups for the Monarch trip. Bolstered by visitation to their Butterfly Rainforest exhibit, this museum is an ideal place to advertise a butterfly-centric OS/OP trip. Acting as a
magnet for people interested in nature and learning, FLMNH has proven time and time again to be an ideal marketing ground for ecotourism, especially with the unique opportunities offered by entomological ecotourism.

Although FLMNH is one of the more ideal scenarios at which to advertise this unique brand of tourism, other venues were integrated into the trials that spread across a spectrum of outdoor interests. Outdoor outfitters, scientific conferences, and travel expos proved to generate significant interest, but as far as connecting interest with actual trip participation, they were less successful than at FLMNH. While interest in these trips was evident at each location, FLMNH continues to prove to be the best arena in which to concentrate marketing resources and attention.

The OS/OP trip model is not wildly divergent from other ecotourism models in the way that it is planned, marketed, and eventually led. However, there are specific considerations that need to be made at each stage in order to optimize the entire process. Keeping in mind that the end goal is to expose as many people as possible to the diverse natural wonders of the world, while giving them significant reasons for why they should be conserved, there must be a balance between high participation and high satisfaction.

The OS/OP concept is perhaps best exemplified by the Monarch butterfly tour, but is replicable in many other cases involving charismatic insects. In the following section, I will discuss future possibilities in which to integrate new species and new phenomena into the dynamic and progressive world of entomological ecotourism.

**Future Possibilities for the OS/OP Model**

The OS/OP model is inherently highly replicable with other species and other phenomena, and, hopefully, more so as a result of this dissertation. The case study
exhibited above details the inner workings of perhaps the most well-suited possibility for the OS/OP model, but that is not to say that other species or phenomena are not sufficiently charismatic with similar potential. Furthermore, discoveries are still being made in science and nature that may unearth the next great OS/OP tour focus.

The overall quality and sensational nature of the species or phenomenon in question largely dictates the length and scope of the ecotour, as does the location in the world in relation to the participant base. For example, while the Monarch ecotour spanned five days for those participants coming from the U.S., a visitation to the Monarch sanctuaries is more of a day-trip for local Mexican citizens or 7-8 days for a visitor from Japan. Along a similar vane, the Glowworm caves of New Zealand would likely necessitate a one to two-week itinerary for travelers coming from the U.S., combining this species and phenomenon with other natural history attractions (illustrating the potential of combining entomological ecotourism models). On the other hand, observing and photographing one of the rarest species of butterflies, the Schaus’ Swallowtail, in the Florida Keys is largely a day trip for Florida residents, yet a multi-day expedition for those travelers coming from other states or countries. Ultimately, it is evident that the duration and scope of an ecotour is largely relative to the audience.

The following examples of OS/OP tour foci represent examples from several locations around the world. While the general outline of the complete tour itinerary may vary significantly, depending on the origin of the traveler, these examples are irrespective of such origin and detail only the highlight of potential tours. Similarly, although it would be valuable to have identified all potential OS/OP tours worldwide in this paper, there are simply too many to properly outline. The following examples are intended to
complement this section’s case study in order to provide the framework for identifying other potential OS/OP tour foci. By showcasing examples of the range and variety of natural phenomena and species with which to work in the entomological ecotourism arena, it is the author’s intention that this presentation helps to facilitate the growth of new OS/OP opportunities.

**Glowworm Caves of New Zealand**

Although hardly unknown by those familiar with either entomology or ecotourism in New Zealand, the Glowworm Caves found in this country are one of the most popular tourism attractions. Tourists started visiting these caves to see this phenomenon in 1889, just two years after their discovery. Now seeing over 450,000 tourists annually, the Waitomo Cave tours operate as a “traditional” tourism attraction where groups are guided through various parts of the cave system, exhibiting the diverse labyrinth of halls and culminating in a spectacular boat ride through the Glowworm Grotto, taking place in total darkness and near perfect silence. Although appearing throughout the cave system, larvae of a fungus gnat fly, *Arachnocampa luminosa* (Diptera: Keroplatidae), peak at over ten thousand individuals in the Grotto (Doorne, 2010). The larvae hang from the ceiling of the cave on long sticky silken threads, with which they catch other insects to eat. Their bioluminescence attracts flying prey in the dark of the caves and is the principle attraction to entomological ecotourists. The majority of tourists arrive in groups by bus and spend 40 minutes touring the cave system. Visitation peaks between 11:00am and 2:00pm with the dominant season being from November to April. It is estimated that about one half of all visitors are comprised of Japanese and Korean travelers, with the remaining percentages split between Taiwanese, Australians, and New Zealanders (Doorne 2010).
Despite the average tour lasting only 40 minutes, it is evident that there is great potential for international markets to participate in this form of entomological ecotourism. As evidenced in Mexico for the Monarch tours, even though the majority of tourists have been documented to stay for brief periods of time, some tour groups will spend significantly longer based on their individual interests, as well as travel time needed to visit the site. While an ecotour designed solely to visit the Glowworm Caves would be impractical for tourists coming from the U.S., a tour of this nature could easily be combined with a broader-focused trip to New Zealand. The important thing to keep in mind is that entomological ecotourism need not be an entire trip focused on just the one species or one phenomenon. A day trip to the Waitomo Caves in the middle of a more comprehensive ecotour of New Zealand still represents a fascinating form of the OS/OP model of entomological ecotourism.

**Migrating Danaid Butterflies in Taiwan**

Butterflies in the family Danaidae, known for migrating to Mexico from the Monarch tour case study, have a proclivity to migrate and overwinter elsewhere, too. Discovered as early as 1971, overwintering populations of danaids in Taiwan are now known for nine of the 18 danaid species found on the Southeast Asian island (Wang and Emmel 1990). Known as “butterfly valleys” by the locals, these areas of overwintering butterfly aggregations are located in the low mountains of Kaoshung County, Pinton County, and Taiton County in the extreme southern region of Taiwan (Wang and Emmel 1990). From October to March of each year, most of these species are relatively absent from the northern temperate end of the island, overwintering 400 miles south in the four principal sites that are more tropical at the southern end of the island. In order to reach these areas in Southern Taiwan, the butterflies undergo a migratory behavior that takes
place prior to the initial cold fronts of winter sweeping across the sea from mainland
China in November of each year (Wang and Emmel 1990).

Much like the overwintering Monarch butterfly (*Danaus plexippus*), these various
danaid species aggregate in predictable patterns that are ideal for supporting tourism
infrastructure. Unlike the Monarch butterfly phenomenon, which covers extraordinary
distances amounting to over 2,000 miles, the migration of the danaids of Taiwan covers
a much smaller distance. In fact, the migration itself is largely observable from various
parts of the country. The overwintering phenomenon in Taiwan offers a unique
dimension not readily available with the Monarchs of the Americas – the ability to
consistently witness the physical migration along the migratory path, in addition to the
overwintering colonies themselves. Although the total number of butterflies is much
smaller than the tremendous aggregations of the Monarch, this added dimension of
witnessing the migratory flight, characterized as a “flying black river”, according to
reports in Wang and Emmel (1990), provides for a strikingly well-rounded experiential
event for entomological ecotourists to enjoy.

Contrasting with the century-long popularity of the Waitimo Glowworm Caves, the
migratory butterfly phenomenon in Taiwan is not well-known nor well-visited. This
occurrence, however, may prove to be valuable for exploring new ideas in the
entomological ecotourism market. Just as with the glowworm example, an entire tour
designed to only witness this migration would be taxing and impractical for U.S.
travelers due to the travel time to Taiwan. Day trips serving local Taiwanese ecotourists
would be a logical beginning to promote tourism infrastructure along migratory routes, or
Periodical Cicada emergences

Known largely for their nighttime calls and the familiar noise on warm summer nights, the word Cicada is the common name for over 3,000 species of insects worldwide. The vast majority of Cicadas are “annual” species with overlapping developmental times that results in adults of the species being present every year. However, “periodical” Cicadas undergo developmental synchrony in which all adult individuals of the population will develop through the nymphal stages and emerge simultaneously. A total of seven species have been recorded to exhibit this behavior. Among these, four species have 13-year life cycles and three have 17-year life cycles (Lloyd and Dybas 1966a, 1966b). From an entomological ecotourism standpoint, this leads to the opportunity to witness the simultaneous emergence of hundreds of thousands, if not millions, of Cicadas within a short span of time. When all the adults start stridulating and calling at once, the noise is spectacularly deafening. Perhaps not as elegant as a migration of Monarch butterflies, or as showy as a cave full of bioluminescent fly larvae, an emergence of Periodical Cicadas is nonetheless a fascinating phenomenon that has the potential to attract interested naturalists, entomologists, and ecotourists.

Occurring predominantly in the eastern U.S., the emergences of Periodical Cicadas present a unique opportunity for ecotourists in the U.S., by allowing for short pinpointed trips. Eliminating the need for international air travel not only reduces the cost, but also increases the potential market of interested persons. Ranging from general naturalists to students on class field trips, this example of entomological
ecotourism represents a more domestic phenomenon than others cited in this Chapter. Fostering interest in these mass emergences (and learning where local emergence will occur predictably every 13 or 17 years) in turn could function as a catalyst for generating interest in larger, more broad scale entomological ecotourism activities, such as those in previous examples.

**Schaus’ Swallowtail**

In a final example of alternative OS/OP possibilities, observing the federally endangered Schaus’ Swallowtail (*Papilio aristodemus ponceanus*) represents a more species-oriented approach in contrast to previous examples, which centered on specific phenomena as the attraction. Because there is no grand migration, emergence, or overwintering behavior in which to witness vast numbers of individual insects, there is less mass appeal with this example of the OS/OP model. For this reason, members of specific interest groups, such as the North American Butterfly Association (NABA), are the primary markets.

The allure of observing the Schaus’ Swallowtail in the wild is due principally to the rarity of the butterfly. Similar to bird watchers, butterfly watchers often have “life lists” to organize and record the various species of butterflies seen throughout each person’s lifetime. The more difficult a species of butterfly is to locate, the more effort a butterfly watcher is likely to put forth in order to see it. Parallel to its rarity is its notoriety. Having been the subject of a long and often dramatic, even tedious, fight to both reestablish wild populations and extend federal endangered species status to include this butterfly, the Schaus’ Swallowtail is as much of a symbol for butterfly conservation as it is a symbol of unrivaled rarity on part of the butterfly watcher.
Tours to witness the Schaus’ Swallowtail do exist at a minimal level, but as with all entomological ecotourism programs, they could be augmented and extended to other markets. Currently, groups such as NABA make pilgrimages in search of this rare insect, but due to the inhospitable environmental conditions (i.e., heat and mosquitoes during the flight season), few other groups as ardent as local NABA members have sought out the butterfly’s habitat solely to visit in search of the Schaus’ Swallowtail. As with the Periodical Cicada emergences, students are a logical audience for future tours. Providing context in conservation work, population biology, gene flow, and other key topics, ecotours designed as class field trips should be promoted, especially to those local schools and universities able to make such visit a simple day trip.

**Evolution of new OS/OP entomological ecotours**

This Chapter largely deals with this topic from the U.S. perspective, or the international tour operator side of things, but how should other countries with entomological ecotourism potential develop their entomological attractions? The following is a step-wise process that pools together experiences and information from this Chapter’s case studies to formulate recommendations.

**Appeal to local communities.** Local communities will be the purveyors of services, ranging from lodging and guiding ecotourists, to maintaining and conserving the habitat that fosters the entomological ecotourism attraction. Local communities must be integrated in the planning at the very beginning of the development of the ecotourism attraction.

**Serve the country first.** A consistent flow of ecotourists will drive progress, whether it be the construction of trails needed to witness a particular species, or the staffing of restaurants that allow tourists to plan on full-day trips to the area, without
having to leave for a mid-day meal. The success of the Monarch sanctuaries is largely dependent on the steady flow of national tourists. In order to create momentum, the ecotourism venture must attract locals to gain support from the region or country. It should not depend solely on the international ecotourism potential.

**Expand to international markets.** After there is sufficient infrastructure to host international tourists, marketing campaigns may be directed to international tour operators and travel agents. As international visitation expands, new opportunities will arise that will further promote community welfare. International ecotourists will require goods and services, such as lodging, souvenirs, transportation services, and bilingual guides, that will increase the potential for local employment and entrepreneurship that would be otherwise unsubstantiated by national ecotourists.

From the previous examples, there is no single paradigm on which the OS/OP model should be based. The case study of the Monarch butterfly represents an ideal scenario of large-scale international entomological ecotourism, but as was evidenced herein, a majority of visitors to the Monarch sanctuaries were in fact local tourists visiting for only a day. The examples that followed the Monarch case study elucidated the fact that the ecotourism focus need not be on only one order of insects, especially when the spectacle is a large aggregation of individuals. The scope and grandeur of the phenomenon is largely dictated by the uniqueness of the event, in the case of the glowing Dipteran larvae, or in sheer numbers and noise, as is the case with the emergence of millions of Periodical Cicadas. Nevertheless, singular species also fit the model for OS/OP. While lacking in numbers like the migrations and aggregations
discussed, singular species can make up for this by exhibiting extreme rarity, beauty, or notoriety.

Many more examples exist that represent each of the above-mentioned subgenres of the OS/OP model, as depicted by the various examples. Much of the intrigue associated with this new dimension of ecotourism is the novelty and constantly expanding list of possibilities, especially from an academic approach. As new phenomena are discovered, and species revered for being the biggest, rarest, or most spectacular in their respective orders are documented, this model, the case study presented within, and examples of subgenres will hopefully serve as examples for future entomological ecotourism endeavors.

**Paired Interest Model for Ecotourism Entomology**

The paired interest model, to be abbreviated to P-I model from here forward, is the technique of pairing entomological ecotourism with other niche forms of ecotourism in order to form a complementary bond between similar activities. In this section’s case study, these complementary activities are bird watching and butterfly watching. As was the case with the OS/OP model, this P-I model was also tested using specific trips repeated over a five-year time period. Also similar to the OS/OP model, this is but one experimental example that is intended to detail the characteristics of the particular tour model, with many other examples across the world being viable for future ecotourism using the P-I model. The following sections will provide more detail on the inner workings of the P-I model and its role in the development of entomological ecotourism as a discipline and ecotour genre.
Costa Rica: Birds, butterflies, and breathtaking scenery

Costa Rica is considered by many to be the birthplace of ecotourism (Honey 2008). Scholars and tourists alike share this sentiment, making it a very desirable destination with over 1.6 million tourists arriving annually as of 2008. As early as 1993, tourism had already become Costa Rica’s number-one foreign exchange earner, leaping over coffee and bananas. Today, tourism accounts for around 22% of foreign exchange earnings and 8% of the country’s GDP (Honey 2008).

The backbone of Costa Rica’s tourism industry is a well-respected and supported national park system that encompasses 25% of all land in the country, valued at roughly $2 billion (Honey 2008). This figure does not take into account private reserves, parks, and preserves, thus underestimating the total amount of protected land by an unknown amount. Between 1990 and 2005, the number of foreign tourists visiting one of the country’s 160 protected areas doubled to over 1 million a year (Honey 2008). The supporting data for Costa Rica’s commitment towards ecotourism could continue on for several more pages, but the conclusion is obvious – Costa Rica is an ecotourism nation and the global community is aware. This makes Costa Rica an ideal trial ground for experimenting with new forms of ecotourism.

Costa Rica is home to a flourishing array of bird fauna that is well known amongst the bird watching community. With nearly 900 species occurring in a diversity of life zones, Costa Rica is a highly desirable tour destination for bird enthusiasts. Although presently representing a much smaller contingent, butterfly enthusiasts also recognize Costa Rica as being highly productive, with an abundance of native tropical species in the highly colorful and charismatic *Morpho*, *Heliconius*, and *Prepona* genera. Boasting
a total of over 1,000 different species of butterflies in nearly all major families, this Central American destination lends itself very well to butterfly watching.

Bird watching and butterfly watching are highly complementary activities. From personal experience, the fervor with which both these groups of nature enthusiasts search for, photograph, observe, and generally appreciate their respective subjects is remarkably similar. In addition, destinations for highly productive watching, be it butterflies or birds, are often the same. Tropical regions host most of the biodiversity, yet temperate regions hold a still exciting suite of fauna that both groups equally appreciate. Equipment and other field gear are virtually identical. Binoculars, a field guide, and perhaps a camera are all that is needed to track down the most spectacular of species. With these tools, both groups may spot distinctive field markings that distinguish closely related, or at least similar looking species (especially in the case of mimicry, which also is commonplace in both birds and butterflies). Perhaps the one thing that does indeed differ is the time of day each group is most active, which actually further supports the complementary nature of the two activities. While birds are most active and easily seen in the early morning and late afternoon, butterflies tend to be more prolific and active during the mid to late morning until the middle of the afternoon. This is not entirely coincidental. Food chain dynamics and the evolution of butterfly behavior as potential prey involves continual need to escape from hungry birds in both time and space. Nevertheless, what different activity maxima do allow for is the same group of people to appreciate both groups of taxa without taking away from one or the other. It seems entirely likely (and has observed personally) that as entomological ecotourism grows, many bird watchers will become butterfly watchers as well.
The complementary nature of these two groups was recognized early on in a suite of case studies, giving rise to what is from this point on deemed the paired interest model (P-I model). Linking entomological tourism with other more established forms of tourism serves to heighten visibility of the lesser-known insect watching dynamic. The following section will detail the components of a P-I ecotour, with specific references to the Birds and Butterflies expeditions trialed in the development of the P-I model.

**Costa Rica P-I ecotourism**

The P-I model for ecotourism was initially developed in 2007 for implementation on the first P-I model expedition in February of 2008. During the course of the five-year study, three expeditions were organized, advertised and led, each on even-numbered years (2008, 2010, and 2012). Just as with the OS/OP modeled Monarch tour, success is measured on individual trip participation, as well as cumulative participation over the course of the trials. During the period of the study, the three trips yielded a total participant base of 71, averaging fractionally less than 24 participants per trip (Figure 2-8). Again, these trips spanned a period of worldwide economic downturn. The consistently high levels of participation during this period further indicate the success of the trip model. Just as with the OS/OP model, the tour planning, marketing, and ultimate execution are directly responsible for the success of the P-I model, in addition to the fundamental tenets and characteristics inherent to the P-I model.

**The P-I Model**

The first thing that stands out with the P-I model is the additional ecotour feature. Whereas with the OS/OP model the subject of the tour was perhaps overly simple, being the one species and/or one phenomenon, we begin to see things becoming more complicated with what is featured and emphasized in the P-I model. When speaking of
the P-I model in its broadest sense, the possibilities are virtually endless when pairing insects with another ecotour feature. This additional feature could range from general wildlife viewing to seashell photography. It is the conservative and prudent approach to pair something as novel as insect ecotourism with something that already has a following. For this reason, insect ecotourism (butterfly watching) has been paired with the highly popular and established tour model of bird watching in these case studies. The following sections will detail the considerations and characteristics of the P-I model with specific regard to the Costa Rica case study.

**Lodging and dining**

Because there is no single focal point of the tour, unlike the OS/OP model, lodging and dining is more flexible, just like the overall tour. However, lodging and dining choices are perhaps more critical to the overall satisfaction of the tour participants because there is not a specific or singular feature that is attracting ecotourists to the tour program. It is the entire package that excites interest. Similar to the OS/OP model, however, the lodging should be chosen based on its proximity to the areas or attractions of interest. For this reason, preference is given to lodges that allow for emersion into nature and are proximal enough to trails so that participants feel that they feel they are in the hotspot for nature. Although participants are not necessarily joining the tour for one specific reason, as is the case with the OS/OP model, they are indeed attracted to the two components emphasized with the P-I model – the birds and the butterflies. Therefore, the more the lodging satisfies this desire to view, photograph, or experience birds and butterflies, the less pressure there is on daytime activities being geared specifically to what each participant expects out of the tour. For example, if staying in a hotel in a city, the daytime activities must put the group in consistently rich areas for
satisfying their expectations of seeing charismatic and interesting birds and butterflies. A lodge emersed in the forest will provide continuous opportunities for bird and butterfly observation, no matter what the daily activities may be.

Costa Rica and its ecotourism base yield a plethora of suitable lodging choices that would appease any nature lover, including those with specific interests in mind. Fortunately, in tropical regions, areas geared towards general nature observation are also geared (whether intentionally or not) towards terrific bird and butterfly sightings. For this reason, it is equally, if not more important, to first decide on a region, area, or preserve to visit before choosing the ideal lodging for the group to use. In the case of Costa Rica, the range of altitudes, slopes, and other topographic elements is one of the most defining and influential characteristics to the country and its diverse flora and fauna. When originally outlining the nine-day trip that served as the case study instrument for the P-I model, three main areas were chosen that represent a diverse range of habitats and climates. The landscape diversity thus gives rise to terrific wildlife diversity as well. Beginning in the lowlands of the Atlantic slope, the tour headed for Monteverde and the mid-montane cloudforest habitat before then descending to the coastal pacific forests near Quepos. This route covers at least three of the main life zones in which birds and butterflies thrive. With the P-I model, considerations for both birds and butterflies (or any other pair chosen) must be made to either optimize diversity or otherwise increase the likelihood of encountering remarkable species.

The most dramatic difference in lodging choices is the general quality of the lodge, to no surprise. It is essential to find the appropriate balance of location (i.e., near, adjacent to, or in the jungle) and amenities. As detailed in the previous OS/OP section,
the quality of the trip is largely dictated by the quality of the lodging. However, quality is not as straightforward as staying in the nearest four-star Hilton resort to achieve top quality. Features such as the presence of self-guided nature trails, access to rivers, presence of fruiting trees (for wildlife spotting), abundance of outside seating, use of fruit stations (to attract fruit eating birds, butterflies, and other wildlife), on-site naturalists and guides, and whether a library or interpretation center is present, are often more important than whether the rooms have hot water showers. There is a negative correlation between the number of remarkable wildlife watching opportunities and the need for modern conveniences (Figure 2-9). When a lodge is able to provide more exceptional opportunities in the way of experiencing nature, the further they are able to deviate from conventional standards of lodging. An example of this would be Rara Avis, which is a primitive lodge located at the end of a muddy road that requires a three-hour tractor drive just to access the cabins. The cabins are rustic, and electricity is limited. However, they boast one of the largest levels of bird biodiversity in the entire country and people flock in great numbers to this ornithological hotspot in the face of relatively high prices and limited guarantees of anything resembling luxury. Nevertheless, as these amenities and conveniences lessen, there is a floor threshold as well, which if surpassed, exponentially fewer people are willing to remain complacent and ultimately participate in a trip (Figure 2-10).

A major theme and message here is that tourism is the search for the authentic. Just as there is a floor below which people are uncomfortable, regardless of the wildlife experiences, there is also a ceiling. When modern conveniences and luxuries abound in an ecotourism lodge, it becomes doubtful that the lodge is able to provide an
authentic experience (Figure 2-10). This is the case with Hotel El Establo, located in Monteverde. This massive lodge complex resembles a ski resort in Aspen, stretching over an immense portion of the mountain slope, and exhibits granite countertops and modern appliances in each of the 155 rooms, including flat screen TVs, brushed-silver microwaves, tea kettles, stereos to plug iPods into, etc. In 2008, this lodge was chosen to host the trial group for three nights in Monteverde in an effort to contrast the more rugged hotel the group stayed at just prior. Although highly comfortable, it offered relatively little in the way of wildlife around the immediate lodge grounds. In addition, it was apparent that the large swath of land cleared to build the lodge altered a significant amount of surrounding forest, going against the typical values of the ecotourism industry. Although there were trails originating at the upper extent of the lodge grounds, with wildlife viewing opportunities present, there was little authenticity, and the group agreed that they would have preferred to stay in a less-fancy more “down to earth” establishment. It did not help that there were transport vans driving from the upper part of the lodge to the lower part 24 hours a day to minimize walking distances for those preferring a quick route to the restaurant building.

In addition to the quality of the lodging dictating the overall quality of the tour, the dining experience assumes high importance. As with most tours, breakfast and dinner are often the first and last activities a group does together during the course of the day. They are most commonly held at the same lodge where the group is staying. Eliminating the need to travel before morning coffee and after dark is safer and more comfortable for the group. It also saves time, allowing for a greater part of the day to be spent on trails observing wildlife.
Contrasting the OS/OP model, the lodging and dining components are marketable parts of the tour that are also expected to be of a particular quality by trip participants. For instance, Costa Rica is well known and well talked about because most people visiting the country return home with great memories of an enjoyable ecotour. While wildlife viewing is a critical component to this enjoyment, there is an inherent expectation on the part of the ecotourist to experience the country via its culinary delights and unique jungle lodges that are commonly featured in travel magazines and online media. For these reasons, it becomes increasingly necessary to choose a reliable lodge that is capable of preparing and providing good food. To summarize, lodging and dining go hand in hand.

Regarding general entomological ecotourism, lodges offering hiking trails that are accessible after dark are essential, since many charismatic insects are found during nighttime hours. Because the success of a P-I tour is largely dependent on the diversity encountered for each component to the model, night walks are particularly fruitful. This can be true of both birds and butterflies, as well as some of the world’s most charismatic insects. More will be discussed on this topic shortly.

**The itinerary**

Planning the itinerary of a P-I tour begins with a relatively clean slate. The confines of the itinerary are initially set by the total duration of the ecotour. In the case of these Costa Rica trips, the total trip length was 9-10 days (one additional night was added to the third trial expedition in 2012), beginning on a Saturday and ending the following Sunday (in order to appeal to the working age – this will be discussed further in the marketing section). Even though Costa Rica is a small country, about the size of the state of West Virginia, curvy mountains, single lane roads, and various pavement
types result in unpredictable and slow travel between sites. Therefore, the areas chosen to be part of the itinerary should either minimize travel, or allow for ample time between destinations on longer travel days. For the Costa Rica trips, a total of three destinations were chosen that spanned two, three, and two nights respectively. (The final night is spent near the international airport, prior to departing the following morning.) The general guideline developed in the planning of these tours is that at least two nights should be spent at each destination regardless of its proximity or location to other nearby destinations. This allows long travel days to be broken up by several full days of local exploration and activities. Since it is nearly impossible to completely predict travel times in Costa Rica, a customary two-hour trip could easily take four hours or more. Should this mean that the group does not get in until late evening or past sundown, it makes for a very short stay at a lodge that may have been hand-picked to be spectacular for a certain suite of species or a particular view of the jungle. This brings us to a follow-up point that it is always prudent to leave a lodge after breakfast for transit to the next area. This allows group members to have packed their suitcases in preparation either the night before or early in the morning. In addition, this allots for an entire day of travel, even if the travel time is predicted to be less.

Generally speaking, the P-I model lends itself to multiple areas and multiple lodges, in contrast to the OS/OP approach. The focus of the P-I model is more about diversity of species seen, which necessitates visiting a diversity of habitats. However, although diversity is highly desirable, this does not mean that the trip planner and leader should not gear any part of the tour to an individual species, which may be rare or highly prized by nature enthusiasts. For example, the itinerary for the Costa Rica trip has one
extra night in Monteverde compared to the other locations. This is largely due to the need to see a Resplendent Quetzal \((Pharomachrus mocinno)\). This magnificent bird in the Trogon family is not uncommon in Monteverde and is thought by many to be the most prized bird to see in Costa Rica (Figure 2-11). Although there is no entomocentric equivalent around which this tour is designed, this is an important bird to find during the course of the trip and Monteverde is the only real chance. This serves to satisfy the birding contingent in knowing that the tour is not subjectively orientated to butterfly watching. However, this does not mean that this is the only thing happening that day. The extra full day is equally valuable to butterfly watchers, with double the chances to see charismatic Lepidoptera like the Clear-wing Ithomiine butterflies, which occur in the montane regions of Costa Rica, as well as several species of \textit{Morpho} butterflies.

The daily itinerary for the Costa Rica case study of P-I tour models is broken down into an early morning, morning, afternoon, and nighttime component. The following sections will detail each time slot, with particular emphasis on the value of each to the ecotourism group.

\textbf{Early morning.} The early morning time slot, typically from around 5:30 or 6:00 am (just before daybreak) until 7:30 am, is ideal for the first wildlife group in the pair of interests – birds. There really is no other time of day like dawn for bird watching, and thus if this activity is to be integrated into an insect ecotour, or any tour in general, this time period must be provided as an option. Although the entire group is not likely to join, which may be composed of people with various interests and priorities, including specialist butterfly watchers and more general nature enthusiasts, the birding contingent
will be thrilled with the opportunity. It is essential to have a combination of specialist opportunities throughout the day when using the P-I model.

When scheduling the early morning bird walk, the trail should be scouted out prior to setting out, perhaps by leaders the evening before, but this is also an opportunity to instill an explorative style to the tour. Although participants expect a certain degree of preparation and planning on part of the itinerary, any opportunity to engage in more basic exploration amidst wild and natural beauty will be appreciated by the group. This is another reason why the choice of lodging is important. Lodges with high quality nature trails allow the group to explore without necessarily knowing what is around each bend (in a good way). The sense of anticipation and excitement is shared with the entire group, and the participants will pick up on the leader's enthusiasm.

Having ample time for this early morning activity is critical. However, this should not be at the expense of the rest of the group, in the case of the P-I model. Higher quality lodges specializing in ecotourism will be familiar with the early morning walks, and will often provide an early coffee and cookie service at a central meeting area where the group convenes prior to setting out. This enables the early morning group to wait until 7:30am for breakfast, at which time the entire group will meet, with the bird watching crowd already telling stories of great wildlife and bird sightings, encouraging others to join the next day's early morning bird walk.

**Morning.** The morning time slot essentially begins with breakfast, because the feasible time at which to depart for the first activity largely relies on what time people are able to be ready to leave. From these trials, one hour is an ideal amount of time from the start of breakfast to when the group is able to be ready to leave for the first activity.
Morning activities are great for nearly all nature activities in highly biodiverse tropical environments. With cooler temperatures compared to mid-day, and before daily afternoon rains begin, wildlife is also more active. Coupled with the fact that the group participants tend to be more active at this time of day, the morning time is best suited for more strenuous activities. Typically, this means hiking and walking, but it can also mean more adventurous things like zip-lining or walking on canopy bridges. By mid-morning, there is a noticeable decline in bird activity, which also coincides nicely with an increase in butterfly activity. Largely based on the amount of sunlight bathing the area, butterflies begin to take flight in search of nectar sources, host plants, and mates. Although wonderful bird watching opportunities remain, those prioritizing butterfly sightings will begin to see the relative activity patterns turn in their favor by 10:00 a.m. Weather providing, the next several hours will be the best part of the day to spot exciting species of butterflies.

The duration of each activity is governed by several things, regardless of the exact pairing of foci in the P-I model. These are mealtimes, general stamina, and use of facilities. Without going into specific detail on caloric requirements, exact levels of fitness, or size of the average group member's bladder, the consensus on how much time each activity should last is about three hours or less. Referring back to departure time for the morning activity being 8:30am (after a one-hour breakfast and time to prepare for the day), this puts the group in a position for a lunch break by noon or shortly before. One key thing to keep in mind is that on the P-I tour, the pace is relatively slow due to the frequent opportunities for nature observation and interpretation. For this reason, it is important to use all available time during the activity.
to provide for such opportunities, as the lack of distance covered on the morning walk may be mitigated by the high levels of diversity observed.

**Afternoon.** The afternoon time slot is perhaps the most flexible. While the type of activity should depend on the type of morning activity, it also depends greatly on the weather, as well as number of possible independent activities available (i.e., things people can do without the aid of transportation or guidance of a group leader). In the tropical environment, where great potential exists for P-I tours, afternoon rain should be expected, even in drier times of the year. This should not prevent an organized group activity from occurring, as weather is both unavoidable and, in many cases, interesting when animals respond with varying behaviors and adaptations. Nevertheless, with full mornings spent hiking, photographing, and wildlife watching, the afternoons are more open to independent exploration. Again, this is where the quality of the lodge comes into play. Self-guided nature trails, rivers to swim in, libraries, and outdoor lounging areas are often an equally rewarding experience for ecotourists. While many ecotourists joining the Costa Rica tour did so specifically for the expert guidance and leadership, certain activities lend themselves very well to independent exploration, giving the participants a sense of personal initiative during their ecotour vacation. Time spent exploring on one’s own was routinely reported as one of the trip highlights year after year.

Independent or “free” time is a necessary part of the P-I model, as people often have their own goals and priorities during the trip that cannot be satisfied when they are part of a group. Photography, although well suited to group hikes, takes on another dimension when unconfined by the pace of a group hiking ahead. In addition, cultural
components that may not be emphasized during an ecotour are also proper
independent activity options. These may include conversations with locals about daily
life or visits to nearby shops or art galleries. For example, on the Costa Rica P-I tour, a
full afternoon is devoted to independent exploration where group members are free to
walk about the city streets and enjoy the unique artisan culture on display in
Monteverde. There are also numerous serpentariums (reptile exhibits), ranarios (frog
exhibits), butterfly farms, and other small nature exhibits that are simply too abundant to
visit as part of the tour. Thus, free time gives individuals the option to visit what they
see as the best and most interesting exhibits. This has proven an ideal time to allow
participants to choose their activity on their own, with a briefing and recommendations
provided ahead of time.

There are good reasons to allow time for independent exploration, but scheduled
activities have also proven very satisfying to group members on the Costa Rica P-I tour.
Again, consideration of the morning activity is important when planning any group
afternoon activity. Successful afternoon activities on the Costa Rica trip included boat
rides through jungle rivers, visits to butterfly farms, and more coordinated souvenir
stops – all relatively passive activities. Although this is not a firm rule, it has proven the
most successful, as it allows for spacing between the more active morning schedule,
while providing more dimensions to the overall trip itinerary.

Even on days with both an organized morning and afternoon activity, time before
dinner for independent exploration is valuable for both bird watchers and butterfly
watchers. Birds tend to have one more period of peak activity in late afternoon, as do
some species of butterflies, such as those in the genus Caligo, the Owl butterflies,
which are abundant and diverse throughout Costa Rica. Although there is some overlap between morning and afternoon species for both birds and butterflies, there is also a significant amount of disparity between the species likely to be seen. This provides for a well-rounded day in a typical P-I ecotour.

**Night-hikes.** Night hikes are a highlight for any entomological ecotour and in many cases can be a self-contained entomological ecotour for groups without an insect focus already. They also provide a dynamic addition to general nature tours (Figure 2-12). Much like the early morning walk is geared towards birders, the night hike is geared to those interested in insects. Once again, this is where the virtues of a quality lodge can make a major difference. Paths into natural areas are a must in order to observe the full potential of a rainforest night hike. However, lighted paths throughout the lodge area, even if not fully immersed into the jungle, can provide incredible insect observation opportunities.

Offered as an optional tour during these P-I case studies, typically less than one half of the group joined each night hike, offered roughly four times per trip during the course of the nine-day trips to Costa Rica. Nevertheless, the group did not routinely consist of the exact same people, as stories of gargantuan beetles, barbed caterpillars, and raids of leaf-cutter ants intrigued the entire group over breakfast the following morning. By the end of each trip, at least 90% of the group participated in a night walk at some point. Because later nighttime hours are seldom reserved for other activities, the night-hike is a spectacular way to involve a rarely seen insect world in any ecotour to Costa Rica and the tropics in general.
Aside from the confines of a set breakfast time or any specific reason to have to be back at the lodge (short of any curfews at the lodge), the duration of the night hike is flexible. Participants generally spend between 30 minutes to one hour engaging in this activity, but others have enjoyed it for longer, staying up to two hours with leaders guiding the way into interesting areas of the lodge grounds or surrounding forest. Insects are not the only attraction, however, with nocturnal birds such as Night Jars, Owls and Paraques, as well as nocturnal mammals, such as Kinkajous and up to seven species of felines, potentially being seen as well. Using trails that are well marked and close to central areas of the lodge are critical for ensuring a high level of participation, as it allows people to return to the central lodge area and their rooms at their leisure.

Another interesting dimension of nocturnal insects is the use of common trapping techniques to bring the insects to the group, rather than having the group go to the insects. Discussed more in the Research Associate section, setting up moth sheets (Figure 2-12) provides not only the opportunity to showcase fascinating nocturnal insects not likely to be seen otherwise, but it also allows the leader to educate the group on scientific procedures for research in the tropics. This serves to enhance the authenticity of the ecotour, a theme heavily emphasized in this dissertation.

A note on insect ecotourism. Tours designed around finding and watching insects are wonderful and rewarding, but are still relatively rare in the grand scheme of ecotourism. However, this is not to say that insects do not find themselves in the ecotour. In fact, insects can be a nature guide’s best friend while exploring the jungles with ecotourist clients. The truth is, despite colorful pictures of Red-eyed Tree Frogs, Jaguars, and Sloths appearing in biology textbooks within “tropical jungle” chapters and
featured on Discovery Channel programs, these creatures are rare and difficult to see. The chance of seeing such charismatic animals on days or seasons of inclement weather is lessened even further. However, insects are prolific even in the rainiest of seasons and on days when other wildlife choose to remain high in the trees, deep in the ground, or otherwise hidden in the foliage. Spotting a colony of leaf-cutter ants, or a dung beetle may be the difference between a jaded and bored participant ready to return to the lodge and one that is amazed by the dynamic life they never knew existed. The opportunity to talk about army ants, and their many associations with antbirds, and even ant butterflies, can turn an ordinary tour into an extraordinary one. Whether the guide finds a sap-covered tree hole with leaf-cutting bees, a termite mound with their “nasute” soldiers, or a helicopter damselfly patrolling for spider prey, insects provide unique and plentiful nature interpretation opportunities. This is true regardless of the weather or what other animals are doing that day. Being familiar with insects in the ecotour can make a dramatic difference for both a naturalist guide and his or her clients on days when the Jaguars are just not cooperating.

**Education**

All trials detailed in these case studies involve strong educational components, as has already been mentioned in the OS/OP section and Monarch butterfly trials. However, the format for educating participants during different types of trip models varies. With the Monarch trips, on-site interpretation was impractical due to the concentrated size and serene nature of the colony sites. In the case of Costa Rica, though, the jungles lend themselves very well to on-site nature interpretation. Partly due to the tremendous diversity, which would be lost or forgotten without near-immediate context and exposition, and partly due to the openness and relative
seclusion of the group, it is more feasible to make announcements, conduct
demonstrations, or otherwise inform the group about what they are seeing. Voices
louder than a whisper and a large gathering of people would be viewed as inconsiderate
by others visiting the smaller and more contained visiting areas in the Monarch butterfly
colonies. However, in the tropical jungle, it is much more feasible to break for a few
minutes to explain something interesting that the group observed.

One of the keys to a successful P-I tour is the expertise of the scientific leaders.
Without an intimate understanding of the two groups of organisms, which are in this
case birds and butterflies, the educational goal of ecotourism is lost. During all trials of
this Costa Rica trip, the scientific leader for the birding component was Dr. David W.
Steadman, a world-renowned ornithologist with extensive experience in both the South
Pacific and Latin America. While a knowledge base of only Latin America would suffice
in a scientific leader, the broader experience and ability to cross-reference bird
behaviors, appearances, and general biology between such disparate global regions is
a definite bonus in his leadership abilities (not to mention terrific field research stories
from exotic destinations). The scientific leader for the butterflies aspect of the tour was
the present author, Court Whelan. However, for one year, Dr. Thomas C. Emmel joined
as an additional scientific leader and butterfly expert. Dr. Emmel is a world authority on
tropical butterflies, current Director of the McGuire Center for Lepidoptera and
Biodiversity, and has a lifetime of field, teaching, and research experience to bring with
him on the expedition. While this author also served as expedition leader for each of
these expeditions, a life-long interest in insects combined with a Bachelor's and
Master’s degree in entomology enabled the author to also function as scientific leader for these P-I expeditions.

On days that the groups engage in jungle hikes, there is a natural division among the group members based on their interest. Stretched along a single trail, each scientific leader would typically have a following based on their area of expertise. For example, participants more interested in bird-watching would favor Dr. Steadman, while those more interested in butterfly spotting would favor Court Whelan (or Dr. Emmel, in the case of the 2008 trial). Still others would join a hired Costa Rican naturalist guide, who had impressive knowledge and sighting abilities for both birds and butterflies as well. Since Costa Rica has much more than birds and butterflies, each leader would be equally cognizant of opportunities to view mammals such as Sloths, Coati, and Howler Monkeys, amphibians such as the colorful and charismatic Poison Dart Frogs, and arthropods like Leaf-cutter Ants, Termites, or Tarantulas.

Opportunities for field-interpretation are immense in tropical ecosystems like Costa Rica, as the animals, and certainly the plants, are often stationary and visible for extended periods of time. Perhaps one of the most satisfying aspects to ecotourism and the general concept of field-interpretation is to explain the life cycle or feeding behavior of an organism unique to the tropical ecosystem while actually watching its behavior. Discussing the unique camouflage employed by the Blue Morpho butterfly (*Morpho spp.*) as it flies through the forest, flashing its characteristic blue upper side in contrast to its cryptic underside, making it difficult to follow in the case of a hungry bird, is a prime example. Discussing this in a textbook is interesting, but being able to see this in real life and actually observing the Morpho’s blue flashes appearing randomly
through the forest as it flits through the air, leaves a more pronounced impression on the part of the visitor. The same goes for observing the defoliation of an entire tree by a persistent colony of *Atta cephalotes* or Leaf-cutter Ants. Enabling the participant to scan the surface of the colony mound, follow the wide foraging trails that connect it to the nearby trees, and look closely at the small minima ants riding on top of the leaf fragments, provides a context really only achievable through witnessing the behavior in person.

Field interpretation is a powerful way to enhance an ecotour, and having the interpretation come from world experts adds to the general rarity and uniqueness offered by the tour planners and leaders. Due to the confines of the duration of each hike or day tour, as outlined in the previous Itinerary section, there is not always enough time to discuss the many complexities of tropical ecology while standing in the middle of the jungle. The next best approach is to hold evening discussions. These may serve to introduce new concepts, animals, or plants, or perhaps tie things together and provide context to the day’s activities. Again led by the scientific leaders, this is a unique opportunity for trip participants to engage in college-level education, while enjoying their vacation. This satisfies the educational component to ecotourism exceedingly well.

In the case of the P-I tour, evening discussions are a terrific time to begin to bridge the gap between the two foci of the trip (i.e., the pair of interests). Conducting recaps of species seen throughout the day by the birdwatchers vs. butterfly watchers, or simply presenting a more structured lecture on tropical butterfly biology, for example, is an effective way to intrigue birders to the world of butterfly watching, as does a lecture on tropical bird biology for butterfly enthusiasts. Ultimately, these discussions serve as
useful tools in promoting the entomo-centric goal inherent in this dissertation and the P-I model, which is to expose like-minded nature enthusiasts to what is now a new niche of nature observation – entomological ecotourism.

Contrasting the nightly discussions detailed in the OS/OP section, those during the P-I tours are likely to be shorter in duration. Part of this is due to the great number of opportunities to hold such discussions throughout the trip. With eight or nine nights, there is a greater amount of time possible to integrate lectures into the daily itinerary. The reason for shorter discussions is due to the more diversified daily schedule, both within and between days. During observations and trials of lecture duration, people responded best to lectures that were around 20 minutes long, and introduced a finite number of topics. With the variety of activities the group participates in each day, a longer and more detailed lecture proved to be less effective in both captivating and educating the participants. Not only does this marginally reduce the group’s overall contentment, but perhaps more importantly, information is not as well retained. The length and detail provided on subtopics for each nightly lecture should be inversely proportionate to the length and variety of activities during the day’s itinerary (Figure 2-13).

**Leadership styles**

The leadership styles differ significantly between the OS/OP and P-I models. As detailed in the OS/OP section, there is a deliberate lack of emphasis on structure and leadership while in the Monarch colonies that has proven to be very successful in managing expectations and satisfying a diversity of interests. However, in the case of the P-I model, the strong field interpretation component necessitates relative cohesiveness among the group. Fortunately, though, the desire on part of the leaders
to provide on-site education is the very thing that promotes the level of group cohesive-ness that ultimately permits the field education, thus forming a very short and direct positive-feedback loop (Figure 2-14). One of the most important jobs of the tour leader is to manage expectations. Because of the bird and butterfly watching expectations set during the trip-marketing phase, one of the primary expectations is to view numerous species of both birds and butterflies and to have them identified. Therefore, the more relaxed style of leadership apparent in the OS/OP model does not work well with the P-I model. Although not as rigorously attentive as leaders in adventure ecotourism, where the participants’ safety is directly in the hands of the leader as they, for example, repel down canyon walls, or ride motorized ATVs through forest tracks, the leadership style of the P-I model tour is the most demanding out of the various models for entomological ecotourism detailed in this Chapter.

**Trip extensions**

The complete and comprehensive nature of the Costa Rica trip trials proved to be ideal in exposing the group to a variety of habitats and ecosystems. While variations are possible in both duration and destinations visited during the course of the trip, there have been no reviews of the trip, on part of the participants, to suggest any dissatisfaction in either aspect. During the five years of trials, the number of trip extensions, where participants would either come early or stay after the trip to engage in additional activities, was limited to only six people out of the total pool of 71 participants (8%). There is virtually an endless number of possibilities for extending one's trip in Costa Rica, but likely due to length of the trip, there is relatively little need to do so, especially when compared to the previous example of the Monarch butterfly trials and the OS/OP model.
Marketing the P-I model

Trip planning. Mentioned previously in the OS/OP section, trip planning and marketing is the backbone of the trip. Without the proper marketing, there is the risk of too small a participant base for the trip to take place, thus causing the trip to be cancelled. Not only is this undesirable in the short term, but in the long term, too many cancellations would reflect poorly on the travel program in general. A critical part of the marketing strategy is how the trip is planned and whether it is set up to meet particular expectations. With the P-I model, this is especially important, as there is no singular attraction like in the OS/OP tour model. Rather, it is the cumulative diversity of what is offered that intrigues the potential ecotourist. The following sections will detail how the various components of trip planning are managed for the P-I tour model.

A note on word-of-mouth and direct contact marketing. Personal recommendations from friends, family, and colleagues are marketing tools that should not be ignored. Because of the novelty of entomological ecotourism, potential trip participants may be slightly wary of the format of the tour, or the overall qualifications of the tour planners and leaders. With any of the tour models detailed in this Chapter, a solidly planned and executed trip is the best way to ensure the spread of verbal recommendations from trip participants to new potential clients in existing and even new markets. However, one way for the tour operator (i.e., trip planner and/or leader) to perhaps instigate word-of-mouth advertising by those not yet exposed to the operator's tours, or entomological ecotourism in general, is to host speaking engagements to interested groups. These engagements may take several forms.

The first method is an informal yet informative lecture on a topic related to the ecotour focus. This lends itself best to groups that may not necessarily have a strong
scientific background, but are nonetheless interested in participating in a remarkable environmental phenomenon (such as the Monarch ecotour) or unique diversity of wildlife (such as the Costa Rica ecotour). Offering to speak at travel club meetings, environmental organizations, or retirement communities is a sure way to become involved from the tour operator’s standpoint. While the discussion should minimize references or solicitation to join a specific ecotour (to avoid a salesman-like approach), having the overall content of the lecture center around the Monarch butterfly migration (in the case of the Monarch ecotour), or butterfly diversity in the tropics (in the case of the Costa Rica ecotour) not only solidifies the connecting between education and tourism, but also serves to create “buzz” among the club, group, or community.

The second method caters more towards the scientific community and is most appropriate in the case of the Research Associate tour model (to be discussed in the following section). Yearly meetings, symposiums, University seminars, and scientific workshops serve as gatherings of the target audience and serves both the scientific community, as well as the ecotourism community. One of the most effective ways to promote word-of-mouth in this arena is to present scientific papers at conferences about recent discoveries and findings, as a result of organized Research Associate trips to a particular destination. Again, blatant solicitation undermines the goal and decreases authenticity of the experience, so it should be minimized. Fortunately, high quality content and an interesting presentation can substitute for this exceedingly well.

Speaking engagements may represent the most cost-effective technique in promoting entomological ecotours, as this allows the trip leader to demonstrate one of the key tour features, which is the ability to entertain while educating. Functioning much
like a free sample at a grocery store, these lectures and discussions serve to intrigue audiences and leave many hoping for more. By creating a buzz in various audiences, whether it is a travel club or annual scientific meeting, potential participants take over the marketing at this point. An engaged and passionate audience member can be the best salesperson in recruiting friends, family, and colleagues, as has been seen on numerous expeditions in all tour models.

**Trip cost.** To reiterate what has already been said in the OS/OP Trip Cost section, price is one of the most important factors in terms of marketing a trip. With the P-I model, one can make the tour as appealing as possible, with expert leaders, a spectacular itinerary, and a brochure with dazzling photos of flora and fauna that are sure to have any nature enthusiast jumping at the opportunity. However, if the price is too high, momentum will be frozen, causing the participant to completely halt any efforts to join the tour, or possibly seek out a more affordable itinerary or tour operator. Any service, whether it be a haircut or an ecotourism expedition, is rated largely by value. Therefore, it is not necessarily the cheapest trip to Costa Rica that is the most successful. In fact, trips too cheap leave the potential traveler wondering what corners have been cut, and what parts of the trip are covered and not covered (i.e., meals, park entrance fees, etc.). If a trip has inexperienced leadership, poor planning, and few things included in the “all-inclusive” price, the trip has a low value, regardless of the price tag. Therefore, when engineering the price of an expedition, price and value are complementary and should be considered equally. This is where the P-I model and the experience of the Costa Rica trials comes in.
What sets these expedition trials, be it Costa Rica, Mexico, or others not yet addressed, apart from other ecotours is the caliber of leadership and planning. To have world-renowned professors co-leading expeditions adds value. Spending considerable time mapping out ideal itineraries with activities, lodges, and restaurants well suited to the tour adds value as well. However, these factors also add to the trip cost, as leader costs need to be covered, as well as expenses for quality lodging and meals in the total cost of the trip. Nevertheless, the value added to the trip surpasses any cost increase, making a $2,000 trip to Costa Rica under such leadership a better value in the eyes of potential travelers than a $1,500 trip with an organization that offers much less in terms of experience, which ultimately translates to the degree of education, interpretation, and authenticity.

Competition plays a large role in the ultimate pricing of a P-I expedition. Even though entomological ecotourism and these different tour models in this Chapter are relatively novel, they are nevertheless still contained in the greater genre of ecotourism and, therefore, compete with virtually all nature tours in terms of capturing the interest of ecotourists. While there may not be another tour that emphasizes the pairing of birds and butterflies, the total number of tour operators and yearly group trips to Costa Rica number in the thousands. The range of prices is considerable, with higher-end trips advertised over $3,000 per person, and lower end trips as inexpensive as $500 for a nine-day itinerary. The accommodations, activities, group size, and various included elements of the trip (i.e., meals, park fees, and guide fees) varies equally across the price spectrum. As these trial expeditions are remarkably similar to the higher end trips in terms of duration, group size, included elements, and destinations, the average price
of these trial tours being $2,024 throughout the three separate expeditions is a great value and has been instrumental in the overall success and high numbers of trip participants throughout the duration of the study. While this is not the cheapest trip out there, it is the belief of this author that it is indeed the best value, which is a much more important consideration than just the price tag of a trip.

**Duration.** The duration of the P-I model is another major difference between this and the OS/OP model. The general idea is that these trial expeditions to Costa Rica are intended not only to attract those with existing interests in birds, butterflies, and general nature tourism, but also to attract those with simply a desire to experience Costa Rica. For this reason, the trip is also designed to be comprehensive and satisfy those participants whom may never get another chance to visit Costa Rica, or perhaps the neotropics in general, ever again. Therefore, a shorter itinerary, as seen in the OS/OP model would largely be unacceptable. Without repeating too much of what was already discussed in the Itinerary section, the nine-day duration has proved successful in meeting and largely surpassing expectations. Spanning from weekend to weekend, this is also ideal for minimizing the amount of time away from a typical working schedule (i.e., only five days off of work). This was done very deliberately for several reasons.

First, efficiently scheduling a trip around the work week makes the trip more attractive to working people. Second, it allows the group to spend the majority of their time in the National Parks during the week when large numbers of local Costa Ricans are less likely to be visiting. This makes the visit more intimate and peaceful. The sharp contrast in visitation has been evident during these trials. Naturally very busy due to the incredible beauty with lush rainforest on the interior of the trail and blue-green tropical
waters and sugary sand on the opposite side of the trail, Manuel Antonio National Park also hosts a tremendous diversity of wildlife in a relatively small area. Appearing somewhat habituated to humans, the White-faced Capuchin Monkeys (*Cebus capuchinus*) will entertain for hours as they play in the trees only several meters from the trails. Frequently, *Morpho amathonte* has been seen in great numbers, using the main trail as a corridor to the delight of visitors. In addition, birdwatchers are able to see many new species due to the variety of habitats, including saltwater estuaries, open coastal beaches, lowland rainforest, and very visible and accessible transitional forest between them all. These desirable characteristics are no secret, and commonly there is a wait to even get into the park, not to mention the larger crowds along trails and beaches. Fortunately the other destinations, which offer rivaled diversity in flora, fauna, and habitats, are explored during the middle of the week and thus much more serene. However, during these trials, these crowds served as a constant reminder as to why it is best to visit other parks during the middle of the week.

**Pre-trip materials.** The many virtues of supplying well-organized and comprehensive pre-trip information packets to each registered participant have been well detailed in the OS/OP Pre-trip Materials section. To expand on this and also to introduce specific components to all pre-trip information packets. Table 2-1 summarizes the information supplied to the participant prior to the expedition.

With all pre-trip information packets, there are relatively few changes necessary between tour models. While some trips may be geared towards more experienced travelers who may need less coaching on what to pack, or the types of electrical outlets found in the host country, it is best to err on the side of oversupplying information. The
Costa Rica trip has seen a larger than normal contingent of inexperienced travelers, so special attention was made to supply an exhaustive list of topics and instructions. However, this is not necessarily characteristic of all P-I tours. In fact, travelers with specific goals, such as bird watching or butterfly watching are often more experienced when it comes to travel. They are more likely to have been to tropical areas before and have proper expectations of what the accommodations will be like, what clothes to wear, and how to pack in order to make the frequent transfers between lodges easier. Nevertheless, the P-I model lends itself very well to promoting travel to newcomers into the ecotourism world. Proper trip preparation is key, and it is up to the trip planner/leader to supply each person with the information needed to begin the expedition informed and confident.

**Hands-on marketing and brochure design**

For obvious reasons, the materials used to promote a P-I tour should highlight the two groups of taxa to be emphasized in the tour. However, managing expectations is critical in ensuring a satisfied group of bird and/or butterfly watchers. Thus, pictures of rare species should only be used if there is a decent likelihood of actually encountering them in the course of the itinerary. This does not mean that one should avoid mentioning or depicting them in the brochure, though, as it is likely that these rare, charismatic, and desirable species are the motivating factor for someone to join the tour. In the case of these Costa Rica trips, the Resplendent Quetzal (*Pharomachrus mocinno*) is perhaps the most sought-after bird by birders. Luckily, with patience and a good guide, it is entirely possible to see one or several in Costa Rica. By adding an extra full day in Monteverde and participating in canopy walks and/or ziplining, this significantly heightens the chances of seeing this remarkable creature. This was
exactly the methodology used in these trials, and resulted in several Quetzals seen in each of the tours conducted in the study. Similarly, seeing a Blue Morpho (Morpho sp.) in the wild is perhaps one of the most desirable sights for a butterfly watcher, especially when a variety of species are encountered. By optimizing the number of habitats and regions that cover a range of altitudinal gradients, the chances of encountering several different species of Morpho are quite high. Photos of these charismatic species make for ideal brochure additions, as they are equally appealing to both ardent naturalists, as well as those just beginning to explore the world of Neotropical expeditions. The number of photos used in a P-I trip brochure should not stop here. Because the trip is designed to observe biodiversity in these and other groups of taxa, the brochure should highlight as many variations of diversity as possible, while also branching out and showcasing completely different groups like mammals, reptiles, amphibians, and plants.

The text of the brochure is often limited by the number of pictures, length of the itinerary, and other unavoidable inclusions like a registration form and, of course, the terms and conditions. However, this area is parallel to that of the photos. Details on what is expected should be abundant, highlighting the various experiences with particular emphasis on wildlife and the activities to be engaged in that will allow such remarkable wildlife observations. As with the photos, any rare occurrence, such as seeing a Jaguar, or Dynastes hercules Beetle should only be mentioned if it truly is a possibility.

In the case of the P-I model, there is less of a need to introduce the focus of the tour compared to the OS/OP model. However, the introduction may be utilized to set the tone and general layout of the tour. Here is where the pair of interests should be
emphasized. If there are particularly exciting opportunities, such as river boat rides or canopy walks, these too should be mentioned. Although it is difficult to say whether people reading the brochure actually begin with the introduction and proceed from there, based on whether they are intrigued or not, one can only assume a logical progression of reading, beginning with the introduction and proceeding to the day-to-day itinerary, if truly interested.

**A note on social media.** Social media websites, like Facebook and Pinterest, lend themselves very well to promoting ecotourism. Allowing users to show videos, photos, and stories from trips and having these automatically posted to their friends’ homepages can facilitate a significant growth in interest. This applies just as much to entomological ecotourism as anything. One of the largest challenges entomology as a discipline must overcome is the stigma of insects being limited to creepy crawlies and other unsavory animals that are perceived as unsanitary or just plain gross. However, as any entomologist knows, these taxa that often have served as ill-fated ambassadors to the world of entomology are a minority of insect species. In addition, many of the preconceived notions of insects as being unsanitary are simply incorrect. Social media may serve as a method to dispel rumors and encourage an appreciation of insects (whether in the context of an ecotour or not) by even the most unlikely of people.

Forming Facebook groups after returning from trips is a useful way in keeping trip members united after the bonding experience had while traveling on an exciting ecotour. The willingness of people to share memories, photos, and videos often allows select photos to be viewed by hundreds or thousands of people, connected to one individual by friends, friends of friends, or networks. Photos of group dinners or
rainforest hikes may promote travel, while photos of spectacular insects like Harlequin Beetles, Fulgorids, or Butterflies, may reveal a very different and largely unknown side of entomology to many. Although social media is still in infancy, the potential is enormous for promoting ecotourism, entomology, and ecotourism entomology.

**Future Possibilities for the P-I Model**

In the previous OS/OP section, there were several examples given as various subgenres within the OS/OP model. Highlighting the diversity of taxa, as well as the scope of the phenomena, there were relatively clear delineations in the various tours, with specific species or phenomena being the foci of the ecotour. With the P-I model, a much less clear delineation exists, as the tandem of interests can take a virtually endless number of forms. In the Costa Rica case study, the pairing involved the well-established activity of bird watching with the lesser-known interest of butterfly watching. This is a highly effective pairing due to the similarity and complementary nature of the two activities. In terms of future tour possibilities involving the P-I model, one should first look at the various destinations worldwide that would support this venture in a similar manner as Costa Rica, where this study has already found success.

**The tropics**

Tropical regions around the world are logically the best suited to hosting P-I ecotours that involve the pairing of birds and butterflies. As rich in diversity as they are rich in mystique and intrigue on the part of the ecotourist, exotic tropical destinations are intrinsically more marketable than their temperate counterparts to the person seeking unfamiliar and novel natural history experiences.

The neotropics is perhaps the best area in which to further expand bird and butterfly watching programs, due not only to their proximity to U.S.-based ecotourists,
making international travel more affordable, but also due to the level of infrastructure for ecotourism already in existence. Countries like Ecuador, Peru, Panama, Brazil, and Honduras already have world-class birding lodges that attract birdwatchers from all over the globe. Integrating the butterfly watching component is relatively simple, as these countries host equally impressive butterfly diversity as well.

Although less diverse in terms of total number of species, the country of Papua New Guinea (PNG) is perhaps the best-suited nation for expanding the bird and butterfly watching P-I model in the Old World tropics. What PNG lacks in diversity, it makes up for in remarkability for its species composition for both groups. Home to the birds-of-paradise, as well as the bird-wing butterflies, PNG is a mecca for each respective group of enthusiasts. For reasons detailed in this section, the complementary nature of these two groups is likely to assist in the promulgation of the virtues of butterfly watching to bird watchers, and vise versa.

Other pairings in the P-I model

Expansion of the P-I model with regards to the well-studied birds and butterflies pairing is relatively simple. Choosing other pairings that are equally effective is not. Concomitant with the methodology outlined in the Costa Rica case study, the best starting point at designing a P-I entomological ecotour is to begin with an established following for one part of the pair. In the case of Costa Rica, birding was chosen due to the overwhelming following bird watching has already. This is an ideal foundation with which to begin. Other such followings are not commonplace, but do exist.

Perhaps the next largest niche in a single group nature tour has to do with flowers. From garden tours of Europe to orchid tours of Ecuador, tours already exist with ardent followers to view, photograph, and learn about flower diversity across the world.
Flowering plants are the very focus needed to form the foundation of the P-I model. While butterflies would present a logical other component, it is also feasible to think outside of the original pairing. What else could complement flowers that has an entomocentric quality? – Pollinators. A Flowers and Pollinators tour has the potential to take place in virtually any country, as the focus is not restricted to wild areas like tropical jungles or cloudforests. Opening the possibilities up to wildflower gardens, with abundances of both subject groups, countries such as the Netherlands, France, and Japan, which would likely rank lower on a traditional birds and butterflies tour, may suddenly fit rather well with the P-I model. Inherently, this sort of tour would lend itself to garden clubs, horticultural societies, and even apiary organizations. The general pollinator term would further extend the possibilities to include not just diurnal Lepidoptera, but also the nocturnal Moths as well. From there, Hymenoptera, Coleoptera, and even Diptera could be emphasized, thus broadening scope of interests, as well as the education delivered during the tour and the inevitable nightly discussions. Although the potential for this type of entomological ecotourism is untested at the time of writing, this author believes that such a program would be successful based on experiences seen in Japanese societal reactions to similar tours (Akito Kawahara, pers. comm.). This is an ideal area for future case studies in future dissertations.

A complete assessment of all potential pairings would extend for hundreds of pages, as there is virtually no limit to the number of combinations and permutations possible in the P-I model. Nevertheless, the two foci need to be complementary, in as seamless a fashion as that of the Costa Rica case study, or the previously-mentioned wildflowers and pollinators tour. With one of the missions of ecotourism entomology
being to increase awareness of insects and their fascinating presence and role in the world, it is a goal of the P-I model to continually promote insect tourism. Hopefully with continued efforts and innovation, one day it is the insect component of the P-I tour that becomes so commonplace that it may be regarded as the foundation of the P-I pairing, allowing for an entirely new suite of taxa with which to experiment as a P-I tour component.

**Derivatives of the P-I model**

Although largely unstudied in the five-year period of these trials, a single interest model has great potential, as the growth of niche forms of ecotourism continues. Resembling the P-I model, a single interest entomological ecotourism model (S-I model) differs mainly in the fact that only the insect component is emphasized, rather than pairing this with another broader interest, such as birds. Examples of these tours exist, with butterfly watching tours being associated with organizations like the North American Butterfly Association (NABA). Ranging from domestic tours in the U.S. to international destinations as far away as Papua New Guinea, S-I model tours represent an additional model that exemplifies entomological ecotourism. For the most part, existing tours using this model focus on total diversity of an area or region, clearly separating the S-I model from the OS/OP model.

Designing an S-I tour would be nearly identical to the steps taken in planning, marketing, and leading a P-I tour. While the potential participant base would be roughly half as large as a P-I tour (because of the lack of a second feature), there is indeed a market, especially as the steps taken in these ecotours continue to promote the insect side of ecotourism. Because of the similarity between the S-I and P-I models, this
Chapter will not repeat details on the specific tour components, such as duration, style of leadership, etc.

**Research Associate Model for Ecotourism Entomology**

A completely different direction than the previous examples, where general ecotourists may participate in new models of ecotourism that promote exceptional insect-observing opportunities, the Research Associate model (referred to as the RA model) is perhaps the most basal form of entomological ecotourism. Rooted in exploration and investigation for the purpose of scientific discovery, prominent figures like Darwin, Rothschild, Bates, and Wallace may have called themselves scientists, but were in many respects some of the first entomological ecotourists.

The RA model is also one of the most niche-restricted forms of entomological ecotourism, as we shall see throughout this section. These tours often take place in the same exotic and fascinating countries as other ecotourism programs, but the format of the tour is entirely different. When compared to a more traditional ecotour, the number of separate destinations visited in the course of an itinerary is often far fewer, allowing for much more time to be spent at each location or locality, as it is termed in the scientific community. In addition, lodging is often much more basic and primitive. In fact, the general outline of the tour is also much more basic and primitive, with the main priority on part of the leaders being to lead the Research Associates into areas where interesting insects occur based on individual interests and expertise.

A Research Associate (RA) is very much a combination between a scientist and an ecotourist. Typically having advanced higher education in their particular field of study, the Research Associate may or may not be a professional entomologist or biologist. In fact, many come from other professional fields such as medicine, law, or
engineering and are best termed “citizen scientists.” Nevertheless, their contributions to science are as vast as they are critical in this time of biodiversity crisis. Some Research Associates have specific interests that are nested in the entomological hierarchy of classification, such as a particular family of ants, beetles, or moths, but others have a more general interest that transcends multiple orders of the Class Insecta. Therefore, it is useful to have medium-sized groups comprising these expeditions that are made up of both generalist and specialist RAs.

The term Research Associate is more than just a fancy name for a participant. Their experience with scientific fieldwork and the extent of their knowledge of insects are the first thing that sets them apart. However, it is their dedicated work and collaboration with the University of Florida, Florida Museum of Natural History, and the McGuire Center for Lepidoptera and Biodiversity that enables them to be truly distinguished and earn the title of Research Associate. Having often spent an avocational lifetime diligently working with staff, faculty, and curators from the entomological world in order to augment museum collections and record behaviors to publish in peer-reviewed journals, they are experienced citizen scientists with the initiative to continuously furnish the scientific world with new discoveries.

With their acute interests in research, this fraternity of experienced Research Associates has proven to be intensely interested in participating in RA-modeled trips focused on entomological ecotourism. The following sections will highlight the successes of a series of trial expeditions in offering entomological ecotours based on this RA model, as well as detail the specific components that proved to be the most successful.
Concomitant with the OS/OP and P-I programs studied and evaluated in the course of five years, from 2007 to 2012, the RA model was instituted as a distinct brand of entomological ecotourism. The methodologies for planning, marketing, and leading such expeditions varied significantly from the previous models detailed in this section, as did each individual trial expedition from others in the RA cohort. During this five-year period, 19 separate expeditions were conducted to six different countries, with 31 localities being visited between all expeditions (Table 2-2). The cumulative tally of trip participant numbers was 147, yielding an average of 7.74 participants per expedition. The success of the RA model is attributed to trip planning, marketing, and leadership approaches that were similar to the OS/OP and P-I models, but also exhibited key differences. The general characteristics of the RA tour, along with comparisons to other entomological ecotourism, will be discussed in the following sections.

**Lodging and dining**

A central theme to the RA ecotour is field research. This puts a significant amount of emphasis on the location or locality that the group is based out of, while at the same time deemphasizes the need for a certain type of quality in accommodations or dining options. For this reason, all priority in planning this aspect of the tour is to lead and situate the group in an ideal area for their research goals. As previously stated, the vast majority of these RA trips are designed to research insects, principally to index their biodiversity and to record specific behaviors and interactions with their environment. During the course of these trial expeditions, it was overwhelmingly favorable to situate the group in natural areas with suitable insect habitat found in the surrounding grounds. This immediately selects for sites that are away from towns and cities, but also away from more established and larger hotels and lodges. While the selected
accommodations vary between these 19 expeditions in terms of proximity to the natural areas targeted for daily exploration and research, a balance was achieved in all instances that put the group as close as possible to the desired research area. In some cases, the particular natural area most interesting to the group necessitated lodging in a nearby town, away from the natural area. Although this is an exception, the benefits of certain remote habitats (which may have no lodging close by) to research outweigh the costs of having to travel each day to the study site, rather than being immersed right in it.

The ideal scenario for the RA model is to have the group stay in the very same area in which it is most productive to study and conduct scientific work. When the lodging is physically in the study site, the other components of the tour are much less demanding for the leader and for the group (i.e., coordinating travel to and from the area, meal planning, leadership role, etc.), as will be seen in the following sections. This allows for considerably more flexibility in terms of how research is conducted. For example, on trips focused on Lepidoptera biodiversity, a popular research method is to hang bait traps high in trees to attract certain species of interest (Figure 2-15). When the basecamp/lodging is in the same area as the study site, frequent checkups and visits to the traps prove to be much more effective in collecting valuable data. In addition, leaving such traps overnight in areas away from lodging can often result in stolen traps, or escaped Lepidoptera between periods of inconsistent monitoring.

Light-trapping is another method employed by researchers studying Lepidoptera biodiversity (Figure 2-16). Aimed at the nocturnal contingent of Lepidoptera (i.e., moths), the method of setting up bright lights against large white sheets has proven
effective for collecting a concentrated amount of data in a relatively little amount of time. Just as with the diurnal butterfly traps, these light traps require time to set up and function best when they are able to be left in one place for multiple nights.

In terms of recording behavior via photos and video, the added time in the study site proves to be much more productive. Being able to set up equipment and have it running for longer periods of time may document exceptional or rare behavior that otherwise would not be possible. Again, though, when a particular area is a focus of the study and nearby lodging is impossible, this does not mean the areas should be overlooked. While preference should be given to those sites that allow for full immersion into the research area, a short daily commute may be quite feasible in exchange for the opportunity to explore a special area of habitat.

The general lack of emphasis on high-quality lodging is mirrored in the dining aspect of the RA model. If a certain lodge, research station, or basecamp is ideally located for research interests, research associates were generally much more content than a subpar locality with delectable cuisine. However, this is an ideal time to mention the added value that a lodge can bring when it is not only situated in an ideal location, but also has superb amenities, accommodations, and cuisine. This situation is not as impossible as one may think, and is exemplified by the single most successful destination during the five-year RA-model trials – The Lodge at Pico Bonito.

**A note on The Lodge at Pico Bonito.** Finding an ideal combination of world-class lodging, wonderful meal options, and superb amenities, all situated in a varied, dynamic, and fascinating insect habitat, is not impossible but is indeed rare. Perhaps best described as a culmination of years of trials and experimentation with various
styles of RA expeditions, The Lodge at Pico Bonito, in Honduras, Central America, represented the most successful RA trial. Its success was based not just on high participation and total numbers of trips (63 researchers on 6 separate expeditions), but also on the total productivity and impressive help to professional research in assessing the Lepidoptera biodiversity. Through combined efforts on the part of Pico Bonito, the McGuire Center for Lepidoptera, and the dedicated staff, scientists, curators, and research associates involved, a major gap in knowledge of Central American insect fauna (particularly Lepidoptera) was filled. With 63 research associates participating in six separate expeditions over two years, citizen science has flourished in this exotic destination in the middle of Honduras, little studied by entomologists since the 19th century team of Godman and Salvin. Lodge managers, directors, and owners at Pico Bonito were shown the societal value of research, as well as this particular research/ecotourism model, and consequent plans to expand the program in 2012 and the years ahead. The program has been very well received by those at all levels of management and ownership at the Lodge.

Initiating research and ecotourism programs are valuable to jungle lodges like Pico Bonito in several ways. First and most obviously, in that they are generating revenue from ecotourists in terms of nightly charges that go to pay lodge employees (of which there are roughly 60 at any one time at Pico Bonito), and to support local communities through expenditures on part of the lodge (i.e., food, staples, and other supplies and goods from local merchants and farmers). Second, lodges gain exposure due to the publicized efforts of such scientists both at home and abroad. From publications in scientific journals, to stories of the lodge and the RA experience published in news
articles, awareness is elevated well beyond conventional avenues for promoting ecotourism. Third, the lodge gains credibility and marketing stature among ecotourists through the increased knowledge promulgated by the visiting scientists. This knowledge may come in the form of official documentation and findings, or more general topics may be passed onto guides and naturalists employed by the lodge. Commonly, lodge guides are curious about natural sciences and are eager to learn all that they can from visiting experts. Whether learning how to properly identify a particular group of insects, or sharing in the discovery of a new plant-insect interaction, when lodge guides benefit through increased knowledge, the lodge benefits, too, by providing better experiences to future guests through more experienced and qualified guides. When these guides are participating in active research in the area, the experience of casual nature walks with more general ecotourists becomes more authentic and therefore higher quality. Figure 2-17 depicts the spread of knowledge and the relationships that form as a result of RA model ecotours.

Pico Bonito represents a rare situation in which the lodge itself is not only situated in an ideal study site, but also retains a comfortable and upscale atmosphere that satisfies high-end luxury ecotourism. Through the lodge’s interests in conservation and scientific research, the trial RA opportunity was made available as part of the early stages (dormitory housing) of a research station trial period, such that the management greatly reduced the nightly lodging costs in exchange for conducting valuable research. This mutually advantageous arrangement has served to attract a number of RA ecotourists to the series of six trial expeditions, which directly contributed to a vast array of scientific discoveries and subsequent publications (e.g., Miller et al. 2012), as well as
having an integral part in increasing value of the lodge and the experience it may offer to future ecotourists.

The itinerary

The most dynamic aspect to the various models for entomological ecotourism is the itinerary. Just as different as the P-I model is from the OS/OP model, the RA model continues to deviate from conventional ecotourism itineraries. Unlike most general ecotours, the attraction of RA ecotours is almost exclusively concentrated on the research and citizen science aspect of the trip. Although this still involves traditional ecotour activities like hiking, photographing, and observing nature, the basic form of the itinerary is almost in complete contrast to the traditional ecotour. Whereas traditional ecotours come with a pre-planned itinerary on part of the tour operator and leader, it is the participant, or research associate, that dictates his or her daily schedule during the RA tour. Once at a particular locality or study site, the individual goals of each researcher or research team vary to the point that it is actually preferable to all involved to refrain from any planned activities (short of meeting for mealtimes). This flexible approach to daily activities puts further emphasis on the proper selection of lodging and/or study site. A diversity of trails is essential that allow group members of varying interests, as well as hiking abilities, to conduct adequate research. Quality of the forest, ease of navigation, and level of trail maintenance play significant roles.

Not only is the daily itinerary much simpler than other ecotours, so is the overall trip itinerary. Because most researchers are intent on thoroughly examining a particular habitat, or aim to meticulously catalogue and index the insect biodiversity of an area, it is important to spend multiple days in one location. Generally, the expeditions in these RA model case studies lasted from 10 days to two weeks with at most three separate
localities chosen (except in the case of Madagascar) (Table 2-2). At each locality, at least four nights were allotted to allow sufficient time to set up various research methods for data collection. In the case of the highly successful Pico Bonito expeditions, the entire nine days were dedicated to research at the Pico Bonito study site, suggesting that it is best to maximize the stay at any one site when possible. Nevertheless, there are other cases in which a particular area is included in the itinerary as more of a transitional area (i.e., stopover point) between two other highly productive localities, and a shorter visit is more appropriate (e.g., Ecuador: Loja and Zamora, 2008, 2009).

Ultimately, there must be a balance between satisfying research and data collection goals with the duration of each site visit during the course of the entire expedition.

**Education**

The role of education in the RA model differs significantly from other ecotourism models. This is largely the result of the contrasting itinerary to conventional ecotourism. With individual researchers on separate agendas during the day, field interpretation is very limited. Furthermore, many researchers are also engaged in nighttime research, as this is perhaps the most productive time of day for Coleopterists and moth-specializing Lepidopterists. Of those researchers not still in the field, the evening is often the only time during the day to record field notes, label specimens, or download photos and videos before another full day of independent field exploration. This is not to say that education is entirely absent in the RA model – only that the more customary education/interpretation flow from leader to participant is comparatively different.

Education is an important product of the tour due to the findings and eventual publications, lectures, and professional seminars that result from the data collected during the ecotour. In addition, there is a flow of information from participants to local
guides, whom often accompany field researchers to learn of new field techniques and to take advantage of many years of experience in the field these ecotourists have acquired (Figure 2-17). Due to their specialist nature, these participants may be some of the most knowledgable experts in the world on a particular taxa of insect, with much to share. The guides benefit greatly by increasing their knowledge base, which is then extended to future ecotourists, enhancing the ecotourism experience for everyone involved.

**Leadership styles**

The overall simplicity of the RA ecotour continues with the role of the trip leader. Fundamentally, the role is the same as that of the leader on any ecotourism expedition – to keep the group safe, informed, on schedule, comfortable, and in a condition that enables them to return safely home afterward the trip is finished. From field interpretation, to daily briefings of schedules, to managing expectations on daily activities, and coordinating numerous transfers from lodges to trails, from lodge to lodge, and so on. Because of the simplified itinerary, often involving only one or two destinations during the course of the trip, as well as the lessened emphasis on field interpretation, the leader’s role eases after the first day or two of the expedition. After managing initial expectations and briefing the group on general information and procedures, such as meal times, proper trail familiarization, and research etiquette among group members, most of the remaining responsibility comes in the form of monitoring for individual safety and assisting with research methods when needed. Overall, this is a very hands-off leadership approach, not unlike that exhibited in the OS/OP model. Just as individual expectations and goals varied during the OS/OP
model, so too do those of research associates in the RA model. Over-coordination of group activities leads to universal dissatisfaction among researchers.

Issues of safety and general wilderness acuity are less prominent in RA ecotours, largely due to the level of experience most participants bring with them on the tour. Researchers that routinely joined these RA ecotours were generally more independent and conscientious about their abilities and surroundings. However, this is certainly no solid rule, as exceptions have proven to demand quick and decisive action on part of trip leaders. Although the general atmosphere of the trip is more relaxed for the trip leader, the role remains to be critical, necessitating the same caliber of leadership as other ecotour models.

The most important role that the trip leader plays is that of the Principal Investigator of any research in which the research associates are engaged. While certain researchers may have more concentrated areas of study than that in which the leader/Principal Investigator has been scientifically trained, the idea is to have the research team complement each other for the purpose of gathering as much high quality data from the field as possible, in accordance with the overall project. For example, a species inventory of insect biodiversity may be led by a general entomologist, with a team of research associates with varied interests in specific orders of insects, such as Lepidoptera or Hymenoptera. The key thing is that the leader facilitates the collaboration of the group, so that data become a cumulative report under the singular project title.

The variety of countries and individual localities in these case study trials required many more leaders than the previous models. For each country, there was a different
leader. Leaders were chosen based on their experience in the project goals, as well as with the general region. As detailed in the upcoming Permits section, the leader is responsible for a unique set of responsibilities. As a result, high caliber scientists must be carefully chosen to ultimately reflect the quality of not only the trip, but the research being conducted, too. Going back to the successful Pico Bonito example of the RA ecotour, the leaders were instrumental in the overall success of these expeditions.

Over the course of the six separate trials, three scientific leaders contributed greatly to the smooth operation of the trip itself, as well as facilitating the research project before, during, and after the expedition. Dr. Jacqueline Y. Miller, however, represented the primary scientist and Principal Investigator for all six expeditions due to the critical linkage with the overall scientific investigation. Acting as Principal Investigator and Scientific Leader for five of these expeditions, she also was integral in obtaining the necessary permits for conducting this research. As required by most scientific permits, she was also responsible for reporting findings after the expeditions were completed. This example illustrates the fact that while the role of the leader during the actual expedition may not assume the same responsibilities as the leader in other ecotour models, new challenges present themselves with the RA model, primarily being the permitting process, which will be addressed in the following section.

**Permits and the RA model.** A great deal of scientific research, especially when measuring the biodiversity of insects, or the life histories of a particular group of insects, requires that specimens be collected. This almost always requires a permit to be attained that allows the researcher(s) to collect specimens needed to accurately complete their study. This is a critical reason for such participant selectivity on part of
the trip leader. In the case of these RA trips, the trip leader is also the Principal Investigator of the research project, which means that they are responsible for not only their actions, but the actions of the entire research team. It is the PI that must outline the scope of the project, along with specific goals and expected outcomes in order to apply and eventually receive the scientific permit. This step can be a major roadblock in the evolution of the RA model of entomological ecotourism. However, this scenario also serves to authenticate the ecotourism experience, which has been a key theme to the successes of entomological ecotourism in this dissertation. With proper collaboration between educational institutions, such as Universities and Museums, the ecotourism industry has no reason to be repelled by the specialist nature of this tour model and the corresponding permitting bureaucracy. Tour operators need not have the expertise in receiving permits in order to offer entomological ecotours, only the ability to identify and work with potential scientific leaders.

**Marketing the P-I model**

**Trip planning.** Planning and marketing the RA model takes a rather different approach than the previous two examples. This is primarily because the ideal participant pool is not infinite, as it is with other forms of entomological ecotourism. For other models, the more people that join these unique expeditions, the more people are engaged in a unique experience with novel educational opportunities. This ultimately creates a more informed society with stronger environmental ethics. However, not only is the general public relatively un-intrigued by the thought of conducting their own insect-based research in the wilderness, with quality of accommodations and food put on the backburner for the sake of emphasizing the quality of the study site, but also the institution and trip leader do not want just anyone with any level of experience as part of
the research team. For this reason, trip planning and marketing efforts must manage expectations directly through the content in marketing materials, as well as how the trip is marketed. The following sections will detail the various components of the RA model that not only ensure that minimum group sizes are reached, but that these groups are composed of experienced research associates that add to the collective aptitude of the group.

**Trip cost.** The trip cost for RA ecotours is just as critical to their success as any ecotour model. Although trip cost was not manipulated in order to select for more experienced participants, it did have bearing on the level of trip participation. In line with previous entomological ecotour models, costs for the RA tour model were kept low in order to make the trip accessible to interested researchers, ideally taking cost out of the equation for wanting to join or not. One of the benefits to the RA model and the importance placed on location, rather than deluxe accommodations and meals, is that costs of the trip are often significantly lower. In addition, the need for constant transportation services, integral in other ecotours, is not necessary, thus further reducing costs. With lodging, meals, and transportation often accounting for the majority of trip costs, minimizing these figures significantly reduces overall trip costs. This greatly offsets the added costs due to the much smaller group sizes typical of RA tours. Even with the smaller group size, which adds to the per-person cost, RA tours have proven to cost less on a per-day basis than either the OS/OP or P-I model ecotours (Table 2-3). This makes them much more marketable to a wider variety of audiences. This, in turn, enables a greater selection of potential markets in which to advertise, with the intention of having the best candidates for participating in scientific
research ultimately join the expedition, not just the wealthiest. The more difficult task of selecting distribution methods for the brochure will be detailed later in this RA model section.

**Duration.** The duration of an RA trip is relatively flexible, with the biggest determinant being that an appropriate amount of time has been allotted to the research being conducted. The vast majority of RA trips in this study were centered around insect biodiversity surveys. These are designed to be efficient yet comprehensive measures of insect richness and diversity in concentrated areas. Thus, the minimum time needed is versatile. As stated previously, minimum time in any area during the course of these trials was set at three to four days. However, as the trials in trip design progressed, longer periods in one location proved more favorable to research associate participants and the model was adapted. Two regimes surfaced throughout the five-year period to be best practices for duration of the RA tour model. The first was a weekend-to-weekend (i.e., Saturday to the following Sunday) time period that centered around one locality. This is best exemplified by the Pico Bonito RA tours. The second was a two-week (weekend to following weekend) expedition that focused on two to three localities. This is best exemplified by the Panama and Ecuador tours. It is not unreasonable for these RA expeditions to last longer, as was the case with the Madagascar ecotour in 2007 that spanned 21 days. It should be noted, however, that although the Madagascar entomological ecotour consisted of four participants, this was combined with a general ecotour that totaled 15 participants. In theory, the Madagascar tour was a hybrid between the P-I model and the RA model. After this initial trial, it was found that integrating the RA model with another ecotour model was relatively
commensal in terms of the impact on the general ecotourists, but with the dichotomy in group interests mixed and the polarity in group size, the entomological ecotourists would have been better served to be on an exclusively-planned RA expedition (i.e., without the more general tourists). Ultimately, with only one trial trip lasting longer than two weeks, it is difficult to comment on the likelihood that this would translate to success with other destinations.

**Pre-trip materials.** The goal of pre-trip materials is to inform registered participants of conditions they are likely to encounter and what gear to bring with them to make the trip as comfortable and productive as possible. The same goes for RA tours, with very little exceptions. Logically, one would think that a list of research gear would also be included, but in fact it is not for several reasons. The first reason deals with managing expectations. Since these trips are largely for independent research, it is expected that each researcher already knows what they typically need in the field to conduct research that they have been doing for a number of years. Anything more than a cursory list of materials or reminders may allude to a firmly set program directed by the trip leader. While direct assistance with the PI’s daily project agenda is often welcome, it is not expected. Essentially, if the participant does not know what to bring on the trip, it is likely that this is not the trip for them. The second reason is that an individual researcher’s interests or past experience may require a completely different set of materials that is either unknown to, or unused by others in the field. Guessing what type of forceps they prefer is unnecessary when preparing a pre-trip packing list. Only one participant out of 147 participants asked specifically for a list of research equipment and gear over the five-year trial period. Additional information is provided,
as with pre-trip materials for all tour models, but most often the participants on RA tours are the most experienced with field conditions in wilderness environments.

**Hands-on marketing and brochure design**

Managing expectations has been one of the recurring themes in this paper, and this section will not see the last of it. Although the entomological community rigorously recruits young people with a passion for science and insects, the vast majority of research associates are more experienced and of a more venerable generation. For this reason, a hardcopy brochure, opposed to electronic media like Facebook or email newsletters, is vital for marketing purposes. In line with the P-I model, rare or exceptional species of interest should be used cautiously, but not left out of the brochure completely. For example, if the trip is designed for a survey of Lepidoptera biodiversity in Honduras, butterflies in the genus *Agrias* should be used sparingly as color pictures in the brochure. Although it will excite topical Lepidoptera researchers, it is relatively rare. Nevertheless, these have been recorded for parts of Honduras, particularly Pico Bonito National Park. Just as with the P-I model, the chance of seeing one of these in the wild may persuade a well-traveled Lepidopterist to join, who may have a particular interest in these rare Nymphalid butterflies. Apart from being aesthetic and portraying the potential of a trip, the brochure (both hard copy and electronic form) needs to have several components that are universal.

Many tour operators approach brochures and trip announcements very differently. Some may distribute print catalogues that contain many trips with an insert designed to request complete brochures for specific trips mentioned within. Others may be a minimalist postcard that briefly describes one particular trip, with what is known as a Call to Action, by directing the viewer to a website for further details. However, the
method chosen for these RA trips is to provide the potential participant with a self-contained brochure that includes everything needed to 1) Be informed, 2) Make a decision, and 3) Register immediately for a trip. Other methods of brochure distribution and design were involved in the initial stages of these trial trips (specifically the two mentioned above, both at the outset of this study in 2007 and 2008), but this latest self-contained version produced a higher level of feedback from potential participants, with both the number of trips per year and the number of participants on each trip increasing dramatically (Table 2-2). Sections of the brochure included the following: 1) Title page, 2) Introduction, 3) Leader Biography, 4) Itinerary, 5) Terms and conditions, and 6) Registration form. Table 2-4 details the functions of each component.

**Marketing and material distribution.** The goal of trip marketing is to get interested people informed about the trip. If the main vehicle for information is a hard-copy brochure, then it needs to get into the hands of those who are most likely to join. With traditional ecotourism trips, as well as the previous entomological ecotourism models (OS/OP, P-I and S-I), the audience is relatively wide and general. Those who are interested in nature, have the motivation to travel, and are physically able to travel comprise the majority of the market. However, with the RA model of entomological ecotourism, the market is naturally smaller due to the nature of the trip, but also is selectively smaller due to the research-based itinerary. Not everyone is a potential researcher. Therefore, the population of marketable individuals is quite different than for the other ecotour models outlined thus far. Fortunately, the small minimum group size, as well as the niche class of trip, makes marketing somewhat easier than most ecotours. Professional societies, University colleagues, and word of mouth comprise
the sources for the vast majority of trip registrants. Mailing lists may be purchased from many of these types of organizations, which allows the information to be given directly to those most interested in such an ecotour model. An important thing to keep in mind is that the more targeted, specific, and accurate the marketing population is to the overall style of trip offered, the greater proportion of those who receive the brochure will ultimately register. A vital outcome is the prevalence of repeat participants.

**A note on repeat participants.** Frequent participation by an individual, family, or group is highly desirable for any and all ecotour models. A combination of proper trip planning and marketing is vital in attracting first-time travelers with a particular tour model or tour operator, and successful leadership and execution of the trip is what yields repeat participants. This is why materials like pre-trip information packets and reading lists not only contribute to more informed, comfortable, and content participants on a particular trip, but also serve to retain these participants as repeat travelers. When a participant becomes familiar with a certain style of operation and leadership, expectations are solidified, increasing the likelihood that they will join another tour.

Repeat participation in tours is a tremendous way to promote cross-model participation. For example, someone who has decided to join an OS/OP modeled ecotour, such as the Monarch migration tour, is a prime candidate to join the P-I model tour. By fulfilling and often surpassing expectations as to what an entomological ecotour can and should be, they are more likely to be interested in other types of entomological ecotours. This goes both ways. For instance, when someone who may be more of a birdwatcher is exposed to the diverse and fascinating world of tropical
entomology on a P-I tour may find it much more feasible to join an OS/OP tour now that they have been exposed to entomological ecotourism.

From a marketing perspective, previous trip participants represent an ideal group to which to advertise. Whether the newest trip to be advertised is the same ecotour model or different, previous participants should be prioritized in terms of advertising new programs.

**Future possibilities for the RA model**

The total of future possibilities using the RA model is great, with many variations possible, especially as one considers new localities and/or study organisms. While the case studies mentioned above concentrate on Lepidoptera and Coleoptera, research on all orders of insects is as important as it is feasible when using the RA model. Similarly, the range of countries and individual localities within each country is extensive. With the proper management of expectations and planning on part of the trip leader, research on insects could take place in an area as remote as Antarctica, should a group of Collembolists want to conduct research there. However, there are specific areas of the world where expansion of the program is most suitable. Tropical areas, which hold most of the world’s biodiversity, are not only the least understood, but also the most likely to generate novel findings. New programs in remote areas have some of the greatest potential for finding new species, behaviors, and records. Stated previously, it is the alignment with qualified and interested faculty from Universities and Museums that help to drive the momentum for RA ecotours. While searching for new destinations may lead one to new scientific leaders, it also may be the case that the search for new scientific leaders leads one to new destinations.
Development of New Entomological Ecotourism Models

Until now, this Chapter has dealt with existing ways that insects are integrated into ecotourism. The list of opportunities is not complete, as there are still a number of ways that insects can be involved in ecotourism with novel approaches not yet experimented with by either this author or other individuals. This section will address future opportunities to expand upon in the world of entomological ecotourism. It is worth noting that many tourism opportunities exist that are either unpublished or otherwise unsearchable in ecotourism databases. The following models are detailed as novel and pioneering to the best of the author’s knowledge.

Entomological ecotourism student courses

Potentially associated with higher education institutions, this model is geared towards directly instructing students with interests in entomology, as part of a field study program. While courses do presently exist that solely concentrate on field-based entomology, this ecotourism-based course would combine basic entomology with ecotourism in order to prepare future generations of entomological ecotour leaders, planners, and guides. Taught on-location in ecotourism destinations, the tour itself would be a form of ecotourism, further supporting experience-based learning. Just as other models have subgenres, a Student Course model (SC model) would have variations in overall ecotour features. Subgenres would likely be targeted at different populations to optimize education and reach the desired goals of students. With the emergence of ecotourism as a bona fide discipline at the higher education level, there grows a need for new methods of instruction. It is the belief of this author that future SC model courses would greatly meet this need.
Guide training

Guide training is a topic to be dealt with more thoroughly in Chapter 3, but it is increasingly becoming a prerequisite to employment for naturalists and guides in ecotourism destinations. Designing entomological ecotours that educate present and future naturalist guides satisfies the mission of entomological ecotourism in a novel manner. By teaching the teachers, information and awareness is broadcasted in a much wider sense, allowing for information to flow from ecotour guides to ecotourists well after the guide training ecotour has been completed.

Chapter Conclusion

There is a sharp dichotomy in the presence of insects in ecotourism destinations versus the presence of insects in ecotourism itineraries. That is, although insects are ubiquitous in places with high ecotourism traffic, they are seldom utilized as ecotour features. However, this only highlights the tremendous potential and growth possibilities in what may be termed entomological ecotourism, where insects are not only integrated as a component of an ecotour, but as the focal point. Beginning with butterfly farming, as a direct and indirect ecotourism feature by both supplying insects to other tourism enterprises and acting as ecotourism destinations themselves, there is strong evidence that there is more than just a casual interest in exhibiting butterflies for tourism’s sake. From an ecotourism perspective, the variations on butterfly farming, with ranching and hybrid models appearing worldwide, they represent more than an opportunity for ecotourists to learn about, admire, or otherwise appreciate insects in the tourism realm. The fact is, these businesses provide critical income in a wide array of economic climates. As production ranges from a few individual butterflies per week to a few thousand, the income generated can support communities in developed nations as
well as remote villages in developing nations. The role of conservation is two-sided in these scenarios. While ecotourists are educated on conservation topics, ranging from Lepidoptera biodiversity to interactions between insects and plant communities, locals and farm workers also benefit from increased environmental literacy. This combination serves the global community in a holistically positive way.

Entomological ecotourism is more than just an attraction, it is an ecotourism category. In fact, because of the expansiveness and potential, entomological ecotourism can be further divided into a number of distinct models that vary in the way they are planned, marketed, and led. Taking different approaches in how insects are featured, these models represent discrete itineraries that most often take the form of a multi-day international expedition, as detailed in their respective examples, including the Monarch butterfly migration (One Species/One Phenomenon, OS/OP model), butterfly watching in Costa Rica (Paired-Interest and Single-Interest, P-I and S-I models), and Lepidoptera research in Honduras (Research Associate, RA model). However, these examples demonstrate that entomological tourism is not restricted to international ecotourism, as national ecotourists often play a significant role in total visitation. Furthermore, these models are relatively unrestricted in terms of focus. There are numerous other orders of insects and localities around the world that are now positioned to play essential roles in the expansion of entomological ecotourism. As these tour models expand in coverage with new species, phenomena, diversity hotspots, and areas with critical research needs, entirely new models will be developed, further expanding the role of insects in the ecotour.
Figure 2-1. Percentage of butterflies sold in each life stage at Shady Oaks Butterfly Farm per month.
Figure 2-2. Examples of various types of breeding cages used at butterfly farming operations. Host plants are generally enclosed within screened cages with adult butterflies present for egg laying to occur directly on the host plant. Photos courtesy of J. Court Whelan.
Figure 2-3. Larval feeding boxes are organized and filled with clippings of host plants for larvae to feed upon. Butterflies are allowed to pupate directly in the containers and then promptly removed. Photo courtesy of J. Court Whelan.
Figure 2-4. Pupal eclosion chambers are found at both farms and exhibits, allowing butterflies to emerge as fully mature adults in a controlled setting. Photos courtesy of J. Court Whelan.
Butterfly larvae are often allowed to feed on naturally occurring or planted host plants with the hybrid EBN model. This reduces the overhead costs of greenhouses, while still providing protection against predators, parasites, and parasitoids through the use of protective cloth bags, which also function to retain those larvae prone to wander off the host plant. Photos courtesy of J. Court Whelan.
Figure 2-6. Total number of ecotourists joining the OS/OP entomological ecotour model during the five-year study period.

Figure 2-7. Levels of trip participation between two Mexico Monarch trips in 2011. Trip 1 represents the typical Friday to Tuesday duration and Trip 2 represents the new Tuesday to Saturday trip duration.
Figure 2-8. Levels of trip participation on three P-I model trips to Costa Rica.

Figure 2-9. There is a negative correlation between the need for modern conveniences at ecolodges and the number or quality of wildlife experiences.
Figure 2-10. Overall visitor satisfaction is at a maximum between two thresholds of quality. Below a certain threshold, satisfaction sharply drops. This, too, is seen on the opposite end of the spectrum: when the rustic qualities are too few, satisfaction decreases as well, due to loss of authenticity.

Figure 2-11. The Resplendent Quetzal (*Pharomachrus mocinno*) is perhaps the most sought-after bird by birdwatchers on an ecotour to Costa Rica. A member of the Trogon family, they are relatively common in the cloudforests of Monteverde. Photo courtesy of Geoff Gallice.
Figure 2-12. Light sheets may be hung in any environment to attract nocturnal insects. By hanging a bright light in front of the sheet, the system acts as one large light source that attracts insects from all directions. Lepidoptera, Coleoptera, Neuroptera, Hymenoptera, and Homoptera are likely to be seen at a well-placed light sheet. Photo courtesy of J. Court Whelan.
Figure 2-13. There is a negative correlation between the length and variety of daytime activities and the appropriate length and detail of nightly lectures while on the P-I ecotour. Generally, with a longer more busy day, the less participants are willing and able to digest detailed information presented to them in lecture format.
Figure 2-14. There is a positive feedback loop between field interpretation and group cohesiveness. Field interpretation promotes group cohesiveness, and group cohesiveness permits field interpretation.

Table 2-1. Components necessary in pre-trip information packets sent to registered participants.

<table>
<thead>
<tr>
<th>Sections</th>
<th>Key Components</th>
</tr>
</thead>
<tbody>
<tr>
<td>Documents</td>
<td>Passport and Visa Requirements</td>
</tr>
<tr>
<td>Travel Health</td>
<td>Immunizations and Health Risks</td>
</tr>
<tr>
<td>Meeting the Group</td>
<td>Arrival and Meeting Instructions</td>
</tr>
<tr>
<td>Flight Recommendations</td>
<td>Full Itinerary for Recommended Flight Itinerary</td>
</tr>
<tr>
<td>What to Pack</td>
<td>Complete Packing List</td>
</tr>
<tr>
<td>Money and Currency</td>
<td>Suggestions on Amount to Bring and How to Exchange Money</td>
</tr>
<tr>
<td>Exchange</td>
<td>Money</td>
</tr>
<tr>
<td>Weather and Climate</td>
<td>Expectations and Clothing Recommendations</td>
</tr>
<tr>
<td>Electricity</td>
<td>Types of Plugs, Voltage, and Recommended Adapters</td>
</tr>
<tr>
<td>Cameras</td>
<td>Key Recommendations for Subject of Tour</td>
</tr>
<tr>
<td>Contact Information</td>
<td>Emergency Contact for Participants and their Families</td>
</tr>
<tr>
<td>Reading Lists</td>
<td>Recommendations on Field Guides and Books</td>
</tr>
<tr>
<td>Phones and Email</td>
<td>How to Call Home and Presence of Email</td>
</tr>
<tr>
<td></td>
<td>Access</td>
</tr>
</tbody>
</table>
Figure 2-15. A butterfly bait trap is set along a road in Panama. The bait is often a syrupy combination of bananas and sugar, or in some cases, a mixture of rotten fish or shrimp. Photo courtesy of Geoff Gallice.
Figure 2-16. An ecotourist admires the variety of nocturnal insects attracted to a single light bulb in Pico Bonito National Park, Honduras. Photo courtesy of J. Court Whelan.
<table>
<thead>
<tr>
<th>Year</th>
<th>Total New Localities</th>
<th>Total Trip Participants</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Ecuador</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Madagascar</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>2008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ecuador</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>2009</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td>Ecuador/Loja</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Ecuador/Misahualli</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>2010</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mexico/Cedros Island</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Ecuador/Loja</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Ecuador/Cuyabeno</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Honduras/May</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Honduras/June</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>Honduras/July</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Honduras/August</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>2011</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>Ecuador</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Honduras/May</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Honduras/June</td>
<td>0</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 2-17. The flow of information in the Research Associate model is wide and varied. This serves to increase the value of ecotourism activities, as many stakeholders see direct benefits through increased knowledge and resulting exposure to numerous audiences.

Table 2-3. Average daily costs for each of the tour models outlined, the One Species/One Phenomenon, Paired-Interests, and Research Associate models.

<table>
<thead>
<tr>
<th>Tour Model</th>
<th>Average Daily Cost</th>
</tr>
</thead>
<tbody>
<tr>
<td>OS/OP</td>
<td>$256.00</td>
</tr>
<tr>
<td>P-I</td>
<td>$220.19</td>
</tr>
<tr>
<td>RA</td>
<td>$165.51</td>
</tr>
</tbody>
</table>
Table 2-4. Typical components of an entomological ecotourism trip brochure and the individual contents for each section.

<table>
<thead>
<tr>
<th>Components</th>
<th>Individual Contents</th>
</tr>
</thead>
<tbody>
<tr>
<td>Title Page</td>
<td>Contains title of trip, dates of trip, and leader name</td>
</tr>
<tr>
<td>Introduction</td>
<td>Details the theme or mood of the trip.</td>
</tr>
<tr>
<td></td>
<td>Expands on the trip title with descriptive goals and expectations</td>
</tr>
<tr>
<td>Leader Biography</td>
<td>Short biography on leader expertise and qualifications</td>
</tr>
<tr>
<td>Itinerary</td>
<td>Provides day-to-day information on schedule and activities</td>
</tr>
<tr>
<td>Terms and Conditions</td>
<td>Addresses what is and what is not included in the trip cost, as well as responsibility of the participant while on the expedition</td>
</tr>
<tr>
<td>Registration Form</td>
<td>Provides registration instructions and space for personal contact information to be used by tour operator</td>
</tr>
</tbody>
</table>
CHAPTER 3
GUIDING FOR ENTOMOLOGICAL ECOTOURISM

Ecotourism guides are the ambassadors to their region, country, or natural area. They are also the educators and environmental interpreters to groups of visiting ecotourists. Throughout the ecotour, whether the tour lasts for a day or for two weeks, tourists often interact more frequently with naturalist guides than with other group members, and sometimes even their own family or travel companions. In theory and in practice, ecotourism guides are supremely important to the overall experience of an ecotour.

As we saw in Chapter 2, guides may come in many forms. They may be scientific leaders, being from the same country as the visiting ecotourists and traveling with the group. Or, they may be local naturalist guides, living and inhabiting the host country and welcoming the group upon arrival. Because all types of guides interact heavily with ecotourists, it is important that they be knowledgeable about the areas visited and the intended foci of the tour. In addition, ecotourism guides serve as environmental stewards, instilling conservation values into their ecotour participants (Black et al. 2001). Pastorelli (2003) fashioned a comprehensive list of responsibilities and roles of the tour guide, stating that they have the role of information provider, social facilitator, cultural host, motivator of conservation values, interpreter of the natural and cultural environment, people mover, safety officer, ambassador for one’s country, teacher, public relations representative or company representative, entertainer, problem solver, confidant, and counselor. To assume these roles all at the same time is difficult enough with a perfectly homogenous group of ecotourists, but even the “typical” tourist group is composed of people with differing expectations and behaviors (Rabotic 2009). A single
ecotour has the potential to change the world for an individual, as well as their future role in it. While individual inspiration very much depends on the overall experience, much is attributable to how the ecotourism guide contextualizes and emphasizes an experience.

A key motivating factor for writing this dissertation is that there exists precious little literature on insects in ecotourism, and the same can be said about published information on the roles of tourist guides in entomological ecotourism. However, one particular publication has made some inroads and has reported findings on the acceptance of invertebrates by ecotourists. Huntly et al. (2005) conducted surveys of both ecotourists and ecotour guides to find several generalities of interest. First, there is a common lack of regard towards insects on most ecotour itineraries. Taking place in South Africa, Huntly et al. (2005) found that only 10% of ecotour guides included any information about invertebrates on their guided tours. However, when asked about the possibility of integrating invertebrate education, 80% of guides were willing to include insects as a feature in their tour itinerary. So, if they are willing, why had they not integrated them already? The study also found that there were common reasons among the guides for why they fail to include information on insects during their tours. The main cause was that the guides did not know how else to focus on invertebrates other than their negative qualities (i.e., disease transmission, stings, agricultural problems, etc.). The guides were generally not knowledgeable about the biology of invertebrates, and were equally unaware of ecotourists’ interests in invertebrate exposure and interpretation. Huntly et al. (2005) found that coupled with the desire to include insects, on the part of the guides, there was also significant interest in learning
about invertebrates on the part of the visitors. In fact, when asked whether invertebrates should be integrated into the ecotour, 95% of visitors indicated that they would be interested in observing and learning about insects on a South African safari. Furthermore, the majority of guides and tourists agreed that indigenous knowledge of invertebrates would be highly favorable additions to any ecotour. Again, though, the overwhelming reason for omitting invertebrate interpretation came back as being the result of a lack of knowledge. Nearly all guides surveyed in this study said they were embarrassed when they did not know answers to questions about invertebrates and wish that they had more training (Huntly et al. 2005).

**Integrating Insects in the General Ecotour**

The topic of how insects may be integrated into entomological ecotours was covered extensively in Chapter 2, which focused on defining entomological ecotourism models. This Chapter will complement Chapter 2 by providing specific techniques and information on integrating insects into any ecotour, not just those designed to have strong entomological foci. This information is intended to serve as generalized guide training tools that are applicable to most ecotourism destinations and provide the necessary knowledge for ecotour guides to confidently discuss insect-related topics while on tour. This Chapter will proceed with a section on the role of guides in ecotourism before continuing with individual accounts, descriptions, and interpretive suggestions for specific insects that are likely to be encountered during an ecotour. Finally, with three general topics of entomology will be covered, as a way to integrate more complex information into a topical guide training framework.
Entomological Guide Training

Education on insects and entomology is available worldwide and comes in a broad range of levels, from structured entomology degrees at colleges and universities, to informal presentations at special interest clubs. The opportunity for the ecotourist to learn about insects while on guided ecotours provides a unique way to understand a detailed topic through experiential learning. However, in order for the ecotourist to learn, a teacher must be present to convey useful, interesting, and accurate information about the world of entomology. Ecotourism guides are the natural focus on which to target efforts, in order to improve the awareness, appreciation, and general regard for insects around the world. This serves the inherent goal of promoting entomology and insect conservation, but also functions to raise awareness about larger conservation and biodiversity issues.

Realistically speaking, it is unreasonable to expect every naturalist guide to have the same knowledge of insects as that of a college graduate studying biology or entomology. Although this training would thoroughly prepare one for the range of topics and questions that could arise, when discussing insects on an ecotour, specific training materials have the ability to provide a solid foundation, if targeted appropriately. For instance, an African safari ecotour is likely to elicit a certain scope and range of questions. The same goes for an ecotour in the Neotropics or the Australasian region. While broader topics, such as the evolutionary origin of winged insects, have their place and are indeed useful to know, more directed topics, such as how a leaf-cutter ant colony is formed or how many species of Birdwing Butterflies exist today, are more useful on a multi-dimensional, or general ecotour.
Complete guide training courses exist at universities and research centers in some countries, but these are often extremely costly and time consuming, especially for guides who must maintain full-time guiding jobs in order to support themselves and their families (R. Odio, pers. comm.). While these comprehensive courses are valuable and go into considerable detail on a multitude of subjects, including plants, mammals, reptiles, birds, arthropods, and even culture and politics, existing naturalist guides may not want or need to retake full courses in order to sharpen their entomological knowledge. In addition, only a small percentage of countries in the world offer such guide-training courses. A stand-alone course designed to prepare naturalist guides for integrating insects in the ecotour would be more efficient and less costly in both time and money. This would be more appealing and more marketable to the majority of existing naturalist guides in countries around the world.

Guide Training Framework

Beginning in 2007, 45 separate ecotours were planned and led by this researcher for the sake of experimenting with entomological ecotour design. Chapter 2 detailed the various conclusions made on the structuring of entomo-centric tours, giving rise to discreet frameworks, such as the One Species/One Phenomenon, Paired-Interest, and Research Associate models. However, these ecotours also served as case studies for the role of guides on ecotours. One of the immediate conclusions was that entomological ecotourism does not need to be confined to specially designed entomological ecotours. That is, insects need not be the primary focus of a tour in order to have insects involved. This unique genre of ecotourism can happen anywhere, at anytime, and on any ecotour.
The vast majority of existing ecotourism programs and companies plan and lead what would be considered general ecotours. They have no specific focus (e.g., birds or butterflies), but instead attempt to integrate all wildlife as much as possible, while also emphasizing scenery and perhaps even culture as well. The focus is primarily on the country being visited, from a somewhat holistic approach. Photography, interpretation, and environmental interaction are stressed as tour components and foci. These comprehensive ecotours appeal to a wide audience and are often more diversified in terms of ecotourist demographics. Individuals and families that participate in ecotourism (in contrast to groups of ecotours) are more often general ecotourists. Although there is no statistic at the present time that accurately estimates the market share of individual travelers versus groups in today’s ecotourism arena, personal experience suggests that the total number of travelers per year is relatively evenly split between individual travel and group travel. General ecotourism clearly represents a major share of all ecotourism.

Roles of Guides

With both general and entomological ecotourism, guides may take one of four forms which are based on the structure of the ecotourism group. In these cases, a group may represent an individual or a multi-person group.

The first type of guide is perhaps the most familiar to anyone who has ever engaged in an ecotour – the Park Guide. Park Guides are stationed at individual natural areas or parks and accompany individuals, families, or large groups of visiting ecotourists. Because they are stationed permanently at a particular reserve or park, they have a detailed knowledge of the flora and fauna found within the boundaries of the natural area. They are often available for hire upon reaching the entrance of a park.
and will guide ecotourists through the area, spotting wildlife, interpreting nature, and leading the ecotourists on the trails, paying particular attention to the specific interests of the group. In some cases, these guides may be stationed at a particular lodge, instead of at the park, accompanying lodge guests as the trained park guide for a particular natural area.

The second type of guide is an Ecotour Guide. These guides are present for the entire duration of an ecotour and will accompany an individual or family, but most often join organized tour groups of ecotourists, due to the costs associated with having a private guide throughout the course of a trip (a group may split the cost, making it affordable to have a private guide). With a typical ecotour lasting from several days to several weeks, the total amount of time spent with the group is much different from that of the park guide. Typically meeting the inbound group upon arrival at the airport, the Ecotour Guide has an extensive knowledge about all areas to be visited during the course of the tour. Since Ecotour Guides remain with the group for multiple days, there are more opportunities for educational talks throughout the trip. Time spent driving between destinations and mealtimes provide options to continue discussions on natural history that may have originated in the field earlier in the day or earlier in the trip. This extra time is opportune for the Ecotour Guide to preface certain experiences and provide context prior to arrival at a particular destination (i.e., reserve, geologic formation, museum, etc.). This extra time may also be used to summarize the day’s events, thus recounting the various sights, sounds, and highlights from individual days.

The third type of guide is the Tour Escort. This person is generally an inbound traveler from the ecotourists’ home country, but may also be from the host country and
meet the individual or group upon arrival. However, unlike the Ecotour Guide, whose primary responsibility is to spot wildlife and educate the group while traveling, the Tour Escort’s role is to coordinate logistical arrangements and ensure a smoothly running ecotour for the entire trip. This position is more commonly coupled with one of the other guide types, but the importance of their logistical expertise should not be overlooked.

In many cases, the previously described Ecotour Guide may also function as the Tour Escort. Although it is uncommon for an individual to be assigned solely to the Tour Escort position, larger groups (i.e., over 40 passengers) often need multiple individuals to help with the trip coordination. For these groups, a dedicated Tour Escort can be invaluable. This position is also integral on expeditions that require numerous flights between locations, making travel days particularly complicated for the group.

The fourth type of guide is the Expert. This position was detailed extensively in Chapter 2 and is a favored type of tour leader for group trips with specific tour foci. However, this leadership position works equally well with general ecotourism, as it does with entomological ecotourism. The expert often has extensive education at the University level about the country or subject of the tour and functions primarily to share information through field interpretation and/or evening discussions. The Expert differs from the other tour guides in that he or she often has conducted higher-level research in the country or region where the tour takes place. Although the Expert may be from the host country, they most often are inbound travelers with the rest of the ecotourism group, being from the same country as the group.

It is evident that each of the four types of guides in ecotourism has its advantages and disadvantages (Table 3-1), as well as some overlap in responsibilities (Figure 3-1).
Ideally, ecotourism guides assume at least one of these roles, for the qualities each brings to the tour are vital, and it is rare that the cost of four separate guides can be justified for a typical trip. Figure 3-1 shows the relationship between the four guide roles, with potential overlap in responsibilities denoted by overlap in the diagram. The only two roles that cannot, in theory, be filled by the same individual are those of the Park Guide and Escort. Because the Park Guide does not travel with the ecotour from place to place, he or she cannot function as the coordinator of trip logistics. Similarly, because a Tour Escort is dedicated to trip planning and logistics, they do not have the same intimate knowledge of specific ecotourism areas, such as parks, preserves, and reserves. These are mutually exclusive roles. If we examine the diagram further and assume that only the upper layer, in any instance of overlap, can assume the other’s role (in addition to their own), we can make further inferences. For example, an Ecotour Guide can function as both a Tour Escort and Park Guide, having both extensive knowledge of the local area, and also able to handle logistical arrangements during the ecotour. However, only the Expert has the ability to assume all roles, for it is the level of education and field experience that is the limiting factor in fulfilling all potential guiding roles.

It is not the aim of this Chapter, or of this dissertation, to create international experts out of all guides. Park Guides have their roles and responsibilities and function as essential components to many ecotour models. The same goes for Ecotour Guides and Tour Escorts. Instead, the breakdown of guides into these four roles and titles is to better understand the relationships that guides have with their ecotour clients. Knowing where the possible opportunities for nature interpretation lie provides for a better
framework on how to best prepare guides for integrating insects into their ecotourism programs. For the rest of this Chapter, we will be directing guide training information specifically for Park Guides and Ecotour Guides. These are the primary ambassadors to a particular country or natural area and take the commanding role as tour leaders when nature interpretation opportunities present themselves. Because of their respective roles, as outlined previously, each will benefit from gaining both general and specific knowledge concerning the field of entomology.

**Insect Exhibits**

The idea of entomological ecotourism exhibits was introduced in Chapter 2, with descriptions of butterfly farms and butterfly ranches acting as ecotourism attractions. By starting with a working farm, the existing infrastructure, such as various breeding houses and nurseries, serves to then incorporate guided tours and ecotourism components. However, a growing trend in tropical countries around the world is the creation of insect exhibits that resemble working butterfly farms, but function solely for the purpose of onsite nature education and ecotourism. That is, the insects they breed and rear are not sold or shipped to dealers or other insect exhibits, but are used exclusively at the ecotourism destination. Generally, these exhibits are butterfly vivariums with native species of butterflies and plants, but in some cases, additional insects are reared that are of particular interest to general ecotourists, such as *Dynastes* beetles and Leaf-cutter Ants.

Having a breeding component with a butterfly vivarium not only creates a self-sustaining enterprise, but also functions as a unique educational tool used by visitors to learn about insect lifecycles and behaviors. For example, La Paz Waterfalls and Gardens, located in Alajuela, Costa Rica, chose to integrate their butterfly rearing
operation directly into their exhibit for the public to view and enjoy (Figure 3-4). Through interpretive signs and a very organized, yet unrestricted exhibit, ecotourists are able to view all life stages of tropical butterflies at La Paz. In addition, behaviors not often encountered in the wild, such as the formation of pupal cases, eclosion from pupa to adult, and even 1st instar larvae hatching from eggs, are displayed throughout the exhibit. Because of the cryptic nature of a butterfly's life cycle, exhibits like the one at La Paz are impressive, educational, and enjoyable to ecotourists.

Another type of insect exhibit is an insect collection. These may take one of many forms, such as insects being artistically mounted on natural vegetation, or simply arranged in columns in a wooden collection box. In contrast to the live insect exhibits, exemplified by vivariums, these collections are entirely composed of dead specimens that have been organized, curated, and displayed for the purposes of education, research, and in some cases, aesthetics. While the notion of boxes of dead insects may be pale and morbid when described on paper, in actuality such exhibits can be vibrant, exciting, and beautiful (Figure 3-5). Taking a more scientific approach to education and interpretation, visits to insect collections are appreciated by ecotourists due to their general reverence for education being one of the key tenets of ecotourism. Quality of the exhibit is paramount in the case of insect collections, as unintelligible organization or poor maintenance can turn a stimulating experience into one that is uninspiring and gloomy. A benchmark for a collection exhibit, Dr. Richard Whitten’s collection at Selvatura Canopy Park, in Monteverde, Costa Rica, is a spectacularly curated and arranged display of insects from around the world. Touted as the third largest private collection of insects in the world, most of the specimens were collected
from Monteverde and the surrounding area, where the collection is housed (Richard Whitten, pers. comm.). As a result, it represents a wonderful way to showcase insects found in the very same area that an ecotourist is visiting, while also highlighting the incredible diversity found elsewhere in the world, encouraging entomological ecotourism on a global level. Just as live exhibits allow ecotourists to witness insect behaviors up close, insect collections enable one to observe fascinating morphologies, color patterns, and textures at a close distance, all while being able to compare specimens side by side, as displayed.

Visiting an insect exhibit is one of the easiest ways to provide a general outline of entomology to a group of ecotourists. They provide opportunities to observe rare or uncommon behaviors, as well as uncommon species that may not be readily seen in the wild. They also allow for up-close viewing opportunities that awaken the scientist in everyone. Nevertheless, there is no substitute for observing a large *Morpho amathonte* Deyrolle fluttering and flashing its blue iridescence down a jungle trail, or observing one’s first trail of Leaf-cutter Ants marching through the forest. For this reason, naturalist guides should be aware that these exhibits are not the one and only point in the ecotour that insects should be integrated and highlighted. Instead, visits to such places serve to ignite interest and provide context to things seen at other points in the ecotour, both before and after the exhibit visit.

There are many valid avenues to take that promote entomology in ecotourism, ranging from informational kiosks at park entrances to full scale insect exhibits. From broad experience in many countries, the best area on which to focus initial efforts is with
the individuals that are responsible for most of the content in the general ecotour – the guides.

The remaining sections have been composed and arranged to represent initial guide-training tools. The text and dialogue contained in these sections is meant to be scientifically thorough, yet fluid and conversational. Highly translatable into various languages, these sections will serve as the text for an ensuing entomological ecotourism guide-training manual, to be completed shortly after the submission of this dissertation. Sample plates and pages from this future publication have been included at the end of the Chapter (Figure 3-2).

**Approaching the Topic of Entomology**

Insects are certainly smaller than most other animals encountered on a typical ecotour (e.g., mammals, birds, etc.). However, what they lack in size, they make up for in sheer numbers. This makes it especially easy to find not only the insects themselves, but also signs of their presence, which are virtually everywhere in nature.

Insects inhabit a unique cross-level position in the trophic pyramid and are linked in many ways to virtually every other life form (Figure 3-3). There are almost an infinite number of connections between insects and their environment. These connections may be direct predation, as even top carnivores and large mammals like Grizzly Bears are known to feast on moths in the Western United States. There are also numerous indirect connections. While higher carnivores may not all directly predate on insects, there are often only one or two degrees of separation between them and insects, with insects in many cases being the primary food source for the prey of higher carnivores. When smaller animals feed on insects, predators of these small animals are indirectly linked to insects as food sources.
Insects are much more than just food for other animals. They are ecosystem engineers that recycle nutrients, aerate soils, and decompose organic matter, serving to promote general ecosystem health. Many top biologists agree that if it were not for insect herbivory, plants could become dangerously hyper-abundant, leading to changes in global hydraulic cycles, dropping soil nutrient quantities, and even oxygen levels. There are numerous topics for a tour guide to discuss, in addition to general identification of the various insect species seen. A natural place to start is with identifying those insects most readily integrated into an ecotour.

Individual Accounts of Insects

An ecotour relies not only on accurate information, but pertinent information. On a typical ecotour, there are a number of predictable scenarios when insects may be integrated. While in the jungles of the Neotropics, the first arboreal termite nest, or glimpse of a *Morpho* butterfly, may be that opportunity. While on a safari in Africa, this first opportunity may take the form of a large dung beetle rolling a ball of elephant dung across the game trail. This is not to say that ecotourists would not enjoy learning about the diversity of houseflies in the area, if described in an engaging manner, but there are certain topics that present themselves on any ecotour. As we shall see, even signs of insect presence are enough to begin the dialogue on entomology. This makes the task of integrating insects into a guided ecotour flexible. The main point is that insect education can happen on any type of ecotour and in any area – the ecotour guide simply has to know what to look for and how to interpret it.

If insects are to be integrated into general ecotourism, the information presented must be interesting enough to balance out their relatively small size, so that their allure competes with that of the charismatic mega-fauna sought after in most ecotour
locations. For example, when tourists in Africa were surveyed on the potential for insects to be integrated into their tour, most agreed that it would be acceptable and interesting, but with the caveat that insects should come second to spotting the 'big five' mammals (i.e., Lion, Leopard, African Buffalo, Elephant, and Rhino) (Huntly et al. 2005). Fortunately, there are numerous instances in the insect world where bizarre appearances, unique interactions with other species, or general life cycles makes up for their small stature. Nevertheless, if insects are going to be accepted as another fascinating attraction to ecotourism destinations, the most charismatic insects should be highlighted as ambassadors to the insect world.

The following section provides detailed accounts of the most charismatic insects in the world, serving as prime targets for integration into general ecotourism. The information presented herein is designed to furnish guides with the knowledge and context needed to share pertinent and accurate information with their ecotour groups. At the end of each section are field-based techniques for locating each type of insect, based on experiences by this researcher, as well as research in the literature.

Based on my personal choices, I have selected the top 30 insects from around the world as instructional material for insect-oriented ecotourism. These are meant to be the ambassadors of entomological ecotourism and, as a result, are those most charismatic in localities across the globe. In addition to general information about the various species, unique information is also provided regarding cultural traditions, myths, and uses in society. As entomological ecotourism continues to grow in popularity, the knowledge base will invariably increase, with more attention paid to the subject by
ecotourists, guides, lodges, and even tour operators. Appropriate provision of reference materials in informative publications in print and online will be integral.

Insect Ambassadors

Common Name: Leaf-cutter Ants

Scientific Name: Atta spp.

Region: Neotropics

Plate: Figure 3-6

There is perhaps no more consistently available, easy to find, and fascinating entomocentric ecotourism opportunity than witnessing a Leaf-cutter Ant colony marching out and back in neat trails through the forest. Commonplace throughout the Neotropics, Leaf-cutter Ants are eusocial insects, meaning that they cooperate in brood care, have overlapping generations, and have divisions of labor within each colony (Holldobler and Wilson 1990). The name Leaf-cutter Ant is the common name to the entire tribe Attini, which is actually composed of about 230 species in 13 genera and found throughout the neotropics (Holldobler and Wilson 2011). Divided into the ‘lower’ and ‘higher’ Attines, the two genera Acromyrmex and Atta represent the most commonly found Leaf-cutters in the neotropical jungles (Schultz and Meier 1995). The original ancestor of today’s Leaf-cutters evolved roughly 60 million years ago in concert with the basidiomycete fungi (Family: Lepiotacea), which they consume as their primary food source. Still today they are dependent on fungi for food, feeding primarily on fungi in the genera Leucoagaricus and Leucocoprinus (Chapela et al. 1994). However, the most common genus, Atta, branched off from earlier ancestors roughly 8-12 million years ago (Holldobler and Wilson 2011). It is this genus that is most likely to be
encountered on an ecotour to the neotropics and serves as an excellent educational tool. For the remainder of this section, the common name Leaf-cutter Ants will denote those ants in the genus *Atta*, unless otherwise specified.

It is a common misconception by ecotourists that these ants are defoliating trees to then consume the leaves. The truth is that the leaves (and flowers, sometimes) are used to farm fungus. Originally introduced to the colony by the founding queen, the fungus is cultivated within special ‘garden’ chambers of the intricate subterranean world of the Leaf-cutters. Prior to being added to the underground garden, smaller members of the colony, known as minima, scrape the surface of the leaf and remove the cuticle before cutting and masticating the fragments into a sticky mass (Weber 1996, 1972, Wilson 1971, 1990). Then by adding a few tufts of fungal mycelia onto the new substrate, the fungus rapidly grows to produce gardens full of delectable swollen tips of the hyphae, which the ants will consume.

This relationship with the fungus is mutualistic, in that both parties depend on one another for survival. Just as the ants need the fungus to remain viable and healthy, as a population and as a species, the fungus needs the ants to reproduce and remain viable, too. On each newly added mash of fresh leaves, a small amount of fecal matter is also deposited. While it is difficult for humans to understand why defecating on a food source would be productive, the ants use their own special fertilizing material to outcompete other invasive fungi. With Leaf-cutter Ants coming into contact with spores of many species of fungus while foraging, and then tracking them back into the colony where conditions are ideal for the growth of fungus, other non-edible species of fungus are routinely introduced that may outcompete the preferred fungus. This could result in
the non-preferential fungus eventually dominating, leaving only a poor food source for the farming ants. However, by defecating on or near the substrate, the preferred fungus is able to harness the proteolytic enzymes from the ant fecal material and to free up nitrogen from the freshly cut leaves (a feat that is rather difficult for this particular type of fungus). This, in turn, gives this fungus an advantage over other species and allowing it to dominate the ant colony microenvironment (Stevens 1983). Without the ants performing this behavior, the fungus may not survive as a population or as a species either.

It is the founding queen that brings the original inoculum of fungus to a new colony site. After removing a small part of the fungus from the previous colony, the female will mate three to five times with multiple males and leave to find a new area suitable to begin her new colony. Synchronized on an annual basis, reproduction of new queens coincides with the production of winged, or allate, males. With mature colony sizes numbering in the millions (and averaging at around five million, for *Atta spp.*) it is easy to understand how thousands of males may be produced in each colony. In fact, during certain times of year, these ants are so numerous that local people in Central America routinely harvest them as a source of food. By sautéing them briefly, the wings fall off, resulting in a crunchy delicacy that can be mixed with seasonings or oil.

After mating, individual females will each search for an ideal nesting site. Once chosen, the lone female will dig the principal chambers and gardens, using her own eggs as the initial substrate for the fungus to grow on. With average queen mortality around 90% up until this point, it is critical for the female to procure a stabile colony of fungus, for the success of the colony depends entirely upon her initial contribution of
fungus. While the queen sustains herself by catabolizing her now-useless flight muscles, the initial brood is fed her own eggs until the first set of workers mature through the egg/larval/pupal stages and are able to begin the farming and foraging process. For the next several years, workers will cut leaves, young twigs and flower petals from over 80 different species of trees and contribute to the growing fungus gardens. Eventually, the colony matures to several million workers and one queen. As with all ant species, these workers will be further divided into separate roles. Caring for the brood, grooming the queen, excavating the colony, and defending the colony against predators and parasites are all vital roles of Leaf-cutter workers (Holldobler and Wilson 1990).

One of the more unique behaviors by a subclass of workers is that of the minima. Noticeably smaller than both the soldiers (often termed maxima) and ordinary workers, the minima go beyond the tasks of farming, brood care, and nest expansion. A common sight on forging trails is for a small minima ant to be riding on a leaf already being carried by the larger worker ant. The fact that the minima are nearly 200 times less in mass than their largest cohorts is not the only thing different (Holldobler and Wilson 2011). Historically, these smallest of the small workers were thought to act as ‘hitchhikers’ on leaves solely to guard the carrier ants against parasitic flies, mainly in the family Phoridae. Should one of these Phorid flies be successful in its attack, it would inject an egg into the base of the ant’s neck, just above the pronotum, and slowly reduce the ant’s fitness as the fly larvae grows. Eventually, the growing parasitoid results in total decapitation of the ant host. New evidence, however, suggests these minima also begin the cleaning and cuticle removal process of the leaf en route to the
nest in order to expedite the farming operation (Feener and Moss 1990, Linksvayer et al. 2002, Vieira-Neto et al. 2006).

The spectrum of sizes within the worker class is linear, in that there are numerous morphologies ranging between the largest and smallest. To no surprise, those ants on the larger side are reserved for defensive roles, and those on the smaller side are for colony maintenance and brood care. Further delineations at either end of the spectrum exist and serve their appropriate roles accordingly (e.g., the smaller workers tend the smaller brood, larger soldiers defend against larger predators, etc.) (Holldobler and Wilson 2011).

**Locating on ecotour.** Leaf-cutter Ants are most easily seen at night in large foraging trails. They are found from northern Mexico (and in some cases, Texas, too) to northern Argentina and extend from sea level to 2,000 meters in elevation. Once a foraging trail is located, one may find the nest by following the trail in either direction until spotting a relatively barren mound encircling several rooted trees, often covering an area as large as 15 meters in diameter. Keep in mind the colony must have enough room for five million ants! Although these ants often use existing trails and pathways to minimize obstacles from grasses and vegetation, they will also cut their own paths. Leaf-cutter Ants may also be seen in the daytime as well, but in fewer numbers. Spotting scattered leaf clippings is a reliable method for locating Leaf-cutter trails during the day, when only a few workers may be traversing the foraging path.
**Common Name:** Arboreal/Nasute Termites  
**Scientific Name:** *Nasutitermes* spp.  
**Region:** Neotropics  
**Plate:** Figure 3-7

Perhaps the most readily seen insect during a neotropical ecotour, *Nasutitermes* Termites are ubiquitous in lowland rainforest and forest-edge habitats throughout Central and South America. Largely arboreal, their nests are generally spherical, large dark brown or black structures, that physically encapsulate a portion of a tree branch or trunk (Thorne 1980). Ranging from the size of a basketball to a large beach ball (0.25 meters to 1 meter in diameter), the nest is made up of a carton material that is, in fact, chewed wood pulp cemented with fecal glue. There are numerous layers and invaginations within the general nest structure, and the inner layers become increasingly more solid and rigid compared to outer ones. Radiating out from the nest are covered runways that connect to feeding sites away from the supporting tree. These covered tunnels function to protect the termites from both desiccation and predation, as the workers are very soft-bodied compared to other eusocial insects (Stuart 1963, Araujo 1970, Thorne 1980, Lubin 1983).

Just as with ants described previously, *Nasutitermes* is eusocial and is divided into three castes – the workers, soldiers, and reproductives. Males are produced at specific times of year in order to coincide with the production of queens, the combination thus enabling the formation of new colonies. While *Nasutitermes* colonies generally have a single queen and king, some species in this genus may have more than one of each (Lubin 1983).
Pheromones are incredibly important to any eusocial insect, but because worker termites are blind, these chemical cues are vital in the coordination of tasks and maintenance of the colony structure in general (Stuart 1963). Pheromones are largely used to lay trails, either to locate food or to signal disturbance. A fun experiment to conduct while on an ecotour is to draw a circle on a piece of paper with a ballpoint ink pen. Then, place several worker termites within the ink circle and watch as they follow the ink trail round and round, using the chemical signals in the ink for navigation, due to its chemical similarity to their trail-following pheromone.

*Lasutitermes* soldiers have a pronounced snout or nasus on the front of their head, from which the genus gets its name. While most soldiers of eusocial insects use their powerful mandibles to intimidate and defend against enemies, these soldiers squirt a strong-smelling, sticky secretion from their snout that acts to entangle other arthropod mandibles in this sticky compound. For larger vertebrate predators, like Tamanduas and other anteaters, this terpenoid compound is an olfactory deterrent (Henderson 2011). The defensive actions appear relatively benign at first, lacking any physical force, like crushing mandibles, but what these soldiers lack in forceful contact, they make up for in the size of the defensive force. Comprising up to 20% of the total nest population, nasute-enabled termites mount a defensive stand that is typically about 10 times the size of non-nasute termite species (Lubin and Montgomery 1980). However, this is a significant cost to the colony. Because the soldiers lack mandibles, they must be fed by workers of the colony. At these high numbers, it represents a demanding task for the worker caste (Lubin 1983).
Besides the fascinating life cycle and caste functions of these *Nasutitermes* termites, they also present other interesting opportunities to the ecotourist. Some of the most charismatic tropical bird species routinely occupy abandoned termite nests, including Trogons, Puffbirds, Parrots, and Parakeets. In addition, these termites serve as a critical food source for numerous ant species, as well as reptiles, and several species of mammals, especially the Tamandua Anteaters (Lubin and Montgomery 1980).

Although less utilized than some of the larger eusocial invertebrates, such as *Atta* spp. of ants, termites may be exploited as a protein source by some indigenous tribes in South America (Posey 1978). However, because of the willingness for soldiers to discharge their noxious terpenoid defenses, *Nasutitermes* is a less-utilized genus of termite for human consumption. Nevertheless, it is possible to eat the workers, which tend to taste like a mint-flavored toothpick (pers. obsv.).

**Locating on ecotour.** The nests of *Nasutitermes* termites are very conspicuous and may be found at several different forest strata. Occurring near ground level all the way to the mid-level canopy, these large round nests can be seen easily while both driving and walking through natural areas. In addition to functioning as a visual opportunity to talk about eusociality among insects, encountering *Nasutitermes* nests while on an ecotour also may yield other interesting discoveries. Several species of charismatic bird groups, such as Trogons, Parakeets, and Parrots, routinely inhabit unoccupied arboreal nests and may readily be seen at openings on the sides of the nest.
Common Name: Dung Beetles

Scientific Name: Scarabaeidae family

Region: Africa

Plate: Figure 3-8

The behavior of these insects, from which they get their name, is not glamorous. However, they rank very high on the “wow” factor by ecotourists. Their life history is heavily concentrated on the search for and use of animal feces.

Dung Beetles occur on all continents around the world except for Antarctica. However, the place exhibiting the greatest diversity of these beetles depends upon their coveted resource – dung. The grasslands and savannas of tropical Africa contain the highest levels of mammal biomass in the world and, consequently, also are filled with the greatest amount of dung beetle resources (Owen 1983). Forested areas also have a great diversity of Dung Beetle species, with tropical forests actually being the most productive type of habitat. Generally speaking, tropical forests have two to three times more dung and carrion (rotting animal tissue) than temperate forests (Whittaker 1975). Where there are more resources, there are more Dung Beetles. In the Ivory Coast alone, Cambert (1984) found that 286 species existed in the savanna, grasslands, and forested areas.

Dung is used as a food source for both the adults and larvae. Adults will feed directly upon a fresh dung patty before partitioning it for their young. By rolling it into a sphere, they will often push the dung ball a great distance before laying a single egg in it (with some species, multiple eggs are laid) and burying it underground. The egg will hatch and the larva will eat the dung from the inside out, before pupating while still
underneath the soil (Halffter and Matthews 1966). Although dung beetles will feed directly from the dung patty, at times when competition is high and many beetles are vying for the same resource, removing a sizable chunk before eating guarantees that the beetle will save enough for itself and its offspring (Hanski 1989). The relocation and processing of dung is a valuable ecosystem function. Research in West Africa suggests that dung beetles inhabiting the savanna will bury and consume one metric ton of dung, per hectare, per year (Cambefort 1984). In the movement and consumption of animal excreta, dung beetles, in fact, do many things that help to sustain healthy ecosystems.

First, they aid in nutrient cycling. Many of the nutrients consumed by animals are excreted. By taking freshly deposited dung, with nutrients still intact, and depositing it below the surface of the soil, they are effectively fertilizing the ecosystem and promoting the growth of vegetation. Valuable nitrogen is abundant in the dung of many African mammals, and if it were not for dung beetles, much of it would be lost through the process of volatilization to the atmosphere (Steinfield et al. 2006). By burying dung underground, nitrogen is recycled directly to the environment from which it came. In addition, by feeding on dung, these beetles introduce new bacteria to the dung which aids in decomposition and mineralization. This further aids in the release of key nutrients to the ecosystem (Yokoyama et al. 1991).

The tunneling behavior of dung beetles is synergistic to their nutrient cycling role. Just as termites and earthworms do, dung beetles promote healthy soils through aeration. This allows for greater movement of nutrients, as well as the flow of water through the soil profile (Mittal 1993). The tunnels that they excavate, in which they store their food and raise their young, may continue for several meters below the surface and
alleviate soil compression by the large mammals found throughout African savannas. All of these factors have proven to significantly increase ecosystem productivity and plant growth (Bang et al. 2005).

Not only do the soil amendments engineered by dung beetles increase plant productivity, but so do the seeds that dung beetles deposit as a byproduct of their behavior. Plant and fruit-eating animals often consume seeds when feeding, which then are passed through and appear in their excreta. Although dung beetles have no interest in the seeds themselves, fierce competition often results in seeds going unnoticed during the construction of their portable dung balls (Andresen and Feer 2005). The act of transporting seeds in nutrient-rich dung, to then be deposited in well-aerated and porous soils, is an ideal scenario for promoting seed germination and new plant growth.

Lastly, dung beetles serve to reduce the incidence of parasites and flies. This is attributed to the rapid removal of fly breeding substrate, effectively outcompeting flies that aim to also feed and deposit eggs in the nutrient rich dung (Bishop 2005). While flies also have their place in the ecosystem, studies of cattle farms indicate that the productivity of their livestock is reduced significantly as fly populations increase (Haufe 1987). This likely extends to African ungulates, as well. Other parasites are often found in dung, including protozoans and various species of parasitic worms. Studies have found that grasslands containing dung beetles have significantly fewer incidents of parasite emergences and parasitism events among animal inhabitants (Fincher 1975, Bergstrom 1983, and Gormally 1993).

Dung Beetles not only exhibit an interesting and somewhat grotesque life history that is intriguing to ecotourists, but they play vital roles in ecosystems. For guides, the
story of the Dung Beetle could begin with any key points made in the above text, or simply by locating a fresh dung patty and watching the show.

**Locating on ecotour.** Dung Beetles occur in variable numbers throughout North and South America, but usually in unreliably low numbers to expect to encounter frequently on ecotours. In the Old World tropics, especially eastern and western Africa, their ubiquity can be legendary. Dung Beetles can be found in most ecosystems in Africa but are most abundant where their dung resource is most abundant. Tropical forests present an opportunity, but the large mammal-filled savannas of Africa also present frequent chances to witness their behavior. While it is not advisable to walk in tall grass in search of fresh excreta, many large mammals use game trails or dirt roads that are clear of vegetation and allow for easy spotting of large dung patties from game vehicles. Fresh dung is best, as it will elicit the most competition and the most activity. Should a large herd of Elephants be passing by a road or moving across a game trail, this is the best time to go looking.

Tropical forests in Africa may be slightly better for viewing individual dung beetles, as more emphasis is placed on walking during the ecotour (i.e., wherein contrast to the savanna, dangerous mammals are not likely to cause problems). However, because there is significantly less dung to be used by the beetles, it is more difficult to watch the process from start to finish. The best chance here is to follow a troop of arboreal monkeys and look for freshly fallen excreta. The dung beetles will not be far behind. This technique can also be used in neotropical rainforests, where forest species of Dung Beetle males frequently perch on leaves at waist height and wait to catch the
scent of newly fallen monkey dung. They will then fly to the dung to encounter and mate with female beetles (T. Emmel, pers. comm.).

**Common Name:** Mopane Worm

**Scientific Name:** *Imbrasia beliina*

**Region:** Africa

**Plate: Figure 3-9**

The Mopane Worm is not a worm at all, but rather the larva of the *Imbrasia beilina* moth in the family Saturniidae. Its notoriety is not necessarily based on its showy appearance (although it is a striking member of the Lepidoptera) but rather in its cultural significance. The Mopane Worm is harvested as a food source across the continent of Africa, being one of the most-traded insects for use as a food source in the world. Taken as late-stage larvae from their host tree, the Mopane Tree (*Colophospermum mopane*), the caterpillars are first squeezed to remove the gut contents, then boiled in salt water, and then sun-dried (Timberlake 1996). At this point, they may be kept for long-term storage, or eaten immediately. In some cases, they may be pan fried and seasoned to compliment a number of dishes.

Historically, these caterpillars functioned primarily as a protein in the diet of rural Africans. However, with their growth in gustatory popularity over the past 10-15 years, they have become more of a trading commodity (Stack et al. 2003). With caterpillar populations numbering in the billions in individual countries, a sustainable harvest will generate over 100 million dollars a year in South Africa alone, 40% of which is retained by the local communities (Styles 1994). However, population outbreaks are common, meaning that there is significant fluctuation and inconsistency in supply from year to
year and from region to region. Nevertheless, the harvest of this local and international delicacy is taken very seriously and represents a sustainable source of income for rural people in Africa.

**Locating on ecotour.** The Mopane Worm is a somewhat special case in terms of locating, for they are perhaps the most well known insect, apart from Mosquitoes or Tsetse Flies, in Africa. One’s best chance is to inquire with local people in local markets, as to the location of these delectable larvae. Finding larvae and adults in the wild should be equally as straightforward and rewarding, with locations of Mopane Trees mapped extensively by local people.

**Common Name:** Giraffe-necked Weevil or Giraffe Beetle  
**Scientific Name:** *Trachelophorus giraffe*  
**Region:** Africa (Madagascar)  
**Plate:** Figure 3-10

One of the best examples of extreme evolution in Madagascar, and Africa in general, is the bizarre body plan of the Giraffe-necked Weevil (*Trachelophorus giraffe*). These members of the beetle family (Curculionidae) are sexually dimorphic, in that males and females look different from one another. Males exhibit an astonishingly long pronotum, or neck, used in male-male battles for territory and mating privileges with the nearby females. Females, on the other hand, have a much smaller neck that they use to assist in rolling leaves into tubes, in which they deposit a single egg. Some accounts show that males may also participate in leaf-rolling, too, but far less commonly.

Like all beetles, they have the ability to fly, and these weevils will do so in order to gain the best position for attracting females by perching at the ends of grasses and
broadleaved plants. However, with their extended pronotum, their flight appears laborious, even for a beetle.

**Locating on ecotour.** Giraffe-necked Weevils are endemic to Madagascar, meaning that they are found nowhere else on earth. In addition, their range is relatively localized to the Ranomafana National Park, found in the middle of the country. Although their distribution is restricted, they may be easily found when in the park. They generally choose sunlit locations in riverine habitats, or areas with ample moisture. Males and females may be found in similar areas, but the males are much more easily spotted due to their larger size and brighter-red coloration of their elytra, or hardened wing coverings.

**Common Name:** Blue Morpho Butterfly

**Scientific Name:** *Morpho* spp.

**Region:** Neotropics

**Plate: Figure 3-11**

There is a lively debate on the number of different species of butterflies in the *Morpho* genus, with the subspecies concept dominating the recent literature. This is not difficult to imagine, as this genus is one of the most charismatic in the New World. Assigning new nomenclature, with the proliferation of the subspecies concept, is eagerly pursued by many systematic entomologists. There is, in fact, no clearinghouse for *Morpho* phylogenies, so for the sake of this Chapter, we will acknowledge that there are roughly 80 species names of *Morpho* butterflies in the neotropics, grouped into familiar species complexes such as *peleides, cypris, menelaus, hecuba, didius, rhetenor,* and others. The most diagnostic difference among these groups, for the average observer,
is how closely the metallic blue coloration of the upperside of their wings extends to the wing edges. By far the most common appearance is for a 1-2 centimeter margin of black pigmentation to separate the wing edge from the blue coloration of the interior of the wing. Among butterfly watchers, this spectacular butterfly is one of the more eagerly awaited sights on an entomological ecotour. Usually found at lower elevations in rain forests, Morphos of some species can be seen as high as 1,500 meters above sea level.

Morphos are not chemically defended and must rely on a combination of cryptic coloration (the underside) and startle coloration (the upperside). This sharply contrasting color pattern serves the Morpho well. While at rest, the cryptic brown color with circular patterns allows it to blend into the forest floor (since it mostly feeds on fallen fruit), or to neighboring vegetation. As it flies and beats its wings, the butterfly seems to disappear when its wings are closed (due to its dark, cryptic ventral coloration) and then suddenly flashes blue when its wings are opened (due to the bright blue upper side). For a bird such as a jacamar or flycatcher in pursuit, a flash mixed with a sudden change of direction upon closing its wings is enough to throw the predator off track. This allows a brief opportunity for the butterfly to dart through the forest and escape, or quickly land on a trunk and blend into the surroundings, remaining motionless until the threat has passed.

Morphos provide a fascinating opportunity for the guide to discuss the two types of butterfly wing pigmentation. On the surface of butterfly wings are numerous scales that are more or less arranged in a series of rows. These scales have numerous longitudinal ridges, as well as cross ridges that effectively create scale “windows” that
frame the scale interior (Ghiradella 1998). Most butterflies have scales that are
individually pigmented, creating the beautiful mosaic patterns that we so commonly
admire. These individual scale pigments absorb some light in the spectrum, and reflect
a range of wavelengths that give each scale its specific color (i.e., black and orange, in
the case of the Monarch butterfly *Danaus plexippus* (Nijhout 1991). However,
iridescence on butterfly wings works in an entirely different way. Known commonly as
structural coloration, butterflies in the *Morpho* genus largely exhibit a latticework of scale
layers (lamellae) and air pockets that serve to create their highly reflective coloration.
Instead of the wing color being determined by individual scales that reflect light back to
one’s eye, *Morpho* wing scales are hardly pigmented at all. In fact, if you were to rub
scales from their wing off on your thumb, you would notice that they are mostly a drab
brown color, rather than a glittery blue (This is not recommended to try, as an
ecotourist!). What makes the wing so blue is the precise orientation and structure of the
individual scales, scale windows, and the air in between. The latticework interferes with
the wavelength of light and actually amplifies the luminosity and intensity of certain
wavelengths in the color spectrum (Kinoshita et al. 2002). In the case of the Blue
Morpho, it is the blue spectrum that is emphasized. However, other butterflies also
employ structural coloration to emphasize greens, reds, purples, yellows, and other
colors.

**Locating on ecotour.** Adults can be seen at anytime of day, but generally are
most common during midday, as the sun warms the forest, and females search for
oviposition sites on one of their many different host plants, which are largely in the
families Arecaceae (*Astrocaryum* and *Geonoma*), Dichapteralaceae (genus
Dichapetalum), Fabaceae (genera Andira, Dalbergia, Dioclea, Erythrina, Inga, Lonchocarpus, Marchaerium, Platymiscium, Pterocarpus, and Sclerolobium) Malpighiaceae (genus Heteropterys), and Ochnaceae (genus Ouratea) (Young and Muyshondt 1973, Henderson 2011). Adults feed primarily on rotting fruit, which presents a wonderful way to “bait” these butterflies for more reliable sightings and photographic opportunities while on an ecotour. They are typically seen feeding on fallen fruits from the genera Ficus, Sapote, Mangifera, Brosimum, Manilkara, Guazuma, Musa, and Spondias (Young 1975, DeVries 1987). However, as an ecotour leader, baiting these butterflies with a bit of rum and banana mush (Central America) or rotten fish (South America) is about as good as it gets for observing them closely.

**Common Name**: Jungle Nymph Stick Insect

**Scientific Name**: Heteropteryx dilatata

**Region**: Malaysia and Indonesia

**Plate**: Figure 3-12 and Figure 3-13

Stick insects are impressive as an entire order of insects, but there are some species that stand out more than others. The Jungle Nymph Stick Insect from Malaysia and Indonesia has separated itself due to its extreme size and weight. Weighing upwards of 65 grams, and even more when gravid females are weighted with full clutches of eggs, they contend for one of the heaviest insects of the world, matching some of the heaviest beetles in live mass (Brock 1999). However, their large size and impressive spiny morphological defenses has not allowed them to fully escape from predation, as spiders have been shown to consume them with little hesitation (Nentwig 1990). There is some evidence that *Heteropteryx* employs an additional strategy,
common amongst a great many other stick insects, which is the expulsion of a toxic and irritating secretion. While such methods are only speculated for the Jungle Nymph, they are well documented for other species and range from violent projections of toxic spray, to passively oozing from secretory glands at various parts of the insect body (Bedford 1978, Bouchard et al. 1997).

The life cycle of stick insects is one of incomplete development, meaning that they do not undergo a complete life cycle of separate transformations from juvenile to adult stages, unlike most other insects in this Chapter (i.e., Beetles, Flies, Butterflies, Moths, Bees, and Ants). From the time that they hatch from an egg, they bear significant resemblance to the adult form, apart from lacking full wings and reproductive organs. They also eat similar food between life stages, feeding on plants, in the case of stick insects. Although the quantity and quality of the food may vary, leading to different preferences for host plants between life stages, they still feed on plants for their entire life. Perhaps one of the most peculiar aspects to the biology of the Heteropteryx is the length of time spent in the egg stage. Documented as lasting 12-14 months, this is one of the longer-lived egg-stages for insects in the tropics (van Zomeren 2012).

Cultural uses for stick insects fall mostly in the consumption category, with a number of insect species eaten in developing and developed countries around the world. However, the human population of an island off the Southeast coast of Papua New Guinea has found a rather specific use for stick insects, other than as a food source. Villagers use the spiny femora of stick insects in the genus Eurycantha as a natural fishing hook. Selecting only males of the genus, as they exhibit more
pronounced femoral spines, the insect leg is used for line fishing in freshwater streams with tremendous success (Balfour 1915).

**Locating on ecotour.** The Jungle Nymph is found exclusively in the Malaysian and Indonesian tropics, and although it appears to be rather conspicuous, with its large appearance, it can be difficult to spot. Relying a great deal on its camouflage, they are nocturnal insects and, like most stick insects, they are most active at night. This is not to say that they are unable to be found during daytime hours, but their daytime inactivity makes them exponentially more difficult to spot. There are no conclusive reports on these insects being attracted to night lights, but night hikes have proven to be successful in finding this insect, with enough time and conviction. As they feed on leaves and attempt to use the branches and leaves to aid in crypsis, searching at or above eye level for objects that break the outline of a tree branch or bunch of leaves often yields the best results.

Also like most other stick insects, Jungle Nymphs are sexually dimorphic, meaning that there are significant size differences between males and females. There is generally about an equal chance of seeing a male and female in copula, as there is finding them separately. In order to safeguard his chance at reproducing and having his genes passed onto the next generation, the male will mate with the female for an extended period of time, preventing competitor males from mating with the same female.
Common Name: Urania Moth or Green Page Moth

Scientific Name: *Urania fulgens*

Region: Neotropics

Plate: Figure 3-14

A fascinating example of insect adaptation has been documented in Central America, and likely occurs elsewhere in the neotropics, too. Although looking much like a colorful swallowtail butterfly, *Urania fulgens* is in fact a diurnal moth. Widespread throughout Central America, its beauty is superseded by the unique migration of the species that takes place every few years. Unlike the Monarch butterfly (*Danaus plexippus*), which migrates in order to avoid freezing temperatures, the Urania Moth migrates largely in response to host plant preferences (Smith 1983). Somewhat unpredictably (every four to eight years), tens of thousands of these moths will fly from the south to the north of Costa Rica, from Panama to the Caribbean coast of Costa Rica, and even south from Guatemala to Colombia (Smith 1972). What is the cause for these considerable movements? They are moving to avoid toxic levels of secondary compounds present in their host plant – the rainforest vine *Omphalea diandra* (Smith 1983, Smith 1983). At low concentrations, these toxins are actually sequestered by young Urania larvae, which then employ the glycosidase inhibitors and alkaloids to deter predation from birds and other vertebrate predators as larvae and adults. However, higher levels of these toxins will kill the larvae (Smith 1983, Trigo 2000). After three generations of larval feeding on Omphalea, the larvae induce the vine to increase the level of toxicity to the point that the next generation of Urania cannot detoxify it as it normally does. Thus, these moths migrate to find Omphalea vines that have not been
fed on recently and have dropped their chemical defenses to a manageable level. As a result, after a large population explosion and subsequent migration of *Urania fulgens*, the forests that once teemed with so many of these moths will be void of them for the next several years. Although the vines will remain, they are too poisonous to eat (Smith 1983, Henderson 2011).

**Locating on ecotour.** Since these are day-flying moths, they are generally more likely to be seen than most other moths during general ecotours. At the same time, though, they are somewhat more difficult to see in the green forest and also are rarely attracted to lights at night. Their migratory cycle is perhaps the most influential parameter affecting whether they can be found in a certain area or not. Because of their somewhat unpredictable pattern of migrating, local contacts are helpful in identifying the start to a migration cycle. For instance, ecotour guides in Corcovado, Costa Rica, may witness the beginning of a northward migration and, thus, be able to alert guides north of San Jose prior to the moths’ arrival. Similarly, guides in Guatemala may begin to notice a southward migration of *Urania* and be able to alert guides in Nicaragua, Costa Rica, Panama, and Colombia. Adults will feed routinely at flowers, preferring those in the *Inga, Leucania, and Eupatorium* genera. Both males and females depend heavily on nectar feeding for rich carbohydrates to fund these long migration flights and have been recorded as frequenting white “fluffy” flowers (Smith 1983).
**Common Name:** Cracker Butterflies  
**Scientific Name:** *Hamadryas* spp.  
**Region:** Neotropics  
**Plate:** Figure 3-15

Easily identified by the rapid clicking sounds as they zoom through the forest, Cracker Butterflies in the genus *Hamadryas* are widespread throughout the neotropics and are represented by over 20 different species (Jenkins 1983). Usually found in sunlit gaps in the forest, these butterflies routinely emit their characteristic clicking sound presumably as a way of defending territory, both against conspecifics and potential predators (Swihart 1967, Young 1974, Jenkins 1983, Monge-Najera et al. 1998). Possessing a rudimentary insect “ear”, known as a Vogel’s organ, Cracker Butterflies effectively have a simple ear drum, with a membrane connected to an air sac and chorodontal sensory organ. Not only are they able to produce sounds, but they are able to interpret it as well (Yack and Fullard 1993, Hoy and Robert 1996). Also known as a tympanal ear, *Hamadryas* use these organs to perceive sounds made by conspecifics. First observed by Charles Darwin during his voyage of the Beagle, he suggested that these sounds function in male-male territoriality, courtship, and sexual attraction (Dawrin 1874, Silberglied 1977, DeVries 1987). However, much less is known about the mechanism behind their sound production. Numerous hypotheses have suggested that it is a percussive action, with apical veins enclosing a discal cell of the forewing (Otero 1990, Monge-Najera et al. 1998). However, others believe it to be a typical stridulatory organ at the base of the forewing (Yack et al. 2000). This would allow for one part to scrape against another, emitting sound in the process. With the many
different *Hamadryas* species exhibiting the propensity to produce this clicking sound, it is possible that sound is used for different purposes in different species of Cracker Butterflies.

Most *Hamadryas* butterflies somewhat resemble each other by the characteristic spotty pattern on both the upper and underside of their wings. However, some are very cryptically colored, while others are aposematic and colored brightly to advertise their unpalatability. Naturally, those with cryptic coloration feed on hostplants without chemical defenses, thus failing to acquire chemical defenses themselves. Those with aposematic coloration are chemically defended through the sequestration of secondary plant compounds during their larval stage (Jenkins 1983). The range of coloration is quite pronounced throughout the genus, from light grey to completely black with iridescent blue dots. Not surprisingly, those with cryptic coloration choose to inhabit areas with appropriately colored trees that allow them to blend into the bark to avoid predation. The aposematic species tend to have a wider range (Henderson 2011).

Adult *Hamadryas* rarely feed on nectar, preferring to feed on rotting fruit, both on the forest floor and high in the canopy, in line with many other species in the family Nymphalidae.

**Locating on ecotour.** *Hamadryas* are best seen perching upside down on tree trunks. However, those species that rely on cryptic coloration are often difficult to detect because they appropriately choose complementary-colored trees on which to perch. Generally, they rest with their wings completely open. *Hamadryas* occur at a range of altitudes, as well as rainforest strata, but generally do not occur above 1,500 meters above sea level (Jenkins 1983, DeVries 1987, Henderson 2011). Should it be difficult to
see these butterflies in the forest, it is very possible to hear them as they communicate through their clicking sounds.

**Common Name:** Stingless Bee

**Scientific Name:** *Meliponinae* subfamily

**Region:** Neotropics

**Plate: Figure 3-16**

Stingless Bees are likely to be encountered on an ecotour in the neotropics at sap-dripping trees and especially when spending time around hummingbird feeders. This likelihood is only increased as ecotourists assemble around bird-feeding stations that are rich in syrupy fruit sugars. These bees are members of the Meliponinae subfamily, which consists of as many as eight genera and 16 subgenera (Wille 1983). However, the extent of speciation and the best systematics treatment of the Meliponinae are still heavily debated. Nevertheless, members of this group share similar morphological features, behaviors, and natural history that suggest close affinity to a common origin.

Like other members of the greater Apidae family (to which these bees also belong), Stingless Bees are eusocial. These bees reside in subterranean colonies, hollow trees, and other structures that effectively enclose and shield them from most of the surrounding environment (Wille 1973, Johnson 1983, Wille 1983). While some species are more exposed than others, all Stingless Bees reside in nests. Their colony size still pales in comparison to other eusocial tropical insects, such as Leaf-cutter Ants and *Nasutitermes* Termites, but this does not stop them from using the abandoned nests of ants and termites. They will occupy these already-constructed nests opportunistically and then reinforce them with their own nest building techniques (Wille
1973, Roubik 2006). By collecting building materials from the surrounding forest, workers will return to the nest with a wide range of organic matter, including mud, fungi, feces, and plant resins (Johnson 1983, Roubik 2006). From the appearance of their nests, it is easy to understand how these materials are used, as nest entrances often look like earthen clay chimneys.

The Stingless Bees are some of the oldest bees in the world, evolutionarily speaking. They have been on the earth for over 65 million years, which is longer than the well-known stinging Honeybees (Camargo and Pedro 1992). As a result, Stingless Bees are significantly more prolific and speciose than their Honeybee descendants. But there are numerous similarities between the eusocial stingless bees and other eusocial bees. Just like most bees, Stingless Bees make honey, they live in perennial colonies, are founded by queens, and have a sterile worker class (Michener 2000). However, they differ in numerous ways that further suggest their more basal position in the phylogeny of Hymenoptera. Unlike Honeybees, Stingless Bees use a variety of materials from the environment to construct their nest, not just wax. In addition, their methods for colony founding and brood production is much less efficient, resulting in smaller colonies and less flexibility to relocate the colony if needed (Michener 1974, Roubik 1989, Roubik 2006).

**Locating on ecotour.** Pheromones are used by Stingless Bees in both defense and foraging, like many other eusocial insects. It has been noted that the recruitment response to foraging is directly in proportion to the sugar concentration of the food source (Johnson 1983). One of the easiest ways to see Stingless Bees on an ecotour in the neotropics is to observe hummingbird feeders, which nearly always attract a scout
shortly after being refilled with concentrated sugar water. This scout will emit a pheromone trail that will then recruit other workers to the food source. In addition to airborne pheromones, the scout often deposits some pheromone on leaves to help orient the group of recruits to the food source.

Stingless Bees are ubiquitous in low to mid elevation tropical dry and wet forests, so it is common to encounter them up to 1,500 meters. With some species, they may be found even higher than this. Oddly shaped protrusions from trees are often nest entrances for these bees, but it will become immediately obvious if such a structure is part of an active nest by looking for workers around the nest entrance. These bees are guarding the nest entrance against other species of Stingless Bees, parasites like Phorid Flies, and bird and mammalian predators (i.e., parrots, woodpeckers, tayras, armadillos, and anteaters) (Johnson 1983).

Common Name: Migratory Locust

Scientific Name: Acrididae family

Region: Africa

Plate: Figure 3-17

The migratory locust phenomenon in Southern Africa is mainly attributed to one species, *Locusta migratoria*. However, there are several other species that are known to be highly gregarious and exhibit “outbreaks” of high population numbers. There are also subspecies of *L. migratoria* in both mainland Africa and Madagascar. In addition, *Schistocerca gregaria* (Desert Locust), *Anacridium melanorhodon* (Tree Locust), *Nomadacris septemfasciata* (Red Locust), *Locustana pardalina* (Brown Locust), and *Dociopterus maroccanus* (Moroccan Locust) have all acquired nefarious reputations.
due to their voracious feeding habits and penchant for causing utter devastation among crops.

*Locusta migratoria* is found throughout the Old World in grasslands from New Zealand to Northern Eurasia. However, the expansive savannas and grasslands of Africa represent an ideal habitat for these insects to flourish. The Migratory Locust is polyphenetic, meaning that it exhibits plasticity in its phenotype, or outward appearance. These differences can be expressed as variance in morphology, color, physiology, and even migratory behavior (Uvarov 1977, Penner and Yerushalmi 1998, Simpson and Sword 2008). This phenotypic plasticity is also density-dependent, particularly with regards to migratory behavior. When population levels are low, Migratory Locusts are generally solitary and sedentary. However, high population sizes result in highly gregarious mass-migrating populations. This density-dependent change from solitary/sedentary individuals to gregarious/migratory individuals is known as gregarization (Chapuis et al. 2008). Although the concept is a simple one, the mechanisms behind this transformation are complex, with over 500 gene differences occurring between solitary and gregarious locusts (Kang et al. 2004). Due to the mixing of populations during these gregarious phases, there are even more complicated dynamics to the entire system, which are a current topic of intensive debate and high-level research.

As with many other insects, one of the most impressive characteristics of the Migratory Locust is the sheer number of individuals in a migration swarm. Sizes fluctuate greatly, depending on the year, the season, and the locality, but it is not
uncommon for swarms to spread over hundreds of hectares, with total swarming numbers averaging in the hundreds of millions (Lecoq 2001).

**Locating on ecotour.** Encountering a migratory swarm on a specific ecotour is mostly going to be up to chance, but during the course of a naturalist guide’s lifetime, they will likely see many of such events. However, this is not to say that finding a few solitary individuals is not interesting, as it provides the opportunity for a great explanation of their interesting life cycle and impressive gregarious behavior. Individuals may be seen in savannas and grasslands flying across game trails, perched on vegetation, or on trees. Because of their phenotypic plasticity, it may be difficult to identify the correct species or subspecies. But again, like the other topics of entomology discussed elsewhere in this Chapter, insects may instigate related discussions, with the presence of a single locust functioning as the beginning point for a discussion on the Migratory Locust, insect herbivory, or other topics.

**Common Name:** Helicopter Damselflies

**Scientific Name:** *Pseudostigmatidae* family

**Region:** Neotropics

**Plate:** Figure 3-18

Appearing like a windmill in slow motion, witnessing a Helicopter Damselfly is quite a majestic sight in the tropical rainforest. Their delicate wing beat and gentle hovering flight are in stark contrast to their highly predaceous behavior. Although one species lays most claim to the common name of Helicopter Damselfly, *Megaloprepus caerulatus*, the characteristic large size is a trait shared among most damselflies in the family Pseudostigmatidae. However, rather than explaining the mechanism for why
these certain Odonates became so large, we must realize that these damselflies are representatives of an ancient group of insects that have actually shrunk in size over the ages. Among the very first flying insects in the fossil record, prehistoric Odonata exhibited wingspans of 750 millimeters over 250 million years ago (Silsby 2001). Thus, while the current “Helicopter” variety seems quite large at 190 millimeters, it is a remarkable reminder of its gigantic relative in the coal forests of the Paleozoic Era (Silsby 2001).

Practically speaking, the common name of Helicopter Damselfly is applied to a number of species in the Pseudostigmatidae family, which has 20 species distributed throughout Central and South America (Fincke 1992). They are all impressively large by today’s standards in the Odonata, and share similar life histories and behaviors. The flight pattern exhibited by Helicopter Damselflies is one of the most characteristic features of these insects, as they appear to float very slowly, with each of the four wings seemingly independent of the others. This is the result of a very deliberate flight pattern, though. With their mostly transparent wings and irregular wing beat pattern, they are able to sneak up on unsuspecting prey, despite their large size. Hovering right in front of spider webs, they will pick off small insects, as well as occupant spiders, remaining nearly invisible to their prey (Stout 1983, Fincke 1992, Clausnitzer and Lindeboom 2002). The actual capture happens with a burst of flight, with the damselfly severing the prey’s abdomen for consumption, allowing the rest of the arthropod to fall to the ground (Stout 1983).

Eggs of Helicopter Damselflies are laid in the arboreal water tanks of epiphytic bromeliads, allowing the maturing nymphs to feed on small invertebrates like mosquito
larvae when young, eventually graduating to tadpoles and small frogs when larger
(Fincke 1992). In some cases, females have been observed to opportunistically lay
eggs in other water reservoirs, including decomposing sugarcane stalks (Stout 1983).

**Locating on ecotour.** As with most of the charismatic insects of the neotropics,
they tend to occur almost exclusively below 1,500 meters. However, within this range
they are ubiquitous. They may be found at nearly all rainforest strata, but avoid light
gaps in order to remain cryptic. Just as other arthropods have difficulty recognizing
them due to their mostly transparent outline, it is often difficult to see them in the dimly
lit understory of the forest. The best chance to see them and witness their unique
behaviors is to observe well-endowed spider webs, particularly orb-weaver webs that
occur one to two meters above the ground in a well-shaded part of the forest. Once you
build a search image for the four distinct markings present at the wing tips of these
damselflies, it is possible to spot them in flight throughout their range, not just by waiting
at their feeding grounds.

**Common Name:** Glowworms

**Scientific Name:** *Arachnocampa* spp.

**Region:** Australasia (Australia and New Zealand)

**Plate: Figure 3-19**

Glowworm caves in New Zealand are one of the most popular entomological
ecotourism attractions. In fact, over 450,000 tourists visit the Waitomo Caves annually,
specifically to witness the display of glowworms that cover the ceilings and emit their
brilliant luminescence year-round.
It is the larval stage of these dipterans that receive the most attention. The worms inhabit caves throughout both Australia and New Zealand, with the largest colony residing within the Waitomo Caves. Whether at the Waitomo Caves in New Zealand or one of the lesser-known glowworm caves in Australia, such as Springbrook, tours operate as a “traditional” tourism attraction where groups are guided through various parts of the cave system, exhibiting the diverse labyrinth of halls. Although appearing throughout the cave system, larvae of this fungus gnat fly, *Arachnocampa* spp. (Diptera: Keroplatidae), peak at over ten thousand individuals in “Glowworm grottos” (Doorne, 2010). The larvae hang from the ceiling of the cave on long sticky silken threads, with which they catch other insects to eat. Their bioluminescence functions not only to attract flying prey in the dark of the caves, but also to attract eager ecotourists to witness this spectacular phenomenon. Through a precise and complicated reaction, the insect mixes oxygen with other chemicals within their light organ to produce over $10^{15}$ photons of light throughout the course of their life (Lee 1976). The larval stage of these flies may last upwards of a year, but after pupating, the adult stage lasts only a matter of days (Baker 2003). Adult flies are very poor flyers, restricting their ability to colonize new areas (Richards 1960, Baker 2003). As a result, their locations from year to year are consistent and predictable.

**Locating on ecotour.** There is significant tourist infrastructure in nearly all areas that boast Glowworm grottos. The Waitomo Caves in New Zealand represent the most famous example, but other sites are becoming better known, such as Springbrook National Park in Southeast Queensland, Australia. Naturally, viewing of Glowworms is best done during nighttime hours, but within caves, the need to view the spectacle after
the sun has set is not entirely necessary. Some entrepreneurs have even created artificial Glowworm habitats that occupy rainforest settings, in order to enable daytime visitation by ecotourists. These are mostly emerging in Australia, as tourism continues to grow, necessitating a concomitant growth in tourist options.

**Common Name:** Clearwing Butterflies  
**Scientific Name:** *Ithomiidae* family  
**Region:** Neotropics  
**Plate: Figure 3-20**

Clearwing butterflies are more common in the montane forests of the neotropics up to 3,000 meters than in the lowlands. The common name of Clearwing butterfly is aptly descriptive, due to their transparent wings, rendering them largely invisible in the dimly lit rainforest. However, there are many clear-winged Ithomiid species, and even examples of whole families of Lepidoptera that have transparent wings, including those in the Satyridae family, as well as moths in the Sessiidae and Arctiidae families. However, the most speciose family of Lepidoptera that exhibits these pronounced clear wings is the family Ithomiidae. Perhaps because this group is so drastically different than anything found outside of the tropics, they are often highly sought after by North American, European, and Japanese butterfly enthusiasts on an ecotour. In addition, they are one of the more charismatic insects routinely found in cloudforest elevations (1,200 meters to 2,000 meters), an attractive destination botanically and entomologically on a comprehensive neotropical ecotour.

Just as the transparent wings of the Helicopter Damselfly make it difficult to see, so do the wings of these Clearwing butterflies, both for predators and ecotourists.
However, their wings are in fact secondary protection against predators, as they are heavily defended by pyrrolizadine alkaloids, a toxic chemical that they sequester from plants (Apocynaceae and Solanaceae) as larvae and as adults (Trigo et al. 1996). Interestingly, this pattern is also seen in many cloud forest and rain forest Arctiid moths, one of the only other groups of Lepidoptera that exhibit clear wings despite being relatively divergent in the evolutionary tree of Lepidoptera.

**Locating on ecotour.** Although they may be encountered in lowland areas, this is an excellent group of insects to prioritize in montane forest habitats, as they are generally more diverse and easier to find. Mostly inhabiting the shade-covered understory, they may be seen perching on leaves from ground level to two meters, and also flying slowly in the same lower understory. They are generally very approachable and able to be photographed with or without flash. Perhaps this is because of their double layer of visual and chemical defense; they have not needed to develop fast-twitch flight muscles, or an intense awareness of potential predators. Although the family Ithomiidae extends from Mexico to Bolivia, there is a change in species composition of local faunas, with the most diversity occurring closer to the equator.

**Common Name:** Bullet Ant

**Scientific Name:** *Paraponera* spp.

**Region:** Neotropics

**Plate: Figure 3-21**

Perhaps not the best insect to change the popular perception of insects as being harmful and vicious, the Bullet Ant is so named because of the painful sting it delivers, typically described as feeling like being shot with a bullet. Often found as a single
individual crawling up and down tree trunks, they are, in fact, eusocial and form colonies with extensive subterranean nests. Although the colony is a fraction of the size of a Leaf-cutter Ant or Army Ant colony, Bullet Ant colonies average about 700-1,400 members total. They are also the largest ant in all of the Neotropics. Measuring at 16-22 millimeters in length, they occupy lower elevations, and the populations drop off sharply above 500 meters elevation (Janzen and Carroll 1983). Bullet Ants forage mostly at night and early in the morning at all levels of the rainforest strata – from the ground all the way to the tops of the tallest emergent canopy trees (McCluskey and Brown 1972). Being protein feeders, they are often seen returning to the colony with smaller arthropods in their mandibles (Herman 1975). However, they are also opportunistic at feeding on nectar and other plant sugars (Young 1977).

The Bullet Ant has no known predators but, like many ants in the neotropics, is vulnerable to host-specific Phorid flies (Apocephalus paraponerae). Studies by Brown (1991) show that it is in fact the olfactory cues emitted by injured Bullet Ants that attracts both male and female flies to the ants. In fact, Brown (1991) suggests that perhaps this is one cause for the great diversity of pheromone compounds present in ants. Over evolutionary time, ants could be changing and adapting their pheromone scents frequently as a tool to avoid attracting such lethal parasitoids, which are capable of learning new compounds as host-finding cues.

Despite the fearsome reputation that the Bullet Ant carries, there are some indigenous cultures that harness the power from its sting. The Satere-Mawe people of Amazonia, Brazil, use the powerful sting from the Bullet Ant in their manhood initiation rituals. As documented by Baily et al. (2007), villagers gather dozens of these ants,
anesthetize them and weave them into gloves with the stingers pointed towards the inside. When the ants become conscious, they are quite riled up from being completely contained in the woven structure of the glove. Before a young man of the Satere-Mawe people can become a warrior, he must wear this glove and be stung by the dozens and dozens of Bullet Ants for 10 minutes. However, this is just the beginning, as it will take 20 repetitions of this ritual for the young man to become a true warrior and respected by the village elders. There are also accounts from the Arawak tribe in Guiana using Bullet Ants as a way to encourage their young children to walk. Being allowed to sting their young infants, the Bullet Ant functions in child enrichment as well (Costa-Neto 2005).

Furthermore, some tribes in Brazil use the stings from the Bullet Ant to relieve rheumatism, cure impotence, remove warts, and act as an aphrodisiac (Costa-Neto 1994).

**Locating on ecotour.** The Bullet Ant does form colonies, but is largely found as a solitary individual. Because they feed at all strata of the rainforest, the best opportunity for finding them is as they walk on tree trunks or branches (either going up or coming down the tree). They are not aggressive unless provoked, so close-up viewing or photography is reasonably safe. They are largely tropical and range from Nicaragua to Brazil at elevations from sea level up to 500 meters. In Costa Rica, they are rarely found on the Pacific slope of the central range, but commonly encountered on the Atlantic side (Janzen and Carroll 1983).
Common Name: Charaxes Butterflies

Scientific Name: Charaxes spp.

Region: Africa

Plate: Figure 3-22

The genus Charaxes represents some of the most charismatic butterflies on the African continent. They are the second most speciose genus of butterfly in Africa, with only the genus Acrea more diverse. Charaxes is composed of 250 species worldwide, over 200 of which are found in Africa, and roughly 30 plus species found in Asia and Australia (Larson 2005). They are large butterflies with colorful and dramatic markings and are extremely strong fliers. In addition, they are found in nearly all habitat types in Africa and are adapted to feed on a wide variety of food sources as adults. To no surprise, these butterflies, which often inhabit the animal-rich plains and savannas, are frequently seen feeding on the copious supply of dung and carrion found there (Aduse-Poku et al. 2009). They will also feed readily on rotting fruit, as well as tree sap flows (pers. obsv.).

Charaxes butterflies are well studied, largely due to their colorful beauty and spectacular patterns. They have been incredibly popular with butterfly collectors and researchers for over two centuries and, as a result, extensive data have been recorded on their distributions, densities, and behaviors (Ackery et al. 1995).

Locating on ecotour. Charaxes butterflies come in a number of shapes, sizes, and colorations, but are all relatively large and colorful. Although they often employ a certain degree of camouflage, they are not as cryptic as one might expect from a butterfly that is not very well defended against predators (Molleman et al. 2010).
Molleman et al. (2010) demonstrated that there appears to be a range of palatabilities in the *Charaxes* genus, when fed to ants. Some were seemingly distasteful, while others completely palatable. Nevertheless, no studies have shown them to be chemically defended. Males are most common at dung piles, or on carrion, which makes spotting them easier than spotting females in the wild. Nevertheless, both sexes may be found on tree sap flows, which may be found readily around safari lodges and at entrances of game parks and reserves. Other than these localities, they may also be found perching on trees, or flying across the savanna with reasonable frequency.

**Common Name:** Goliath Beetles

**Scientific Name:** *Goliathus* spp.

**Region:** Africa

**Plate: Figure 3-23**

There are five members of the genus *Goliathus* and all are found in tropical mainland Africa. They are considered some of the world’s largest insects, both in mass and volume. Although they are all gigantic, there is a noticeable size range between species and between sexes, with the largest species measuring up to 110 millimeters in length, while smaller species may be as little as 40 millimeters in length. Nevertheless, they are impressive, no matter which species one encounters. In order to support this large size, they require significantly more protein than most other scarab beetles (Meier 2012).

As members of the beetle family, they undergo a complete metamorphosis, where the juvenile *Goliathus* larvae remain in the soil and feed on organic matter for months before pupating and emerging as a fully mature adult. For this reason, they are
contributors to nutrient recycling by decomposing organic matter into usable components. Once fully mature, adults are sexually active and focus all of their efforts on reproducing. Males routinely will engage in dramatic battles for courtship rights to nearby females. Also, for such large insects, they are relatively agile climbers and fliers, with males following pheromone trails upwind to search for viable mates. To sustain their vigorous lifestyle, they may often be seen at tree sap flows, feeding on the sugary secretions. They have also been recorded to feed on ripe and rotting fruit, both in nature and in captivity (Meier 2012).

**Locating on ecotour.** Larvae of *Goliathus* are just as spectacular as adults, but are seldom seen due to their subterranean lifecycle. However, adults may be encountered in much of tropical Africa, especially in moist and humid forests. These insects are diurnal, but have been known to come to lights at night. The best chance to encounter these beetles during daytime hours is to observe productive sap flows, where adults may come to feed. However, the opportunity to see several species at once, including both males and females, may best be achieved through patient light-trapping.

**Common Name:** Bogong Moth

**Scientific Name:** *Agrotis infusa*

**Region:** Australasia

**Plate: Figure 3-24**

The Bogong Moth is a migratory insect that inhabits Australia year-round. Despite its minimal popularity elsewhere in the world, especially compared to the well-known and publicized migration of the Monarch butterfly in Mexico, indigenous people of Australia have known about this phenomenon for thousands of years (Flood 1980).
Each year, as summer approaches in the southern hemisphere (November-April), tens of millions of adults begin a 3,000 kilometer journey from Southern Queensland to South Australia and fly southeastwards to the Snowy Mountains. For the remainder of the summer, they will aestivate at an altitude of roughly 1,200 meters in the Australian Alps, remaining reproductively immature and flying for only brief periods each day. This flight occurs mostly at sunset and appears to follow no particular pattern (Common 1954). As is common in many aestivating organisms, the consumption of food and water is at a minimum, with fat reserves functioning to fuel the organism during periods of activity throughout their period of aestivation (Common 1954).

When in the mountains, they reside in cracks, crevices, and caves, lining rock walls, and physically stacked in layers in order to take advantage of all possible space within ideal habitat (Common 1990). In fact, space is becoming an increasingly more serious issue, as a carpet 1.5 meters deep lines some of these caves, composed of nothing but dead moths from hundreds of generations past (Thomas 2002).

This large reserve of fatty, nutritious, and sedentary organisms naturally attracts predators. Of these, the Mountain Pigmy Possum represents their greatest predator, as it depends heavily on reliably large populations of Bogong Moths (Mansergh and Broome 1994). In addition, Bogong Moths have served as an important summer food source for aboriginal peoples inhabiting Australia for thousands of years (Flood 1980).

Come late summer and fall, Bogong Moths will return to their winter home, taking the reverse northwesterly route towards Queensland in order to avoid the colder temperatures found in the Australian Alps, for larvae cannot withstand cold temperatures (Common 1990). It is during this winter period that the Bogong Moth has
become infamous during its larval stage. Renamed the cutworm, larvae of *Agrotis infusa* are known to feed on numerous grain crops, causing significant agricultural damage (Common 1958).

**Locating on ecotour.** Due to the predictable nature of the migration of the Bogong Moth, they are relatively easy to locate on ecotours. Consistently inhabiting caves and rock crevices in localized areas of the Snowy Mountains in the Australian Alps, their locations from year-to-year are tracked and well known. The Ngan Girra (meaning Bogong Moth) festival takes place each year on the last Saturday of November and is hosted by the indigenous people of the Murray Valley. It is regularly attended by over 5,000 people and is intended to display their unique cultural traditions, as well as the importance of the Bogong Moth to their way of life (Thomas 2002).

**Common Name:** Palm Grubs

**Scientific Name:** *Rynchophorus* spp. and *Oryctes* spp.

**Region:** Worldwide

**Plate: Figure 3-25**

Palm Grubs have been popularized as a culinary delicacy for hundreds of years in countries across the globe. Harvested as larvae, these particular edible grubs belong to the weevil genus *Rynchophorus*, and to a lesser extent the scarab beetle genus *Oryctes*, which occur in tropical and subtropical regions in the Americas, Africa, and Asia.

Apart from an edible treat, these beetles represent one of the most serious pests to palm trees and other agricultural crops, including sugar cane and several root and fruit crops (Hagley 1965). In their larval stage, they burrow into the crown of the palm,
feeding on young growth and sometimes even the apical meristem, causing death of the entire palm within a short time period. Even when they do not feed on the vital growing point, they often mine the trunks of these plants, causing significant weakening of the structural support (Hill 1983). In addition, they have been known to transmit the nematode *Rhadinaphelenchus cocophilus*, which is the vector of red-ring disease (RRD) (Morin et al. 1986).

Harvesting palm grubs is an environmentally friendly and culturally beneficial solution to control these serious pests. Some have demonstrated that positioning dead trunks near infected plots can be used as bait for adult oviposition and larval consumption. Then, by burning or poisoning the entire trunk, the entire generation of grubs will be eliminated from the population (Hill 1983). However, many indigenous cultures have long been practicing their own method of control, by instead routinely harvesting these baited palm trunks and eating the larvae (DeFoliart 1993). After cutting down certain vulnerable palms and allowing them to remain untouched, they become filled with dozens of individual larvae and hundreds of grams of table-ready food within months (Beckerman 1977). Dufour (1987) reports that many indigenous cultures will routinely harvest palms for their fruits and heart-of-palm by cutting down the trees first, which then provide the opportunity to “farm” for these nutritious grubs. When operationalized, this has led to an acquisition rate of 2,000 grams of larvae per hour during the harvesting process (Dufour 1987).

**Locating on ecotour.** These insects are not in the same category as other ecotouristic features, as they are not likely to be encountered on a nature walk, no matter how rich in diversity an area is. However, they present a unique opportunity to
the ecotourist through emersion into local cuisine and culture. While it would likely be a faulty generalization to say that nowhere in the world are tours offered of indigenous farming techniques for these grubs, there is indeed room for expansion of this type of entomological ecotour. As ecotourism grows, the population of individuals seeking novel and authentic experiences grows as well. It is the belief of this author that with the greatly increasing presence of oil palm plantations in tropics around the world today, there exists great possibility for farming operations to organize tours to showcase this delectable insect, both for the sake of both ecotourism and export. This would provide visitors with a unique view of traditional livelihood, as well as expanding horizons on what is acceptable food in areas around the world. Integrated pest management strategies may also benefit the environment, by reducing the need for chemical pest control by providing preferential oviposition sites in managed farm areas for both *Rychophorus* and *Orcites*.

**Common Name:** Army Ants  
**Scientific Name:** *Eciton* spp.  
**Region:** Neotropics  
**Plate:** Figure 3-26

There is perhaps no display of force more impressive than a large colony of swarm-raiding Army Ants in the neotropics. Often comprised of thousands to millions of individual ants, the full size of the colony is readily perceivable, as they do not have a permanent nest or colony site. Instead, they spend most of their time in a migratory or raiding behavior pattern, where the entire colony will charge through the forest and form columns of workers and soldiers that stretch out for 3-15 meters in a fan-shaped ‘wolf
pack’ (Rettenmeyer 1983). Through intricate coordination by pheromones, Army Ants are not necessarily more aggressive or venomous on an individual level, and in fact have very limited vision (Franks 1982). Their success lies in their ability to organize as a group and predate in a synchronized effort. Driving arthropods and small vertebrates like cattle in front of the swarm, the colony will attempt to incapacitate prey by sheer inundation, covering an area of over 1,000 square meters in a single day (Franks et al. 1991). This carpet of ants will capture their prey, which consists mostly of other ant species, social wasps, and any arthropod too slow to escape, and then return to strategic points of the raiding column in circular loops. Upon reuniting with the central part of the raid, worker ants will drop off the captured food to be used in feeding the brood, and then return to the primary raiding column.

The brood often travels with the raiding swarm, being carried beneath the body of the workers as they run along the forest floor (Franks and Fletcher 1983, Franks 1989). However, these raids do not continue throughout the day. Generally at some point in the night, the raid begins to consolidate and form what is known as a bivouac. Usually found in a hollow log, underneath the roots of an upended tree, or underground in a cavity, these bivouacs are nests composed entirely of living ants. Interlocking legs of workers form the walls and foundation that encase the precious brood and a single queen (Watkins 1978). During the swarming or nomadic phase of most Army Ants, a bivouac is formed nightly, with daybreak eliciting migration when ants will once again pour out of the bivouac and begin their raids for the day. Sometimes the bivouac will remain in place for an extended period of time, with the raiding swarms returning back to it with food in a looping fashion, providing the queen and workers with food, as the
new brood is in the egg stage or while larvae enter the pupal stage. This statary phase lasts roughly 20 days, and contrasts with the swarm-raiding nomadic phase, which lasts roughly 15 days (Franks and Fletcher 1983).

There are a number of different species of Army Ants, with slight differences between them. Although all species exhibit the characteristic raiding behavior, the size, frequency, and statary/nomadic pattern of the raids differ (Rettenmeyer 1983). *Eciton burchelli* present the most dramatic example of Army Ants, for this species’ colonies are the most numerous with the most widespread raids. Often consisting of 200,000 or more individual ants, the raids of *Eciton burchelli* are so massive and elicit such a dynamic reaction by forest floor dwelling organisms that scientists have identified an interrelated microenvironment of interactions, all stemming back to these raids (Franks 1982, Franks and Bossert 1983). For example, predacious and parasitic flies and numerous species of antbirds have discovered that they can follow Army Ant swarms in order to prosper from the escaping arthropods. As arthropods attempt to flee from the swarm, parasitic flies may lay eggs on them and antbirds may directly predate upon katydids and other prey that attempt to avoid the swarming ants (Rettenmeyer 1961, Willis and Oniki 1978). Some flies will even steal food directly from the ants by snatching it out of their mandibles (Gotwald 1995). Several species of butterflies have taken this one step further by accompanying the ant swarms to then feed on the antbird droppings, which are predictably left behind after the swarm has come and gone (Drummond 1976, Ray and Andrews 1980). Birds of prey have also been recorded to feed on antbirds by tracking these ant swarms (Henderson 2011). In addition to organisms that follow these swarms, there are many that actually are integrated into the
swarm, including Silverfish (Thysanura), Rove Beetles (Staphylinidae), Histerid Beetles (Histeridae), Phorid Flies (Phoridae) and multiple species of mites, which live directly on the Army Ants (Rettenmeyer 1983). The role of these various arthropods is unclear, but seeing as how they are provided with nutrients and harborage by the ants, they are either beneficial to the ants’ survival, or are taking advantage of the ants’ sole reliance on chemical perception and are fooling the ants through chemical mimicry.

The soldiers of Army Ants, with their oversized mandibles, have been used by indigenous people and featured on TV shows and movies for their ability to act as sutures for wounds that would otherwise require stitches to mend back together (Gudger 1925). After affixing the soldier to either side of the wound, the massive jaws close tightly, pulling the skin together. Then, by decapitating the ant, the jaw muscles contract and keep the wound closed (Sapolsky 2001, Gottrup 2004).

**Locating on ecotour.** Army Ants are one of the most widespread insects in the neotropics, inhabiting multiple life zones and at elevations from sea level to above 2,000 meters. Identifying them in the forest is quite easy – you simply have to look for a carpet of ants. One may see the flurry of escaping arthropods ahead of the swarm, first, though. As these ants are common in most neotropical ecotourism areas, the more time spent in higher quality forest, the greater the chance of encountering one of these dramatic raids. Despite their fearsome name, they are only harmful by their numbers. Individual ants should not be feared, but safety should be maintained by keeping the ecotour group at a non-contact distance of several meters from the raiding column. Because raiding columns often branch out in unpredictable directions, it is best to anticipate the presence of additional columns or loops while standing in admiration.
**Common Name:** Bot Fly

**Scientific Name:** *Dermatobia hominis*

**Region:** Neotropics

**Plate:** Figure 3-27

More a scourge of nature-travel in the neotropics than an ecotour feature, bot flies are gruesomely interesting. They are not tremendously numerous, like the ant species described throughout this Chapter, nor are they colorful and showy, like the Blue Morpho or Charaxes butterflies. Instead, it is their unique parasitic life cycle that earns them a place among the top insects of ecotourism.

There are many species of botflies, and similar to other parasitic organisms such as lice, they are relatively species specific, with only certain species exhibiting common incidents of cross-over from one species of host to another. For humans, *Dermatobia hominis* is the usual culprit, known to cause the majority of myiasis cases (infestation of a fly larva into the body) in Central and South America (Guimaraes et al. 1983). More commonly known to parasitize livestock, draft animals, and dogs (Roncalli 1984), there is extensive overlap into human communities (Guimaraes and Papavero 1999), causing it to be feared by local citizens of these tropical nations, as well as ecotourists.

Bot flies do not parasitize the host (in this case, humans) in a way that most parasites on animals do, where the parasite comes into direct contact with the host on or in which to lay its eggs. Instead, human bot flies deposit their eggs onto a carrier, which comes naturally into contact with the bot fly’s host. In the case of the human bot fly, this carrier is a zoophilous fly – one that feeds on animals (e.g. mosquitoes). The egg is cemented onto the carrier by the bot fly, ensuring that the egg remains there until
it is ready to hatch into a larva (Cogley and Cogley 1989). As the mosquito or other zoophilous fly feeds on its host, the bot fly larva emerges from its egg and then burrows into the skin of its new host (Mourier and Banegas 1970). The larva will then develop inside the host’s skin for 5-12 weeks, often causing great pain in the process (Acha and Szyfres 1994). While incidents of biologists and entomologists returning from the tropics with a bot fly is somewhat common, few choose to allow the larva to live out its entire life cycle. However, for those brave enough, and patient enough, the larva will continue to feed on cutaneous exudates, growing in size and respiring through two spiracles that come into contact with the surface of the host’s skin (Kahn 1999, Haruki et al. 2005).

When ready to pupate, the last larval stage will emerge from the host and undergo pupation in the soil. After two to three weeks, the adult will emerge and begin the lifecycle once more.

**Locating on ecotour.** Generally, most people do not look for bot flies during an ecotour. Perhaps the better advice would be on how to avoid human bot flies while in natural areas in the neotropics. Because the host must be in contact with a zoophilous carrier, in order for the bot fly larva to be transmitted, it is best to focus on preventing contact with mosquitoes and other blood-feeding flies. Crepuscular hours (i.e., dawn and dusk) represent the most active time of day for mosquitoes. While bug spray works, an equally effective defense is to wear protective clothing that minimizes the amount of skin showing, especially around ankles, neck, and elbows. Treating clothing with Permethrin acts like bug spray in repelling flies, just without most of the negative side effects of most sprays, like oily or sticky skin, or harsh smells. These precautions
are especially important when near freshwater areas, as these are common breeding
grounds for the carrier organisms. More carriers (i.e., mosquitoes) mean more
opportunities for parasitism to occur.

**Common Name:** Mound-building Termites

**Scientific Name:** *Macrotermiteinae* subfamily

**Region:** Africa

**Plate: Figure 3-28**

Termites are considered ecosystem engineers in many ecosystems because of
the valuable processes they control. The most conspicuous termites in Africa, and
consequently those most likely to be encountered on an ecotour there, are the mound-
building Macrotermiteinae. Occurring from Eritrea to South Africa, their large nests can
be seen in African savannas at concentrations of up to eight mounds per hectare, with
as many as 15,000 termites per square meter of each nest (Sands 1973, Wood and
Sands 1978, Wanyonyi et al. 1984). In tropical Africa, termites represent up to 65% of
the soil faunal biomass (Goffinet 1973). While individual termites, and even individual
mounds and colonies may not significantly alter soil composition, the cumulative
influence of termites in these high concentrations greatly affects levels of soil nutrients
and even gas emissions (Jones et al. 1990). Next to wildfires and ungulate grazers,
termites shape the landscape of the African savanna more than any other factor.

The mounds of African termites can be rather large, measuring up to five meters
high and cover an area of 50 square meters (Hesse 1955, Schuurman and Dangerfield
1996). The shape and structure of the mound is dependent on the species of termite,
but all are adaptable to meet the confines of soil composition and climate. If they are
unable to build their mound in their preferred way, they will adapt and build it dependent on the confines of their environment. The soil excavated by termites is regarded by indigenous tribes, agriculturalists, and scientists to be rich in nutrients and ideal for use in growing crops. Accounts also exist that animals may use termite mounds as salt licks, suggesting that the minerals and other nutrients unearthed in the mound construction process are preserved and integrated right into the mound structure (Hesse 1955, Jones 1990, Fox-Dobbs et al. 2010).

The termites found in Africa have a unique ally in the way that they feed. While they forage for dead wood and other rotting organic matter, they employ an interesting tactic to help them digest these foods. They farm a specific type of fungus to help them digest these plant-derived materials (i.e., wood, grass, leaf-litter) (Johnson et al. 1981). However, unlike the Leaf-cutter Ants discussed earlier in this Chapter, the termites do not eat the fungus. Instead they maintain what is known as a fungus comb.

Maintaining this *Termitomyces* fungus by adding partially digested plant material to it, they eat older parts of the comb (consisting of converted plant material), while the fungus spreads to the newer parts. Nearly all species of termites require some type of symbiosis in order to digest their food, but apart from these fungus-growing *Macrotermiteinae* termites, the symbionts are generally intestinal bacteria, archaea, or protists (Abe et al. 2000). There are currently 11 accepted genera of the *Macrotermiteinae* and 10 of them occur in Africa with a global total of over 330 species (Abe et al. 2000). The fungus *Termitomyces* is divided into over 40 species worldwide, with an unknown final count of the total variety found in Africa (Kirk et al. 2001). The
imbalance of termite to fungus species numbers suggests that multiple species of termites use the same species of fungus.

The mounds are perhaps the most topical aspect of African termite colonies, due to the visual reference possible during an ecotour. Often tall and chimney-like, these mounds are formed little by little, through the efforts of the termite workers excavating tunnels below the surface and using the soil to construct the aboveground structure. Typically composed of soil and decaying organic material mixed with saliva, the hollow cylindrical nature of the visible portion of the mound serves to thermoregulate (air-condition) the interior of the colony, while maintaining adequate moisture levels within (Luscher 1961). Just as with other eusocial insects described in this Chapter, the mound-building termites are separated into castes. An egg-laying queen produces the brood, the soldiers defend the nest against intruders, and the workers are further divided into numerous other roles, doing just about everything else required to maintain a healthy colony. While the above-ground structure of the termite mound can extend for many meters upwards, the underground portion of the nest is equally large, with various chambers to rear brood, store food, and house the queen. Not surprisingly, more sensitive members of the colony are kept deeper underground, where the temperatures are more stable throughout the day and night (Dangerfield et al. 1998).

Mounds are constantly expanded to make room for growing colonies, resulting in the movement of soil from deep within the earth to the outer edges of the mound structure (Pomeroy 1977). Although this seems like a simple procedure, the ramifications are vast, for this is why termites are often considered ecosystem engineers. By moving mineral-rich soil to the outer edges of the termite mound, they
are effectively releasing these minerals to the environment, especially as rains wash some of the soil off of the above-ground structure (Dangerfield et al. 1998). In addition, many mound-building termites choose areas that are naturally high in soil nutrient levels and mineral composition, as these soil components aid in creating the rigid structure of the mound. They are also integral in maintaining proper moisture levels (Hesse 1955, Fox-Dobbs et al. 2010). Lastly, the method in which mound-building termites excavate their nest further releases nutrients to the topsoil. By using their mouths to dislodge and carry soil to various parts of the nest, they are effectively breaking the soil into smaller components (Jones 1990). Generally speaking, the greater the total surface area exhibited by reducing the size of soil particles, the more that minerals and nutrients become available.

The implications of releasing more soil minerals and nutrients to the upper soil profile are wide-ranging. Grasses and shallow-rooted plants have better access to available carbon, nitrogen, phosphorous, and potassium (Jones 1990, Fox-Dobbs 2010). Large mammals not only use both occupied and unoccupied termite mounds for salt licks, acquiring minerals that are otherwise limited in the environment, but they also benefit from the increase in vegetative growth that results from increased soil nutrients (Hesse 1955, Loveridge and Moe 2004). For ungulates, they may benefit directly from more grasses to eat, and predators may benefit from the presence of larger, more numerous, and more nutritious ungulates (Loveridge and Moe 2004).

**Locating on ecotour.** Termites are ubiquitous in Africa and are especially abundant in arid zones, such as plains and savannas. They can be seen up to 2,000 meters in elevation, and due to the typical open topography where they are found, they
can be spotted quite easily from safari vehicles. At concentrations of up to eight mounds per hectare, they often dot the landscape, introducing ecotourists to mound-building termites on even the briefest of ecotours.

Mound-building termites present a fantastic example of how all of nature is connected. Even if a safari group is in Kenya primarily to observe large mammals, information like that presented above is not only critical in understanding why there are large mammals to be seen, but is also informative and interesting as an entomological ecotour feature.

**Common Name:** African Driver Ants  
**Scientific Name:** *Dorylus* spp.  
**Region:** Africa  
**Plate:** Figure 3-29

Driver Ants are to the Old World what Army Ants are to the New World. They are legionary ants that assemble and disperse in well-organized raids numbering in the millions (Rettenmyer 1983, Holldobler and Wilson 1990). The principal difference between Driver Ants and Army Ants, other than their origin, is that Driver Ants will routinely construct and reside in both above and underground colonies that persist for weeks and months. Nevertheless, they are most well known in Africa for their propensity to engage in foraging raids when food supplies are low within the colony (Holldobler and Wilson 1990).

Just as with all ants, they are eusocial insects, meaning that they have clearly defined castes (worker, soldier, and reproductive classes), an overlap in generations, and engage in cooperative brood care. Also common amongst ants and other eusocial
insects, the importance of chemicals used in communication is paramount to their survival. This is especially true with Driver Ants, as all members of the colony are completely blind (Holldobler and Wilson 1990). These chemical cues are critical in finding food, relocating the colony, defending against enemies, and provisioning the brood with resources.

Swarming raids can pose serious threats to humans and livestock, as a typical raid can have millions of individual ants, many of which are extremely aggressive. Soldiers will often act as sentries, even forming living tunnels of ants through which the smaller workers may pass safely. Although these swarms represent a potential threat, only those humans and animals that have restricted mobility are at risk. In fact, many rural villages in Africa embrace visitation from Driver Ants, as they will clean houses of food scraps, insects, rodents, and even venomous snakes.

Members of the Maasai tribe in Eastern Africa have found another use for these insects. Just as indigenous tribes in Central and South America have discovered, the powerful jaws of the soldier class of these ants may be used as an emergency suture to close open wounds. By capturing live soldier ants and instigating them to clamp down across two sides of a wound, they effectively form a medical-grade suture. Unfortunately for the ant, their bodies are then ripped off from the head to ensure that the muscles remain contracted and allow the jaws to stay closed for several days (Gudger 1925, Gottrup and Leaper 2004).

**Locating on ecotour.** Much like the Migratory Locust, Driver Ants are remarkable for not only their unique biology, but also for their numbers. Also like the Migratory Locust, finding a raiding swarm of Driver Ants is somewhat left to chance.
Nevertheless, there are several features that one may keep an eye out for in order to increase the odds of encountering a swarm. A swarming raid travels relatively slowly, and by the time the first part of a raid passes through an area, to when the end of the swarm has moved through, a raid may move only 20 meters in an hour (Holldobler and Wilson 1990). Although not obligately associated with rural settlements, swarming raids use them facultatively, meaning that these settlements serve as an optional food source for ants in the area. Talking with villagers is one way to get a sense of how recently a swarm has passed through and whether or not it would be feasible to still see a swarming raid in other parts of the village, or nearby areas.

Looking for ant mounds on the grassland landscape is also profitable, as Driver Ants are some of the only legionary ants that will form nests (Holldobler and Wilson 1990). In addition, Driver Ants are known to raid the mounds of other ants and sometimes termites, too (Bodot 1961, Gotwald 1974, Darlington 1985, Gotwald 1995). During the course of an ecotour, one may encounter a dozen or more ant and/or termite mounds. Apart from being lucky to encounter a raid while passing by a village, perhaps the best chance of seeing these insects is to keep an eye on their food sources, in order to try to witness a raid occurring in the wild.

**Common Name:** Birdwing Butterflies

**Scientific Name:** *Ornithoptera* spp., *Troides* spp., and *Trogonoptera* spp.

**Region:** Australasia

**Plate:** Figure 3-30

The Birdwing butterflies, aptly named because of their large size and resemblance to birds when in flight, include about 30 species and many more subspecies that occur
throughout southern Asia, Indonesia, New Guinea, Australia, and the Solomon Islands (Parsons 1992, Sands 2008). In addition to being some of the largest butterflies in the world, they are also some of the most vibrantly colored, attracting scientists and collectors alike for centuries. As some of the first entomological ecotourists explored these areas of the world, attraction to birdwing butterflies preoccupied even the most serious naturalists (Wallace 2007). However, western admirers are not the only humans to value the colors and patterns inherent in these organisms, for native populations of islanders and tribesman have long shown a penchant for collecting and proudly displaying these butterflies independently of outside influences. For example, Huli tribesman of the Wari Valley in Papua New Guinea use the wings of birdwing butterflies as headdress ornamentation, with the most colorful and rare specimens demonstrating seniority and prominence in their societies (pers. obsv.).

Birdwing butterflies undergo a lifecycle similar to other butterflies, in that they begin life as an egg before hatching into a larva with an insatiable appetite. Feeding on plants in the Aristolochiaceae (pipevine) family, they sequester chemical toxins early in life that render the adult butterflies unpalatable to most would-be predators. Nevertheless, several species of spiders and birds have found ways around the chemical defenses and actively feed on Birdwings (Common and Waterhouse 1981, Sands et al. 1997). Birdwings are found in a variety of habitats throughout their range, from lowland jungles to montane cloudforests. While species have individual ranges corresponding to their hostplants and preferred nectar sources, there is also a gradient of voltinism, as one goes from lowland coastal habitats to more mountainous ones. Generally, Birdwings are known to be bivoltine (two generations per year) at lower
elevations and univoltine (one generation per year) at higher elevations (Sands 2008). Adult Birdwings will generally survive anywhere in the range of several weeks to several months, with environmental conditions, such as availability of water and food, having the largest impact on their longevity (Braby 2000).

The beauty and intrigue associated with Birdwing butterflies makes them a perfect focus for entomological ecotourism. In fact, they were some of the first insects to be passionately involved in this unique brand of nature travel, as commercial butterfly farming and ranching has been in practice in the Australasian region for nearly 50 years (Parsons 1992, 1995, New 1994, U.N. 1997). While farming and ranching continues to provide economic support via the sale of specimens, both living and dead, new models in entomological ecotourism have identified the benefits of focusing on observation and photography. Perhaps no group of insects on earth is more suited to this new enterprise.

The most famous member of this group of insects is Queen Alexandra’s Birdwing (Ornithoptera alexandrae) of Papua New Guinea. As the largest butterfly in existence today, with female wingspans measuring over 25 centimeters, it is also one of the most restricted in range. It is as much a symbol of the beauty of nature as it is of fragility and conservation in Papua New Guinean biodiversity (Parsons 1984, 1992). Listed as a CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix 1 species, it remains heavily protected in its tiny remaining lowland habitat in the Popendetta region, where it lays eggs exclusively on the vine Aristolochia diehlsian (Cranston 2010). In an effort to safeguard the long-term protection of birdwings and other insects in general, Papua New Guinea created the Insect Farming
and Trading Agency (IFTA), which oversees any commercial production or trade of birdwings and other valuable insects. By permitting controlled trade of common species of birdwings (but not Alexandra), black market values have decreased significantly for all Birdwing species, discouraging illegal capture and trade (Parsons 1992, 1995, Gullen and Cranston 2004). This model has been adopted by over 450 villages throughout the country of Papua New Guinea and functions to not only curb illegal commerce in insect trade, but also to popularize the study and admiration of Lepidoptera (Gullen and Cranston 2004). Replicable in numerous other countries, and with many other flagship species of insects, the Queen Alexandra’s Birdwing has been responsible for many positive changes in the way that insect conservation is carried out in developing countries.

**Locating on ecotour.** Birdwings are found at a range of elevations, from sea level to over 2,000 meters. While they must breed in areas rich in *Aristolochia* vines, adults may be found outside of this range when searching for nectar sources. Nevertheless, they are most often found in primary and healthy secondary forests searching for food resources and/or mates. Well-endowed nectar sources, such as bushes of *Hibiscus*, are opportune areas at which to sit and wait for the arrival of Birdwings throughout the day. Although males are the more brilliantly colored, female birdwings are often larger and, despite their more muted black-and-white appearance, are equally exciting to see in the wild. As their name suggests, these butterflies very much look like birds flying, so observation from afar should take this into account. Perhaps not coincidentally, these butterflies will often fly in areas that are also frequented by swallows and swifts, which are very similar in appearance from a distance.
**Common Name:** Monarch Butterflies

**Scientific Name:** Danaus plexippus

**Region:** World-wide, with annual migration in North America and Mexico.

**Plate:** Figure 3-31

Well-studied by scientists and well known by the general public around the world, the Monarch butterfly may be considered the most popular butterfly on earth. In fact, in tropical butterfly exhibits, it is the Monarch butterfly that is most eagerly sought after, even as iridescent Blue Morphos, African Charaxes, and Birdwing butterflies flit by visitors (J. Hansen, pers. comm.). This is not to say that the Monarch is lacking in charisma, though, as it has rightly earned its regal reputation. It exhibits striking coloration, is found around the world, and demonstrates fascinating migratory behavior. Similar to most other butterflies, Monarchs lay their eggs on larval host plants to begin the life cycle of the next generation. In the case of Monarchs, these larval host plants are Milkweeds (in the family Asclepidaceae), which contain various levels of toxins that the larvae readily consume in order to protect themselves from hungry predators during all life stages. After progressing through five larval stages, or instars, they pupate, and then after a few days will emerge as a fully formed adult Monarch. In general, adults will live for about one month and males spend the majority of their time searching for a mate with which to reproduce. For females, after an early mating, their life is spent searching for host plants and laying eggs, in order to begin the cycle all over again. However, this simple life cycle is not observed for all monarchs, as a great number of them in the last generations of each summer deviate from this program and engage in an annual fall migration from North America to Mexico to pass the winter.
Each year, approximately two billion Monarchs migrate from the eastern United States, flying over 2,000 miles before reaching a series of overwintering sites in southern Mexico to spend the winter (Urquart and Urquart 1976, 1978). Divided in recent years among 12 separate colonies, these overwintering Monarchs cluster by the millions on Oyamel Fir Trees (Abies religiosa) in relatively predictable areas throughout the apex region of the Transvolcanic Range between the southern termini of the Sierra Madre Oriental and Sierra Madre Occidental. From November to March of each year, these butterflies attempt to remain relatively dormant, or quiescent, leaving their tree roosts only occasionally to drink from nearby streams, or to feed on nectar from flowering plants (the genera Senecio, Lupinus, Salvia, and Verbesina being most common sources) (Brower et al. 1977). However, as mid-day temperatures warm throughout the season to the 60s and lower 70s degrees Fahrenheit, butterflies exposed to sunlight will leave their roosts by the tens and hundreds of thousands. Flying through the air for brief periods of time in order to thermoregulate, they will resettle and join the colony clusters in shaded areas once again after reducing their body temperature (Brower et al. 1977, Calvert and Brower 1986). Because of the incredible efficiency with which they fly and glide, the convection of cool air passing over their wings during flight significantly lowers body temperature, conserving their fat and lipid stores, which could be depleted if they become too warm (James 1986, Masters et al. 1988, Alonso-Mejia et al. 1997).

The storage of fats and energy is vital to their survival, as only a small percentage of Monarchs will feed while in their overwintering grounds. They must use their stored food and energy, acquired during their southward migration, to last for the entire
overwintering period before powering them to start out on their last leg of the journey – their return flight northward in the spring (Masters et al. 1988). Just as the Monarchs are triggered in the fall to migrate southward by shortening day length, cooling temperatures, and a lowering of the sun’s zenith in the sky, the lengthening of the days, warming temperatures and raising of the sun’s zenith stimulate Monarchs to migrate northward in the spring (Goehring and Oberhauser 2002). As the spring equinox approaches, the Monarch’s reproductive diapause ends, meaning that they begin to search for mates and reproduce. The overwintering colonies then start to break up, initiating the northward migration and return to the U.S. (Herman, 1981, 1986, Herman et al. 1989). It is during these middle four months that some of those colony sites open to ecotourism (five at present count, pers. obsv.) will collectively receive upwards of a quarter million visitors each year (Barkin 2003).

What makes the migration of the Monarch butterfly so unique is not just the fact that it occurs with such a simple organism, but that nearly every part of the migration is owed to genetic programming (Reppert et al. 2010). Each migrating monarch is participating in the journey for the very first time, without any benefit of parental imprinting or learning (Brower 1985, 1995). In fact, there are at least two generations of Monarchs between migrating generations each year, meaning that it is the grandchildren or great grandchildren of each generation that participate in the migration the following year (Malcolm 1993). Those intermediate generations are considerably shorter in lifespan (one month, as an adult) and also have shown no tendency to migrate, even when subjected to environmental conditions comparable to those
experienced by the migrating, or methuselah, generation (Urquhart 1960, 1966, Brower 1961).

Navigation by Monarchs is perhaps one of the most fascinating components to their biology and incorporates several tactics, since no learning between generations takes place to help in guiding the Monarchs to the ancestral overwintering grounds. The first level of navigation employed by Monarchs is the use of what is known as a time-compensated sun compass (Reppert 2007). The path of the sun is a predictable tool for orientation, in combination with a circadian clock that allows the Monarch to adjust for the movement of the sun at 15% longitude each hour by employing an internal timing device. The Monarch continuously tracks the sun across the sky in relation to the time of day, anticipating its location and able to take accurate readings, no matter where the sun is in the sky. Therefore, the compass part of the term signifies the use of the sun as a directional tool, with the time-compensation part allowing for adjustment in accordance with the sun’s movement across the sky. In order for these two components to be integrated and continue to work throughout the migration, both the circadian clock and sun compass must be adaptable to changes in environmental, atmospheric, and geographic conditions.

The second tool that is employed by monarchs is an internal magnetic compass (Jones and MacFadden 1982). Possessing magnetite, a magnetic iron-oxide metal, migrating Monarchs may exercise magnetic navigational tactics to aid in their orientation. Although this would certainly help to explain the persistence of proper orientation on cloudy days when even the e-vector of polarized light may not be visible, there also exists evidence against this theory. The use of magnetic poles in monarch
navigation theory remains to be controversial, with evidence both for and against it appearing in the literature.

It is difficult to assume that this simple bearing is sufficient for the remarkably precise navigation ability observed, for Monarchs roost in the same locations year after year. Monarch antennae have been seen to be critical in the navigation process when perceiving sunlight, and it is possible that they are further involved at the chemoreception level. Although relatively unsubstantiated, many scientists working with Monarchs believe that olfactory cues, either from dead monarchs, monarch scales, or volatile chemicals from the Oyamel Firs, could be cues for locating appropriate colony sites (Bingman and Cheng 2005). Additionally, distinct changes in barometric pressure or wind speed, when Monarchs cross particular mountain passes or other geographic landmarks, could be perceived by monarch antennae. This has already been shown to occur in other insect species and likely apply to Monarchs, too (Kamicouchi 2009, Sane et al. 2007, Yorozu et al. 2009).

The migratory behavior and navigation techniques remain a mystery, to some extent, as researchers continue to come up with new questions at the same rate that others are answered. However, a more complete picture is being assembled that sheds a great deal of light on this amazing phenomenon. Coupled with new discoveries regarding their migratory behavior are discoveries in many other fields to which the Monarch butterfly complex may apply. Novel research, including such areas of study as genetics, disease transmission, and medicine. Current research on the Monarch butterfly serves a multitude of research goals.
Locating on ecotour. Monarchs are now found on every continent except for mainland Asia and Antarctica, but are clearly neotropical in origin. Because they feed on plants in the Milkweed genus, *Asclepius*, they may be found in a diversity of habitats, from rural fields, boreal forests, tropical jungles, and savannas. While any sighting of a Monarch butterfly is an opportunity for an ecotour guide to begin the discussion on their incredible migratory behaviors, the major migration event itself takes place in North America and Mexico (there is regular small north-south movement now established in eastern Australia). As Monarchs fly south on their journey to the overwintering grounds each fall, they invariably stop at multiple localities to feed on nectar and briefly rest before the remainder of the journey. In early 2012, there were 5,299 registered Monarch Way Stations that serve to provide Monarchs with suitable habitat at any stage of their journey. Organized by Monarch Watch, these way stations are excellent places to observe the southward migration in the fall, as well as the northward migration in the spring of each year. In addition, there are several well-known Monarch stopover areas in the United States and Canada that experience visitation by thousands of Monarchs each year (Walton and Brower 1996). These localities include Cape May, New Jersey (Walton et al. 2005), Chincoteague National Wildlife Refuge, Virginia (Gibbs et al. 2006), Long Point, Ontario, Canada (Crewe et al. 2007), Peninsula Point Recreation Area, Michigan (Meitner et al. 2004), and the St. Marks National Wildlife Refuge, Florida (pers. obsv.). All represent great areas to witness large numbers of Monarchs. However, these cannot compare to the magnificent spectacle of Monarchs in their overwintering colonies in Mexico. Located roughly 100 miles west of Mexico City, there are currently five monarch colonies open to the public. Three of these are significantly
more consistent for high population numbers from year to year. These include the El Rosario, Sierra Chincua, and the Cerro Pelon colonies, located near the town of Angangueo, in the State of Michoacan.

**Common Name:** Acacia Ants

**Scientific Name:** *Pseudomyrmex* spp.

**Region:** Neotropics

**Plate:** Figure 3-32

Mutualistic relationships between organisms in the tropical rainforest may best be personified by the fascinating world of the Acacia Ants. This type of symbiosis yields benefit to both species involved, which in this case are the Acacia Ant and the Acacia tree. Although this mutualism involves a matching between several different species of *Pseudomyrmex* ants and several different species of *Acacia* trees, the behavior and life cycle are very similar in any combination of ant-acacia mutualisms (Janzen 1966, Janzen 1983).

The relationship begins with a newly mated queen. Upon mating in flight, she sheds both her wings before searching for a suitable Acacia on foot. Depending on the species, the queen may prefer Acacia trees in open pastures with full sun or trees found in dense understory with little sunlight (Janzen 1983). Others may be opportunistic and be adaptable to any habitat they find. Once she has located a suitable tree, she will chew a hole in a new green thorn and then hollow it out from the inside, forming a nesting cavity. Here, she will deposit her first batch of eggs to create much-needed workers (Janzen 1967, 1983). Next, the queen will need to feed, as her initial search for an appropriate tree could last as long as a month without eating (Janzen 1983). The
Acacia Tree fortunately provides two sources of nutrition to nourish its ant inhabitants. The first is what is known as Beltian bodies. Located at the tip of leaflets of tropical Acacia trees, they represent an essential protein, nitrogen, and lipid source for these mutualistic ant species (Belt 1874, Darwin 1877, Janzen 1967, Rickson 1975). These plants are also endowed with foliar nectaries that are located at the base of mature leaves, a vital source of sugars and carbohydrates for the Acacia Ants (Janzen 1966).

The founding queen will take advantage of these nutrients, but judiciously, for if a rival queen finds her newly excavated thorn unattended, the rival queen will kill the brood and displace the original founding queen. In fact, Janzen (1983) observed that in areas of high Acacia density, a young Acacia will have several thorns occupied by competing queens, with up to a dozen more “thornless” queens searching on the surface of the plant for an available home. Once a single queen acquires a mature group of workers, they will evict and kill the competing colonies until only the single colony remains (Janzen 1966, 1975, 1983). These workers will also indulge in the productive nectaries and Beltian bodies for their own nutrition, as well as to feed the brood. A mature colony will often have 15,000 workers, 2,000 males, 1,000 virgin queens, and 50,000 larvae and last upwards of 20 years, all dependent on the longevity of the single egg-laying queen (Janzen 1983).

This seems like a lot of intrusion on part of the ants, so the benefit to the plant must be significant. It is, for the ants protect the Acacia vehemently against other organisms, including herbivorous insects and vertebrates, by stinging and biting trespassers. They will also defend the Acacia against the encroachment from other plants, especially vines (which could compete for soil nutrients or sunlight) by “mauling
them with mandibles” as described by Daniel Janzen (1966). This habit also creates a natural fire-break free of dry vegetation around the ant-occupied Acacia, which frequently saves both the tree and the ant colony during periodic fires in the dry season of each year. Having lost the ability to produce plant secondary compounds for defense, Acacia trees depend heavily on ant protection (Janzen 1967). In fact, during the early stages of life, Acacia trees without ant inhabitants are noticeably unhealthy and vulnerable, growing very slowly due to the constant need to invest energy in the regrowth of leaves due to herbivore attack. When comparing the growth and viability of occupied versus unoccupied Acacia, those trees with Acacia Ant inhabitants demonstrate exponential growth and superior viability (Janzen 1966).

Although the Acacia Ants actively guard against intruders, both in the animal and plant kingdom, several organisms have found a way to bypass the defenses of these vigorous ants. The best example is with several bird species, including Orioles, Wrens, and Kiskadees. Upon first establishing a nest in an occupied ant-Acacia tree, Acacia Ants will attack the intruding bird and the developing nest. However, after a variable amount of time, the colony becomes acclimated to the bird nest and the ants cease their attacks. Presumably, the nest goes through a period of chemical acclimation, where the scents of the ant colony are deposited on the bird nest from contact, thus masking any foreign presence. Acacia Ants rely greatly on chemical perception and although seemingly obtrusive to the eye, a properly scented bird nest is ignored (Janzen 1969, Young et al. 1990). The risk of serious harm due to ant attack is possible for the bird choosing to establish a nest in the ant-Acacia tree, but just as the tree gains rewards from the ants, so does the bird. Essentially becoming a feature of the tree, the nest is
defended against intruders as intensely as the tree itself by the Acacia Ants. Egg predation is a major concern for nesting birds in the tropics, and Young et al. (1990) showed that choosing the right Acacia tree greatly reduces this risk with the help of ant defenses.

The ant defenses are quite potent and serve to dissuade most intruders from Acacia trees. However, the Ant-Acacia Beetle is impervious to the stinging and biting attacks of Acacia Ants and represents one of the major threats to the health of ant-Acacia trees (Janzen 1983). Having a heavily sclerotized cuticle, the only vulnerable areas on these beetles seem to be the mouthparts. However, when a lucky ant targets this area and succeeds in delivering a sting or bite, the beetle merely sweeps it away and continues to feed on the new growth of the Acacia leaflets (Janzen 1983).

**Locating on ecotour.** The ant and Acacia mutualism is best observed in the dry forests of the neotropics, but can be found in most lowland and montane rainforests as well. Locating individual trees is relatively easy, as they have conspicuous bull-horn-shaped thorns, giving way to one of their many common names – the Bullhorn Acacia. Most mature Acacia trees are occupied, but looking for circular holes near the tips of these large brown-colored thorns is a sure sign of occupation by Acacia Ants. Oftentimes, the ground surrounding the Acacia will be cleared of leaf-litter, as if someone swept the soil with a rake. This is just another tactic by these tedious ants to guard their home from invading vegetation (Janzen 1966).

If ants are not present on the outer surfaces of the Acacia leaves and stems, simply tapping the trunk or individual thorns will elicit a response, generally resulting in
dozens of ants pouring out of the various thorns, aggressively attacking anything still in contact with the tree (i.e., a finger or a hand).

**Common Name:** Hercules Beetle

**Scientific Name:** *Dynastes* spp.

**Region:** Neotropics

**Plate:** Figure 3-33

With over 300,000 species of beetles on earth, this order of insects has tremendous potential for being significantly integrated into the ecotour. In addition, they are often large and easily encountered both at night and during the day. While there are many exciting species of beetles that can be showcased on any ecotour, those in the genus *Dynastes* are some of the most charismatic. For examples, males of *Dynastes hercules* (perhaps the most likely to be seen representative of this genus on a neotropical ecotour) can be up to 82 millimeters in length and over 25 grams in mass. In addition, the males often have large curved horns protruding from the front of the head, and smaller thorns off the pronotum. They have been tested to carry up to 850 times their own weight, making them, gram-for-gram, the strongest animal on earth (Moron 1997). Although their coloration is usually some combination of subdued brown, black, and sometimes greenish yellow, their size and superlative strength makes them an ecotour highlight when found. Females are no less spectacular, but are generally smaller and lack horns. This is because the horns largely function as tools used in dominance battles between males (Beebe 1949). Using the curved horn, they will attempt to flip the competing male onto its back (Howden 1983). Although these beetles are capable of flight, their tremendous mass prevents them from being able to
open their elytra (the hard-shelled forewings) to expose their two membranous wings in order to flip themselves back upright. A loss in a dominance battle does not necessarily mean assured death to the loser, for these beetles can eventually flip themselves back over, but precious time is lost in courting females with which to mate.

Once mated, a female must find an appropriate log in which to deposit her eggs. Because the development time for most Dynastine larvae is on the scale of three or four years, the female must choose a log of considerable size, for several years of weathering and decomposition in neotropical jungles will disintegrate all but the largest of fallen trees. Once the egg hatches, the beetle grub (or larva) will consume the wood pulp until ready to pupate and ultimately emerge as an adult. Just as the larvae of Dynastine beetles feed on wood, so do most adults. Peeling away the bark and feeding on the cambium layer, scaring on various species of trees presents evidence of their behavior (Menke and Parker 1988). However, adults of many species of Dynastine beetles, especially those in the neotropics, will readily eat sugary fruit, as well.

**Locating on ecotour.** Because the life cycle of these beetles depends so heavily on large trees, these beetles are good indicators of high quality forest. Areas that have been cleared in recent history, without ample time for larger trees to grow and then die naturally, are generally void of these large beetles.

Since there are many species within this subfamily, a wide range of altitudinal zones are covered, with these beetles found in some cases up to 2,500 meters. However, they are more likely to be seen at mid and lower elevations, from 1,500 meters and below. Locating the grubs may be fascinating, but destructive, as it would necessitate the opening of fallen logs. This could ruin prime habitat for these beetles.
The best way to include these creatures on an ecotour is to patrol lighted paths at night around lodges and hotels. They are readily attracted to bright lights at night and will often fly into lighted areas individually, “landing” with a large thump and collision. They have not perfected the art of landing very well. Most adults have been noted to come into lighted areas in the middle of the night, therefore, waking up early to walk along lighted paths is equally rewarding, when searching for these insects.

**Common Name:** Hercules Moth

**Scientific Name:** *Coscinocera hercules*

**Region:** Australasia

**Plate:** Figure 3-34

The Hercules Moth is appropriately named, as it is one of the largest moths in the world, measuring over 27 centimeters in wingspan (Zborowski and Edwards 2007). A member of the Saturniidae, or silk moth family, it actually faces quite a bit of competition for largest moth, as a great many other species are within close range of the Hercules moth. Most notably are the Atlas Moths (*Attacus atlas*), which can exhibit wingspans over 25 centimeters (Common 1990).

Much like other members of the Silk Moth family, adult Hercules moths do not feed and in fact do not even have mouthparts. Hercules Moths are very short-lived, with the time between eclosing from their pupal stage and dying only lasting three to five days (Common 1990). Although short adult lifespans are common amongst Silk Moths, in general, it is relatively uncommon that insects of such large size expire so quickly. During their adult stage, they are solely consumed with mating, reproducing, and laying eggs. Since they have very little time to accomplish this, they naturally have evolved
extremely sensitive mate-locating sensory organs. Male moths are able to fly upwind of pheromone plumes, emitted by female silk moths, at extremely low concentrations and erratic distributions (Baker et al. 1985). While the concentrations and pheromone compositions may differ between species, both males and females utilize these highly specific tools with incredible efficacy, able to locate mates from several miles away (Kaissling et al. 1978).

Larvae of Hercules moths are equally impressive in size, measuring up to 10 centimeters in late-stage instars (Common 1990). Upon reaching their final instar, larvae will undergo the typical transformation that all Lepidoptera go through, by reorganizing their internal cells and external morphology, in their pupal stage. However, Silk Moths undergo pupation within a silken cocoon, acting as a protective case for the pupa which is spun out of silk excreted by the larva itself prior to pupation. The most famous silk moth, *Bombyx mori*, has been used in Asia for centuries as a producer of silk for commercial use in the clothing industry.

**Locating on ecotour.** Silk Moths in general are somewhat of a staple in the entomological ecotour. Attracted to lights at night, a diversity of Silk Moths may be found by doing little more than spending several minutes checking lights at the perimeter of natural areas around ecotourism lodges and hotels. Hercules moths are no exception to this strategy. In fact, they are rather difficult to find without using this night light technique. Only a few minutes spent checking the immediate areas surrounding lights may yield several Hercules moths.

As Hercules moths are found in tropical Australasia, their seasonality is dependent more on rain cycles rather than traditional summer/winter cycles found in more
temperate habitats. Silk moths in general are most likely to be found during rainy seasons on nights with cloud cover, or during the new moon phase.

**Common Name:** Homerus Swallowtail

**Scientific Name:** *Papilio (Pterorus) homerus*

**Region:** Caribbean (Jamaica)

**Plate:** Figure 3-35

The Homerus Swallowtail is recorded as being the largest butterfly in the western hemisphere and is found only in Jamaica (Garraway et al. 1993, Emmel 1995). Adult wingspans measure over 15 centimeters and, as with most butterflies, the female of the species is larger than the male. Males engage in dramatic territoriality battles between themselves, colliding violently in mid-air, resulting in permanent wing-damage for battling individuals (Lehnert 2005).

The size of *Homerus* alone would attract considerable attention to this insect, but this butterfly is also critically rare and endangered. It is currently listed in the IUCN Red Data Book, *Threatened Swallowtails of the World* (Collins and Morris 1985) and is an Appendix 1 species under CITES and the Jamaican Wildlife Act of 1988. An icon for conservation in Jamaica, it is used as a symbol for the Jamaican National Park system and is also an emblem of rarity in the world of butterfly research and ecotourism.

Originally found throughout the island nation of Jamaica, in seven of the 13 parishes, the range of the Homerus Swallowtail is now found in only two primary locations in the country (Emmel and Garraway 1990). Separated by relatively inhospitable habitat, made up of urbanized towns, coffee plantations, and other agricultural landscapes, the two extant populations are on opposite sides of the country,
with one found in the eastern John Crow and Blue Mountains and the other in the western Cockpit Country. In fact, the divergence in these populations is significant enough to have resulted in employment of different larval hosts, with the western population feeding on _Hernandia jamaicensis_ and the eastern population feeding on _Hernandia catalpifolia_ (Emmel and Garraway 1990, Emmel 1995). However, in this case, host plant usage may have more to do with the availability of such plants in their respective ranges, rather than an evolved selection.

Adults have been recorded to fly during all months of the year, except for January and sometimes February, making the Homerus Swallowtail reasonably reliable from a tourism standpoint (Garraway et al. 1993). However, throughout the past several decades, additional conservation concerns have emerged from time to time, mostly stemming from deforestation practices and implementation of monocultures in cleared lands surrounding protected areas. As mining, deforestation, and agriculture encroach on _Homerus_ habitat, protection becomes tenuous. Ecotourism may play a key role in the future, as local landowners begin to realize the monetary potential of showcasing this spectacular organism to interested nature travelers from around the world.

**Locating on ecotour.** The eastern population is better known, in terms of accessible localities, and more studied, yielding a better overall understanding of the needs and priorities involved in conservation work. However, the land area over which _Homerus_ may be found is significantly larger in the western population than the eastern one, suggesting that the two areas are equally balanced for pursuing the butterfly and witnessing its soaring flight, impressive territoriality, and various life stages. In the eastern population, the villages in the Rio Grande Valley and the Rio Grande Field
Station, as well as the town of Bath, have served as important waypoints in locating *Homerus*. However, for spotting this butterfly anywhere in the country, trained guides should accompany any group, as while territories can be predictable and reliable, they may change throughout the seasons (pers. obsv.). In the western population, the town of Elderslie serves as the starting point for entering habitats in the Cockpit Country in which *Homerus* may be found. Open clearings with suitable nectar sources are ideal areas to use the sit-and-wait approach, but as Lehnert (2005) reports, adult males may be located by listening for the crack of their wings striking against one another, while engaging in territorial battles.

**Common Name:** Lantern Fly  
**Scientific Name:** *Fulgora lanternaria*  
**Region:** Neotropics  
**Plate:** Figure 3-36

Contending for the most bizarre-looking insect to be showcased on an ecotour, Lantern Flies are not actually flies at all. They are sucking insects (Hemiptera: Fulgoridae), more closely related to a common cicada than to any sort of fly (in the order Diptera). Their most diagnostic feature is the large peanut-shaped head protrusion, often leading to the common name of Peanut-head Lantern Fly. This gaudy appearance has landed it into tropical mythology. Well-known throughout Central America and northern South America, there is folklore that if a girl is stung by one of these insects, she must go to bed with her boyfriend within twenty-four hours or she will die (Janzen and Hogue 1983). While it would break the hearts of teenage boys all over the neotropics to learn that Lantern Flies are in fact harmless and have mouthparts
adapted to piercing the phloem of plants, not humans, there exists no evidence for the myth’s validity (O’Brien and Wilson 1985).

The unusual appearance of the Lantern Fly is not solely to increase its popularity among entomologists and to fascinate ecotourists. The peanut-shaped head protrusion is believed to function as a defense against predation. Resembling the head of a lizard or small caiman, some suggest that this deters predation from some bird species (Anonymous 1933, Janzen and Hogue 1983). However, this is not their only defense. They also have pronounced large eyespots on the upperside of their hind wings that serve to induce a “startle reflex” by predators (Janzen and Hogue 1983, Costa-Neto and Pacheco 2003). With the eye spots up to 10 centimeters apart from each other, it gives the impression that the insect is much larger than it actually is. From the predators perspective, the Lantern Fly could instead be a large vertebrate that would like to predate upon the potential predator. If the reptile mimicry and eyespots are not enough to deter predation, they also are known to employ a chemical spray, much like a skunk. Should a predator come too close, the Lantern Fly will rapidly take flight and broadcast this spray in an attempt to coat the predator, providing the Lantern Fly with enough time to escape.

These defensive behaviors would rather not be employed by the Lantern Fly, as this would mean that they were on the brink of survival. Their main tactic is crypsis. They choose to rest on trees that allow them to be camouflaged. Aligning themselves vertically to match the lichen, moss, and bark pattern, they remain motionless for much of the day (Janzen and Hogue 1983).
There is an overwhelming fear of this insect among indigenous communities in the Amazon region. Mostly, this is due to the threat of being stung by their ferocious-looking mouthpart – termed their murder dart by Cruz (1935). However, it is not just their effect on humans that has people worried about their presence. There are numerous sentiments by indigenous communities that the Lantern Fly is responsible for most tree deaths in the jungle (Costa-Neto and Pachaca 2003). It should be noted here that there is no scientific evidence of Lantern Flies causing widespread damage. However, because they are phloem-feeders, it is entirely possible that if they are feeding continuously, they could reduce the health of a small tree to the point of causing mortality. In addition, diseases transmitted by phloem feeders have been widely documented, further supporting their claim (Coley and Barone 1996).

**Locating on ecotour.** The best chance of seeing a Peanut-head Lanternfly is to attract it to the lodge, hotel, or field station at which the group is staying the night. By setting up a light trap facing the jungle, there is a chance that they will come to you, instead of you going to them. Nevertheless, they may be found without the use of traps, too. Generally, they are found positioned vertically on a tree trunk, singly or in pairs. They are cryptically colored, so it is best to look for lichen or moss covered tree trunks that are light green to yellow-brown colored. Occupying lowland habitat, they are rarely found above 500 meters. Despite their lowland preference, they tend to avoid wetter areas and give priority to drier forests in rain shadow areas, topographically speaking (pers. obsv.). This does not mean that they avoid rain altogether, as they have been noted to be most common at the start and end of rainy seasons (Janzen and Hogue 1983).
Additional Entomological Ecotour Topics

The previous section identified individual insects that should be prioritized as attractions within general ecotours. However, many important insects are too difficult to locate due to their cryptic coloration, their small size, or remote habitat (e.g. deep in the leaf litter or high in the forest strata). This is not to say, though, that they cannot be integrated into general ecotourism in a similar manner as the previously described insect ambassadors. In many cases, insects are involved in critical ecosystem processes that are equally interesting and important subjects for entomological ecotourism interpretation. The following sections will highlight three key topics of entomology that can be easily integrated into existing general ecotours, regardless of the destination. While these topics are specific, focusing on (1) insect herbivory, (2) pollination, and (3) nutrient cycling, they present opportunities to talk about a broader range of entomological topics as well. Terms and concepts such as holometaboly vs. hemimetaboly, or kairomones vs. allomones, are difficult to bring up independently during an interpretative discussion in the field, but with the help of these guiding topics, detailed entomological discussions will present themselves cogently throughout the course of any ecotour. In order to provide context for each interpretive opportunity, suggested catalysts for such opportunities are also provided, as ways to trigger naturalist guides to bring up the topic of insects.

Insect Herbivory

**Triggers – Insect leaf damage.** There is widespread evidence visible to any observer, that insects feed on plants. Often in their larval stage during this process, insects will feed on leaves and plant material to gain the necessary nutrients to undergo complete development to adulthood. Having distinct larval and adult stages separated
by a pupal stage is termed Holometaboly. This is the typical case of an insect egg hatching into an immature larva (e.g., a caterpillar, in the case of Lepidoptera), before transitioning to the pupal stage, and ultimately becoming an adult insect that bears little resemblance to any of its previous life stages. Holometaboly is in contrast to Hemimetaboly, where the insect makes a gradual shift from immature adult (or nymph) to fully mature adult, often changing only slightly in appearance, other than overall size. Usually, these differences are exemplified by the enlargement of wings, externally, and the maturation of genitalia, internally.

Insect herbivory is critical to the health of insects, as it is during their younger stages that the insect is very much an eating machine, adapted to consume large quantities of plant material through the use of powerful mandibles, and a specially designed digestive system to handle large amounts of course plant material. While plant-eating insect larvae have stomachs that are lined with a protective membrane and facilitate constant consumption, digestion, and absorption of nutrients, other insects exhibit different kinds of adaptations. Blood and liquid-feeding insects, such as mosquitoes and other biting flies, have little need for any protective lining in the stomach due to their liquid diet and have traded unnecessary tissue for the ability to expand their stomachs upon feeding. Because blood feeders feed more intermittently than plant feeders, their stomach must be able to handle large stores of food, much like snakes or large felines that gorge themselves opportunistically, but infrequently.

Plants, although rooted and sedentary in nature, are somewhat opposed to being eaten and thus have evolved several types of passive defenses to discourage herbivory. Depending on the species of plant, one or several of these defenses may be
used at the same time to deter insect feeding. One defense is for the plant to emit volatile plant compounds upon the initiation of feeding by insects. These compounds serve several purposes, but generally one compound type is favored by the plant (i.e., more resources are allocated to its functionality). The form and function of the chemical depends on the type of habitat, insect, or general environmental conditions. First, the emission of these volatile plant chemicals may be used to alert predators and parasites to the availability of the insect herbivore as a potential prey item or host. This acts like a dinner bell that can signal predators and parasites that food is available. The more insects that are feeding, the more volatiles that are released, which all signify the availability of a greater potential food source (i.e., more insects to eat or parasitize). These types of volatiles described here are termed kairomones, because they are perceived by a different species than that which is producing the chemical, and serve to benefit the perceiver. In this case, the perceiving organism follows the chemical trail to find the plant that produced the chemical, and then encounters the insect prey. Kairomones are in contrast to allomones, which are also volatile chemicals emitted by an organism intended to interact with a perceiving organism. However, allomones are produced solely for the benefit of the emitter, not to the benefit of the perceiver. These chemicals may yield a noxious smell or other feeding deterrent that discourages the perceiving organism (i.e., insect) from feeding on the producing organism (i.e., plant).

Another way for plants to discourage herbivory is by producing feeding deterrents. These are often secondary plant compounds (primary compounds being those that the plant uses for its own health and maintenance) that are either toxic or indigestible to the insect herbivore. These are metabolically costly to make on part of the plant, and
consequently are used sparingly. Milkweed is a good example, as the white latex that flows from damaged plant tissue, in response to feeding, is toxic to many invertebrate and vertebrate herbivores. Oak tree leaves contain large quantities of indigestible tannins, which are best exemplified by their effects on the color of fresh water, often turning rivers brown with the color of these tannins. These same tannins discourage feeding by insects, as they reduce the ability of an insect to digest the plant food. Because feeding by insects increases the time spent moving about and more visible to other organisms, feeding makes them relatively vulnerable to predation and parasitism. Therefore, it is a waste of time and generally unsafe to consume indigestible leaves, which discourages feeding on such plants.

In some rare cases, plants employ a livelier means of defense. Some species of Acacia plants house Acacia Ants within the confines of their thorns and branches. These ants will actively defend the Acacia against herbivory by attacking any intruder, whether it is a small beetle or a full-grown deer. However, these ants do not put their own lives on the line for nothing. They are rewarded for their loyalty to the Acacia with sweet foliar nectaries that provide sugar and protein and lipid-rich Beltian bodies, which are located at the tip of the leaves.

The majority of plant herbivory is due to Lepidoptera (butterflies and moths) and Coleoptera (beetles) feeding as immature larvae. Although not exhibiting actual herbivory, because they do not physically consume the leaves, Leaf-cutter Ants also represent threats to plants because they harvest leaf material to feed to fungi. Figure 3-2 shows the types of plant damage likely to be found on an ecotour in the neotropics.
Pollination

**Triggers – Presence of flowers, pollinators (e.g. bees, butterflies).** Insects are excellent pollinators, with much of their success due to the fact that insects and flowering plants have coevolved with each other for the past 60-85 million years (Ehrlich and Raven 1964). In fact, diversification of flowering plants and insects seem to be concomitant, according to the fossil records of both (Dilcher 2000). While insects contribute much to pollination in all environments, tropical habitats often see more insect pollination, as plants in temperate habitats frequently rely on the wind to aid in pollination, a process known as anemophily. Gymnosperms, like conifers, pines, and firs, benefit most from wind pollination, as is evident from their highly exposed cone-shaped reproductive structures. In contrast, flower-producing angiosperms rely on insects and vertebrates to share pollen between conspecifics and ultimately reproduce. As a reward, these flowering plants offer various food sources to the potential pollinators. The most common reward is sugary nectar. Fueling a great many insect species, carbohydrate-rich nectar is a staple food source that lures pollinators to the reproductive parts of these plants – the flowers. An insect feeding on flower nectar is forced to come into contact with the plant reproductive organs, either by brushing against the pollen-producing structures, thereby picking it up accidentally on its body hairs, or unknowingly depositing pollen that had been picked up from a previous visit to a different flower of the same species. It is a widely accepted belief that insects and angiosperms have coevolved throughout the millennia, resulting in flower nectar sources being located in areas of the plant that virtually guarantees such “accidental contact” between the insect and the plant reproductive organs. While some plants have both male and female reproductive parts on the same flower, others do not, and,
therefore require these insect vectors to aid in transferring the male pollen gametes to the female ovaries. Still, even in those plants with both pollen-producing structures and ovaries on the same flower, it is advantageous for insects to cross-pollinate. This exchange of gametes between adult flowers (rather than self-pollination) serves to promote the genetic health of the seeds of individual plants, and thus the species as a whole.

Simply put, cross-pollination increases genetic diversity, and the greater genetic diversity found in life, the more robust life is. By allowing individuals a broader ability to constantly adapt to changing conditions, whether it is the introduction of disease, adverse environmental conditions, or a new type of herbivore, increased genetic diversity increases the chance of survival. Such diversity increases the likelihood that some individuals of the species will always have the proper genetic code to adapt to changes in the world, be it climate, disease, or something else. The proper genetic code may be something as simple as a thicker wax layer on the leaf surface, to wick away excessive moisture during rainy years in order to prevent rotting, or as complicated as the ability to produce toxic compounds to discourage herbivory from large vertebrates, such as deer. All of these changes arise from simple genetic diversity and the resultant possibility of new combinations of genes at each reproduction event, and in the case of plants, much is owed to their insect pollinators.

**Nutrient Cycling and Decomposition**

**Triggers – Leaf litter, herbivory, soil-dwelling insects.** The previous section on insect herbivory told only part of the story. While insects help regulate plant growth, and in many cases keep their abundances balanced, they also play a critical role in nutrient cycling. In some instances, insect herbivory can actually function to stimulate
production of new leaves and stems and thus promote plant growth, much like human-
instigated annual pruning of shrubs and trees.

Insects occupy a vital niche in nutrient cycling. Contributing primarily through their
feeding behaviors, being herbivores, carnivores, and detritivores, their small size and
abundant numbers allow them to make consistent change to an environment. This
change is ever-present, and is in fact a cycle of constant environmental manipulation.
For this reason, it is difficult for the casual observer to appreciate the role that insects
play in maintaining critical nutrient levels in soils by removing decaying organisms from
forest floors. Massive outbreaks of large vertebrate herbivores (i.e., rabbits, deer,
ungulates) are certainly more noticeable, in terms of the effect they have on their
environment. Nevertheless, insects play an even larger role.

First, insects can alter the chemical composition of the soil, which has a
pronounced impact on the rate of soil decomposition and nutrient mineralization
deposition of insect frass, honeydew, and carcasses by insects, as their by-products,
have been shown to alter the chemical composition of the soil (Stadler et al. 2001).
Second, through plant feeding, insects have been shown to alter the chemical
composition of living plants, as well. Changes in nitrogen and phosphorous levels in
live plants directly impact the levels of nutrients found in leaf litter and detritus, which
ultimately becomes available for other organisms that derive nutrients from the soil. In
addition, insect herbivory often promotes the formation of secondary plant compounds
(as a defensive behavior) that further alter chemical properties of soils and thus soil
nutrient composition (Rosenthal and Berenbaum 1991, Coley and Barone 1996, Karban
Lastly, regarding herbivory’s role in nutrient cycling and decomposition, premature abscission of plant parts (i.e., fruits, leaves, flowers) has been shown to dramatically increase soil nutrient levels (Faeth et al. 1981, Williams and Whitham 1986, James and Pritchard 1988). As plants senesce naturally, nutrients are relocated within the plant. However, when plant parts are cut from the plant by insect herbivores, any bits that are not consumed represent nutrient-rich compost that is recycled, allowing for other plants to benefit from the increase in available soil nutrients.

The primary organisms that contribute to decomposition in the soil are bacteria and fungi. However, this is not to say that insects do not play a vital role. Insects break down larger pieces of organic matter into smaller ones, releasing key nutrients back into the environment throughout the process. Although insects are not believed to represent the majority of detritivore diversity (Bacteria have earned that title), they are still extremely abundant in both tropical and temperate habitats. Most importantly, they serve to break down larger matter into more manageable units for other decomposers, bacteria included. By increasing the surface-area-to-volume ratio of organic matter, insects play a key role by allowing the much smaller bacteria to efficiently recycle once-living plant and animal material into usable nutrients for future generations of living plants and animals. Carrion feeders (organisms that feed on dead animal material), saprophages (organisms that feed on rotting organic matter), and detritivores (organisms that feed on decomposing organic matter) all essentially do the same thing, which is to consume non-living organic matter. In the insect world, there are many different orders that fit into this niche. Beetles (Coleoptera), Flies (Diptera), Earwigs
Dermaptera), Springtails (Colembola), Thrips (Thysanoptera), Silverfish (Thysanura), Cockroaches (Blattodea), Termites (Isoptera), Psocids (Psocoptera), and True Bugs (Hemiptera) all play a direct role in the decomposition of rotting organic material. From Dung Beetles to Cockroaches, insects are ecosystem engineers with a critical role in nutrient cycling in all environments.

Finally, subterranean insects play critical roles in nutrient cycling, even if they do not directly decompose dead organic matter. Certain species of ants, bees, wasps, termites, and beetles are known to develop underground colonies and refuges where they tunnel out relatively extensive areas in which to live and rear young. In most cases, these species will actively provision their nests with food items, both for themselves, as well as for their offspring. Sometimes this food is living organic material, as is the case with some wasps that provision their young with live insect larvae, and sometimes it is non-living organic matter, as is the case with Dung Beetles that harvest animal dung balls as food sources. Either way, these behaviors serve to not only aerate the soil, through the construction of tunnels and chambers, but they also serve to provision the soil by delivering high quality organic material to the subterranean environment. Here, the insects themselves may convert the food to more directly usable forms, such as frass, or simply provide a microenvironment for certain species of bacteria and fungi to convert the organic matter to simpler compounds, such as simple hydrocarbons and water.

Chapter Conclusions

The previous sections that detailed specific accounts of insects and general entomological topics for use in ecotourism are by no way meant to be a definitive list of the topics. The potential for more insects to become involved is tremendous, especially
as the growth and awareness of entomological ecotourism continues. Nor are these lists intended on being final solutions for providing the necessary instruction to naturalist guides or ecotourists about the fascinating world of insects. The development of additional methods for instruction is critical in disseminating this information and building upon it during these formative years of entomological ecotourism’s rise. Training models should not seek to reinvent the wheel, so to speak, nor should they completely resemble those already in place for broad-spectrum nature education.

An ideal way to proceed with entomological ecotourism guide training is to assimilate the information in this Chapter into an instructional course, hosted in easy-to-access areas within ecotouristic localities and countries. Along with lecture-style presentations, print materials should be provided for guides to use as references long after the workshop has finished. In addition, classroom-based lectures should be supplemented with field excursions in order to demonstrate the documented techniques for locating insects and identifying cues for entomological interpretation, as detailed in this Chapter.

The neotropics would be a natural testing ground for this new type of workshop: not only because of the high level of insect biodiversity, but also because of the prominence of ecotourism in most neotropical countries. However, this is not to say that instruction should include only those insects to be found in the immediate areas of the neotropics. By providing instruction on insects found outside of one’s own country or region, guides are able to use this information to present more comprehensive interpretation to ecotourists, by citing examples of similar insects or behaviors from around the world. For example, when explaining the details of the Monarch butterfly
migration, it is beneficial to compare it to the migration of the Bogong moth in Australia, and vise versa. This serves to not only enhance the individual educational opportunity, as the guide is able to provide unique and more thorough interpretation, but also to promote greater awareness of entomological ecotourism on a worldwide basis. This ignites a desire to learn and experience other forms of entomological ecotourism, as well as market via word-of-mouth (emphasized in Chapter 2).

This author is pursuing these projects as a way to take the information presented in this Chapter and integrate it all into a user-friendly, efficient, and practical format. The first step already taken, is to design course materials that will act as a workshop supplement. It will also function as a stand-alone publication to be used by both naturalist guides and ecotourists. Sample plates from this future publication are shown in Figure 3-2, as well as the examples of numerous insect-species plates.

The continued growth of entomological ecotourism requires not only better-informed guides and improved techniques for finding, exhibiting, and interpreting insect natural history, but it also requires an academic side that is equally engaged. In order to have the most pronounced impact on the ecotourism field, and the ensuing conservation implications, there must be a balance between academia and industry. While both have their place in the promotion of entomological ecotourism, they must act in concert with one another as often as possible to advance the field from a highly scholastic foundation. Industry is integral in playing a part in day-to-day interactions with ecolodges, guides, and tour operators, by directly managing relationships and implementing strategies. Academia is critical in developing such strategies that function as best practices, ensuring that the industry stay culturally and environmentally
responsible. By understanding impacts that ecotourism may have on people and wildlife, the field of ecotourism may go forward and perpetuate the ideals by which it was originally defined and contemporarily promoted.
<table>
<thead>
<tr>
<th></th>
<th>Park Guides</th>
<th>Ecotour Guides</th>
<th>Tour Escorts</th>
<th>Experts</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Advantages</strong></td>
<td>Have practical knowledge and the most detailed understanding of a localized area.</td>
<td>Being with the group from start to finish enables a more fluid dialogue. Certain topics may span multiple areas, and their comprehensive approach leads to more in-depth discussions about the areas visited.</td>
<td>Will promote interpretation and group learning by ensuring organized and well-planned visits.</td>
<td>Provide a higher level of knowledge and insight. Have access to most up-to-date information.</td>
</tr>
<tr>
<td></td>
<td>Through experience, they know where wildlife is most likely to be found at certain times of year.</td>
<td>Have wide-scale knowledge of the destination visited, leading to a better general understanding of the country, its wildlife, and various ecotourism attractions.</td>
<td>Keenly familiar with service industry, taking pressure off other leaders.</td>
<td>Are professionals in the field and are prepared with the most accurate information to share with ecotourists.</td>
</tr>
<tr>
<td><strong>Disadvantages</strong></td>
<td>Often have the least training and are the most likely to share inaccurate information.</td>
<td>Have less detailed knowledge of individual destinations, compared to Park Guides.</td>
<td>A dedicated Tour Escort may have little knowledge about the natural history or wildlife found in destinations.</td>
<td>Less versed at handling logistics and group needs, as their training and profession concentrates on the pursuit of knowledge, rather than providing services to clients.</td>
</tr>
</tbody>
</table>
Figure 3-1. Each circle denotes the set of responsibilities each type of guide must assume. There is significant overlap between sets of responsibilities, with overlaying circles indicating the ability for one type of guide to function in a number of different guide positions during an ecotour.
Herbivory

There is widespread evidence that insects feed on plants. Often in their larval stage during this process, insects will feed on leaves and plant material to gain the necessary nutrients to undergo complete development to adulthood, termed Holometabolism. This is the typical case of an insect egg hatching into an immature larva (e.g., a caterpillar, in the case of Lepidoptera), before transitioning to the pupal stage and ultimately becoming an adult insect that bears little resemblance to any of its previous life stages. Holometabolism is in contrast to Hemimetabolism, where the insect makes a gradual shift from nymphs of immature adult to fully mature adult, often changing only slightly in appearance, other than overall size. Usually these differences are exemplified by the enlargement of wings, externally, and the maturation of genitalia, internally.

Insect herbivory is critical to the health of insects, as it is during their younger stages that the insect is very much an eating machine, adapted to consume large quantities of plant material through the use of powerful mandibles, and a specially designed digestive system to handle large amounts of coarse plant material. While plant-eating insect larvae have stomachs that are lined with a protective covering and facilitate constant consumption, digestion, and absorption of nutrients, other insects exhibit different kinds of adaptations. For example, blood-feeding insects, such as mosquitoes and other biting flies, have little need for any protective lining in the stomach and have traded that for the ability to expand significantly upon feeding. Because blood feeders feed more intermittently than plant feeders, their stomach must be able to handle large stores of food, much like snakes or large felines that gorge themselves opportunistically, but infrequently.

Figure 3-2. Three pages of potential guide training information for entomological ecotourism guides. Demonstrating potential guide training materials, these pages combine the text located in this Chapter and integrate visual aids and additional information. It is the intention of this author to replicate these types of materials for guide training courses and classroom lectures with all of the information provided in this dissertation.
Plants are somewhat opposed to being eaten and thus have evolved several types of defenses to discourage herbivory. Depending on the species of plant, one or several of these defenses may be used at the same time to deter feeding by insects. One defense is for the plant to emit volatile plant compounds upon the initiation of feeding. These compounds serve several purposes, but generally one is favored by the plant (i.e., more resources are allocated to it) and depends on the type of habitat, insect, or general environmental conditions. The emission of these volatile plant chemicals may be used to alert predators and parasites to the availability of the insect herbivore as a potential prey item or host. This acts like a dinner bell that can be for opportunistic predators and parasites. The more insects that are feeding, the more volatiles become released, signifying the availability of a greater potential food source (i.e., more insects). These specific types of volatiles are termed Kairomones, because they are intended to be perceived by a different species than that which is producing the chemical, and serve to benefit the perceiver. In this case, the perceiving organism follows the chemical trail to find the plant that produced the chemical, and then encounters the insect prey. Kairomones are in contrast to Allomones, which are also volatile chemicals emitted by an organism intended to interact with a perceiving organism. However, allomones are produced solely for the benefit of the emitter, not to the benefit of the perceiver. This may be a noxious smell or other feeding deterrent which discourages the perceiving organism (i.e., insect) from feeding on the producing organism (i.e., plant).

Another way to discourage herbivory is by producing feeding deterrents. These are often secondary plant compounds (primary compounds being those that the plant uses for its own health and maintenance) that are either toxic or indigestible to the insect herbivore. These are metabolically costly to make on part of the plant, so they are used sparingly. Milkweed is a good example, as the white latex that flows from damaged plant tissue in response to feeding is

**New Terms**

**Kairomone:** A chemical produced and emitted by one organism that is perceived by another organism that benefits the perceiver, but not the producer.

**Allomone:** A chemical produced and emitted by one organism that is perceived by another organisms that benefits the producer, but not the perceiver.

**Secondary plant compound:** Complex chemicals made by plants that are not essential to the life of the plant. However, they often play critical roles in plant defenses against herbivory.

Figure 3.2. Continued
Herbivory

Toxic to many invertebrate and vertebrate herbivores. Oak tree leaves contain large quantities of indigestible tannins, which are best known perhaps by their effects on the color of fresh water, often turning rivers brown with the color of these tannins. These same tannins discourage feeding by insects, as they reduce the ability of an insect to digest food. Because feeding by insects makes them relatively vulnerable to predation and parasitism, wasting time by undigestible leaves greatly discourages feeding from such plants.

In some rare cases, plants employ a livelier means of defense. Some species of Acacia plants house Acacia Ants within the confines of their thorns and branches. These ants will actively defend the Acacia against herbivory by attacking any intruder by biting and stinging, whether it is a beetle or a deer. However, these ants do not put their own lives on the line for nothing. They are rewarded for their loyalty to the Acacia with sweet foliar nectaries that provide sugar, and protein and lipid rich Beltian bodies, which located at the tip of the leaves.

The majority of plant herbivory is due to Lepidoptera (butterflies and moths) and Coleoptera (beetles) feeding as immature larvae. Although not actual herbivory, because they do not physically consume the leaves, Leaf-cutter Ants also represent threats to plants. The figures in this section show various types of plant damage likely to be found on an ecotour.

**New Terms**

**Beltian Bodies:** Located at the tips of leaves on *Acacia* trees, they are rich in proteins and lipids and serve to reward ants, which guard the tree against natural enemies.

**Foliar Nectaries:** Located at the base of the leaf blade where it joins the petiole, these are areas that offer sugary secretions as a reward to ants that guard the tree.

**Orthopteran** (Grashoppers, Katydid, and Crickets) feeding damage may be confused with that of Lepidoptera, as both groups feed at the leaf margins and employ mandibles. Generally, the feeding is symmetrical as with Leaf-cutter Ants.

Lepidoptera feeding damage exhibits characteristics of Leaf-cutter Ant feeding damage, in that damage is at the margin of the leaf and generally consisting of large circular abscissions. However, Leaf-cutters typically exhibit a hemi-circular cut, whereas Lepidoptera larvae chew a rougher, unevenly cut edge.

Figure 3-2. Continued
Figure 3-3. The trophic pyramid. Situated at a key position in the trophic pyramid, insects interact directly with most life forms. They largely represent primary consumers, feeding upon plants and then being consumed by secondary consumers. However, predatory insects like wasps, beetles, mantids, and ants, can function as secondary and even tertiary consumers, as well. Through both direct and indirect connections, they impact entire ecosystems because of their near-infinite interactions with flora and fauna at all trophic levels.
Figure 3-4. Living insect exhibits are excellent ways to integrate insects in the ecotour. A) Two ecotourists compare photos of adult butterflies with living pupae. B) At La Paz Waterfalls and Gardens, in Costa Rica, pupae are cleverly displayed within their live butterfly exhibit, being placed on display just prior to eclosion for visitors to observe. C) Ecotourists are able to photograph multiple life stages of insects within organized exhibits. D) Although fully enclosed, exhibits are able to maintain environmental aesthetics to fully immerse ecotourists in the world of entomology. Photos courtesy of J. Court Whelan.
Figure 3-5. Insect collections represent a unique way for ecotourists to view, photograph, and appreciate insect diversity. A) Collections of dead insects do not need to be dull compared to live insects, as displayed by the vibrant Dr. Whitten Collection in Monteverde, Costa Rica. B) Adjoining Dr. Whitten’s collection is a beautiful live butterfly exhibit. A Park Guide interprets to ecotourists the techniques that are used in rearing Blue Morpho Butterflies. C) Insect collections may also contain useful stories and cultural meanings of insects from around the world, engaging ecotourists on the many levels of entomology. Photos courtesy of J. Court Whelan.
Figure 3-6. Leaf-cutter Ants. A) Leaf-cutter Ant minima riding on top of a leaf fragment. B) Foraging group using pheromone trails for navigation. C) On occasion, Leaf-cutters will also cut and use flowers in their fungus gardens. D) Leaf-cutter Ants routinely carry leaf fragments many times their size and weight. E) A large ant mound, potentially with millions of colony members. Photos courtesy of Geoff Gallice.
Figure 3-7. Arboreal Termites. A) Nasute soldiers mount a defensive response. B) An arboreal nest, now abandoned, is occupied by parrots. C) Soldiers and workers are disturbed when a termite tunnel is breached. D) An arboreal nest located closer to the forest floor. Small tunnels can be seen radiating out from the central nest structure, which are used as termite highways. Photos courtesy of J. Court Whelan.
Figure 3-8. Dung Beetles. A) A sign in a South African game park, reminding ecotourists of the importance of Dung Beetles. B) A Dung Beetle stands atop a recently formed dung ball. C) “Yield to Dung Beetles”. D) Using their hind legs for guidance, Dung Beetles will walk backwards while pushing their dung ball to a preferred location. Photos courtesy of Julie Allen.
Figure 3-9. Mopane Worm. A) Mopane worms are eaten, once dead and dried. B) An adult of the Mopane worm, these caterpillars turn into handsome silk moths. C) Not just an indigenous protein source, Mopane worms are traded all over the world and considered a delicacy in many countries in Europe and Asia. D) The harvest of these caterpillars generates significant income due to the volumes produced year after year. Photos courtesy of Thibaud Decaens.
Figure 3-10. Giraffe-necked Weevil. A) A male Giraffe-necked Weevil perches on a branch, displaying its characteristic “neck”, or pronotum. B) Seen from above, the pronotum generally measures three times as long as the abdomen. C) A single female awaits a male on a leaf in Ranomafana National Park, Madagascar. D) Females may or may not exhibit a red abdomen (depending on the species), but are nonetheless identified by their significantly shorter pronotum. E) Perched on the underside of a leaf, Giraffe-necked Weevils may be spotted with relative ease, but are often difficult to find due to their small size. Photos courtesy of J. Court Whelan.
Figure 3-11. Blue Morpho Butterfly. A) An adult rests on top of a leaf. B) A late-instar larva has been feeding. C) An adult perches on vegetation. D) Blue Morpho pupae are prepared at a butterfly farm, nearly ready for shipment. E) An adult perches on a leaf, giving a good view of the cryptic pattern on the undersides of the wings. F) Individual scales, although small, are readily seen in this eyespot pattern. Photos courtesy of J. Court Whelan.
Figure 3-12. Jungle Nymph Stick Insect. A) A Female *Heteropteryx* exhibits multiple spines along her head, thorax, and abdomen. B) Males exhibit dramatically different color patterns, as well as overall body size. C) Males and females often remain in copula for an extended period of time (days to weeks). Photos courtesy of Linda van Zomeren.
Figure 3-13. Balfour (1915) reports that indigenous tribes in Papua New Guinea use the femur of certain stick insects as fishhooks.
Figure 3-14. Urania Moth. Urania moths are usually seen individually, but during migratory years, they can be seen in aggregations, as depicted by this photo taken in Panama by Dr. Neal Smith in August of 2005. Photos courtesy of Neal Smith.

Figure 3-15. Cracker Butterfly. A Cracker Butterfly perches upside down on a palm trunk to blend into its surroundings and also be prepared to launch itself in quick “clicking” pursuit of any intruding male approaching its perching site. Photo courtesy of J. Court Whelan.
Figure 3-16. Stingless Bees. A) The earthen entrance of a Stingless Bee colony is lined with guards. B) The profile of a Stingless Bee. C) Scouts and workers return to the entrances of a colony. D) Going after nectar at the base of a flower, Stingless Bees have powerful mandibles that allow them to chew through vegetation. Photos courtesy of J. Court Whelan and Geoff Gallice.
Figure 3-17. Migratory Locusts may come in several different shapes, sizes, and colors, largely dependent on whether they are in their migratory phase or not. Although females and males may be sexually dimorphic, most phenotypic variation occurs between solitary and migratory phases. Photos courtesy of J. Court Whelan.

Figure 3-18. A Helicopter Damselfly is displayed in a man’s palm, exhibiting its large size. Photo courtesy of Stephen P. L. Luk.
Figure 3-19. Glowworms. A) The “Glowworm Grotto” of the Waitamo Caves in New Zealand. B) Larvae lay sticky traps in order to collect flying insects as food. C) When displaying their bioluminescence, the sticky beads reflect the light and cause the larvae’s microenvironment to become illuminated. Photos courtesy of Garry Maguire.
Figure 3-20. Clearwing Butterflies. Clearwings routinely perch on the uppersides of leaves and commonly prefer more shaded areas of the forest. Their transparent wings serve to camouflage the butterflies, especially when perched or flying in dimly lit areas of tropical forests. Although the prominent white patches on the forewings of these two species seem to take away from their cryptic nature, the hindwings are almost completely transparent, making them appear much smaller, if not altogether undetectable, while in flight. Photos courtesy of J. Court Whelan.

Figure 3-21. Bullet Ant. Bullet Ants are most commonly found alone, either resting or walking on vegetation, including leaves, branches, and trunks of trees. Photo courtesy of Arthur Anker.
Figure 3-22. Charaxes Butterflies. A) A single Charaxes Butterfly is perched on a branch outside of a safari lodge in Kenya. B) Assembling around a sap flow, a group of Charaxes eagerly consumes the nutrient-rich flow, competing with other insects for this opportunity as well. C) Undersides and uppersides of Charaxes can be quite striking, making them a highly desirable species to be seen by entomologically-minded ecotourists. D) The green proboscis of a Charaxes is extended into the bark of a sap-covered tree trunk in an effort to consume every last drop of this precious resource. Photos courtesy of J. Court Whelan and Andrew D. Warren.
Figure 3-23. Goliath Beetles. Goliath Beetles have been popularized greatly by collectors and insect breeders. Found throughout Africa, these insects are shipped all over the world for display at insect houses and insect breeding operations. Photos courtesy of Milan Ilnyckyj.
Figure 3-24. Bogong Moths. Bogong Moths are most fascinating in their adult stages, when they look like shingles in their assemblages on cave walls in southern Australia. Photos courtesy of ScienceImage.
Figure 3-25. Palm Grubs. A) Various types of Palm Grubs collected by a tribesman of Papua New Guinea. B) Palm Grubs can be eaten raw (alive), or drained of their fluids and roasted. C) While a number of palm beetle species are actively harvested and eaten, the majority of those grubs sought after are in fact the larvae of a type of large weevil. Photos courtesy of Stavros Markopoulos and Mike Jones.
Figure 3-26. Army Ants. A) A raiding swarm relies primarily on pheromone cues, traversing obstacles with ease. B) When larvae are large enough to carry, workers join the raiding swarm during the nomadic phase and tote larvae along with them. C) A bivouac is formed with no materials but bodies of living ants. Photos courtesy of Geoff Gallice.
Figure 3-27. Human Bot Fly. A) An adult bot fly perches on a leaf. B) A larval bot fly, exhibiting its two spiracles, used for respiration while beneath the skin C) A larval bot fly after being removed from the subcutaneous tissue of a human. Photos courtesy of Alan Cressler, Diego Almeida and Geoff Gallice.
Figure 3-28. Mound-building Termites. A) A group of Banded Mongoose uses termite mounds as lookout points, along with other African mammals. B) A large termite mound in the African savanna. C) Standing over 20 feet tall, this African termite mound uses its large columnar shape to circulate air throughout the interior of the colony. D) African termite mound of still another species. Photos courtesy of June S. Tooley.
Figure 3-29. African Driver Ants. A) A raid of Driver Ants surrounds an insect. B) Although blind, Driver Ants will traverse a range of obstacles due to their exceptional ability to perceive trail pheromones. C) From afar, a swarming raid of Driver Ants resemble a soil washout or other natural feature. D) Driver Ants are unique in that they are some of the only legionary or swarm-raiding ants in the world to build nests. Photos courtesy of J. Court Whelan and Sunni Black.
Figure 3-30. Birdwing Butterflies. A) A male *Ornithoptera urvillianus* perches on a leaf in the Solomon Islands. B) A farm-raised Queen Victoria’s Birdwing (*Ornithoptera victoreae*) is freshly emerged, allowing its wings to harden before taking flight. C) Typical habitat of Rajah Brooke’s Birdwing (*Trogonoptera brookiana*). D) A female Goliath Birdwing (*O. goliath*) feeds from *Hibiscus* nectar in the highlands of Papua New Guinea. E) The only Birdwing in Madagascar, the Spotted Swallowtail Birdwing (*Pharmacophagus antenor*) takes flight near Isalo, Madagascar. F) Males of Rajah Brooke’s Birdwing are known to puddle in great numbers on Malaysian riverbank habitats. Photos courtesy of J. Court Whelan and Ian K. Segebarth.
Figure 3-31. Monarch Butterflies. A) A single Monarch is found perching on a *Vernonia* flower, found throughout the overwintering colonies in Mexico. B) Monarchs cluster so densely on tree trunks and bushes that it is nearly impossible to see through the layers of butterflies. C) By mid-day in the overwintering colonies, Monarchs will take flight by the millions to thermoregulate, or perhaps flying longer routes to nearby water sources. D) Mountain streams often have thousands of Monarchs puddling at the edges of the water. E) Densely clustered Monarchs, hanging from branches of the Oyamel Fir Trees. Photos courtesy of J. Court Whelan.
Figure 3-32. Acacia Ants. A) Acacia trees are relatively easy to identify due to their large thorns and bipinnately compound leaves. B) Proteinaceous Beltian Bodies reward the occupant ants for their diligent work defending the tree against herbivores. C) A sparse Acacia tree in the middle of small understory growth stands alone, as ants will actively clear the surrounding forest floor to eliminate any competition that the colony tree may face from other plants. D) An ant is about to enter one of the many nest entrances, found at the tips of the swollen thorns. Photos courtesy of J. Court Whelan, Dan L. Perlman and Tom R. Davis.
Figure 3-33. Dynastes Beetle. A large male *Dynastes hercules* beetle is displayed, showing the extent of its size when compared to an adult man's hand. Photo courtesy of J. Court Whelan.
Figure 3-34. Hercules Moth and other Silk Moths. A) Silken cocoons of an unknown member of the Saturniidae family. B) The Hercules Moth is one of the largest moths in the world and is characterized by its size, as well as the clear windows found on each of its wings. C) Silk Moths generally rest with their wings open in order to display their eyespots. D) Sometimes Silk Moths will rest with their wings closed, but will readily flash their hidden eyespots if disturbed. Photos courtesy of J. Court Whelan.
Figure 3-35. Homerus Swallowtail Butterfly. A) A single large Homerus rests on a leaf. B) Adult Homerus can soar for long periods of time, searching for host plants, nectar sources, or potential mates. C) A soaring male, patrolling a light gap in the Cockpit Country of Western Jamaica. D) A characteristic light gap likely to be frequented by Homerus Swallowtails. Photos courtesy of J. Court Whelan and Thomas C. Emmel.
Figure 3-36. Peanut-head Lantern Fly. A) A pair of Lantern Flies rest on a lichen-covered tree trunk. B) The protrusion extends past the eyes of the insect. C) With wings spread, they exhibit distinct eyespots that function to startle predators, using a quick flash of their wings. D) Many believe that the head protrusion attempts to resemble the head of a caiman, possible deterring attacks from predators. Photos courtesy of J. Court Whelan.
CHAPTER 4
EFFECTS OF ECOTOURISM ON WILDLIFE AND INSECTS

Effects of Ecotourism on Wildlife

Ecotourism is widely regarded as a valuable tool in promoting environmental awareness and conservation. The principal concept behind it is that a natural area will be better protected when there are economic incentives to promote its preservation. Such economic incentives are directly tied to the overall condition of the natural area. For example, a healthy ecosystem will generate more tourism and more revenue than if it were to be transformed to a less natural condition, such as an agricultural field, timber, commercial or residential development. When an ecosystem or natural area is conserved, the floral and faunal inhabitants are also protected. In what is known as a “stakeholder’s theory” by ecotourism laureates like Martha Honey (2008), people will protect what they receive value from. Whether stakeholders to natural areas are ardent conservationists, or simply entrepreneurs focused more on monetary gain, ecotourism has the ability to conserve ecosystems and wildlife, while improving the welfare of the local communities that directly protect these areas. As stressed throughout this dissertation, the growth of ecotourism has positive ripple effects far beyond the actual ecotourism activity or destination. However, as ecotourism surges, studies are showing that there may also be negative consequences for the wildlife and environment that ecotourism is designed to protect. The following sections will examine this further in order to understand not only the benefits of ecotourism, as discussed elsewhere in this dissertation, but also the costs.
Disturbance to Wildlife

Human disturbance has been shown to negatively affect wildlife in a number of different ways. From excessive noise, to light pollution, to sheer encroachment on habitat, an ecotourist is no exception when it comes to harassment of wildlife, even though it is unintentional in most cases. In some instances, ecotourists are thought to be more threatening than typical tourists, as they often seek out and approach wildlife for better viewing (Jacobson and Lopez, 1994).

While the form and function of these disturbances may vary, the perception of the ecotourist’s actions by the wild animal is often the same, regardless of how benign the ecotourist’s intentions actually are. From the wildlife’s viewpoint, disturbance by ecotourists generally represents a perceived risk of predation (Lima and Dill 1990, Lima 1998, Steidl and Anthony 1996, 2000). With this threat, encroachment by ecotourists may divert time away from critical roles and activities of wildlife, such as parental responsibilities, feeding, or mating. A simple diversion from everyday life may be detrimental to an animal’s fitness and wellbeing. Although a predation event is not actually occurring when an eager ecotourist stalks a bird to snap a photo, and the “prey” animal does indeed survive, one must ask at what cost to the animal? Because an animal that is responding to a perceived predation risk will readily extend itself in an act of survival, a false predation risk often elicits an equally abnormal and extreme response on part of the wildlife. Instigating such behaviors repeatedly (i.e., human tourists regularly encroaching on animal habitat via a particular trail or road) is likely to be physically demanding for the animal in question (Frid 2002). Fortunately, most animals employ a sense of economy when fleeing from what they perceive as a potential predator or similar threat.
A fleeing animal must reach a balance between evading capture against the cost of expending excessive energy or abandoning a resource patch (Ydenberg and Dill, 1986). Not surprisingly, the probability of fleeing increases as the rate of advancement and size of the predator increases (Burger and Gochfeld 1981, 1990, Cooper 1997, 1998, Dill 1974). The chance of an animal fleeing also increases as the number of predators increases, as can be seen in Walther (1969), who compared the responses of Thomson’s Gazelles to individual hyenas versus packs of hyenas. It is not difficult to see the parallel between the animal world and the ecotourism world, with individuals and groups of humans easily appearing as a threat to smaller animals such as birds, reptiles, invertebrates, and small mammals.

**Encroachment as a Disturbance to Wildlife**

The most common behavior that an ecotourist engages in, which is also one of the most significant in terms of eliciting defensive responses from wildlife, is simply encroaching into an animal’s habitat. Differences in the angle of approach (i.e., how directly one approaches an animal), the speed of approach, and the size of the perceived predator all have effects on the behavior of the ‘prey’ animal. Ecotourists that directly approach animals have been recorded to trigger reactions from a wide range of species, including Ringed Seals (*Pusa hispida*), Dall’s Sheep (*Ovis dalli*), Common Terns (*Sterna hirundo*), Mexican Spotted Owls (*Strix occidentalis*), Snowy Plovers (*Charadrius nivosus*), Pacific Brants (*Branta bernicla*), Canada Geese (*Branta canadensis*) and Bald Eagles (*Haliaeetus leucocephalus*) (Steidl and Anthony 1996, Burger and Gochfeld 1998, Burger 1998, Born et al. 1999, Delaney et al. 1999, Ward et al. 1999, Frid 2001, Lafferty 2001) (Table 4-1). Most instances of disturbance are cases where an increase in speed by the approaching ecotourist increases the probability of
escape behavior on part of the “prey”, as can be seen by the reaction of the Common Tern to motorized watercraft (Berger 1998). However, some animals appear to exhibit the opposite reaction. For example, Snowy Plovers, when approached by joggers vs. walkers, were more likely to flee from walkers. Lafferty (2001) shows that the stalking-like behavior of a slower walker elicits a greater response, perhaps more strongly linking the ecotourist’s behaviors to that of a predator. This begs the question as to whether similarities in behaviors between the animal’s native predator and the ecotourist have possibly the most profound impact on whether or not an animal decides to flee from an advancing human. While humans may feel that slow and cautious approaches when observing wildlife are safest and most appropriate, this may not be universal.

Habitat characteristics also play a role in whether or not an animal flees in reaction to human disturbance via encroachment. For example, when approached by helicopters, Dall’s Sheep on rocky slopes were less likely to flee compared to sheep on smoother slopes (Frid 2001). The protection offered by the rocky slopes serves as an ideal habitat for Dall’s Sheep, thus weighing in on the decision to flee. They know that their chances of outrunning or outmaneuvering a predator in difficult terrain are greatly improved compared to other areas due to their relative agility (Frid 2001). Similarly, Big Horn Sheep (*Ovis canadensis*) are less likely to flee from hikers, bikers, and road traffic when on rocky habitat, furthering the belief that an animal’s perception of danger (i.e., less danger when in a more protected habitat) plays a significant role in their propensity to flee when disturbed by tourists (Papouchis et al. 2001).

Observable behaviors like avoidance or fleeing are testable, but this does not mean that unobservable behaviors have fewer effects on disturbed wildlife. The time
that an animal spends anticipating disturbance also has negative consequences. Studies indicate that an animal spends more time being vigilant when the perceived risk of predation is higher (Elgar 1989). Increased vigilance results in fewer successful predation events, to the overall benefit of the prey, but at the cost of less time spent foraging, mate locating, or other critical activities (Frid 2002). The same factors that contribute to an animal fleeing as a result of human disturbance, such as the directness and speed of approach, also affect the animal’s likeliness to remain overly vigilant after the disturbance has come and gone. For example, the amount of time Bighorn and Dall’s Sheep spent in vigilance increases (i.e., vigilant responses began earlier and lasted longer) when small tourist aircraft approach more directly (Stockwell et al. 1991, Frid 2001b).

**Effects on habitat choice**

Concomitant with these lasting impacts, the perceived risk of predation also directs habitat choices by wildlife. The choice of habitat is largely a trade-off between resource richness (i.e., food, water, harborage) and the risk of predation (Gilliam and Fraser 1987). Therefore, it is of little surprise that there exists wide-ranging evidence from a variety of taxa indicating that animals spend less time in a resource-rich habitat where there is greater predation risk (Edwards 1983, Gilliam and Fraser 1987, Morris and Davidson 2000). In fact, it has been documented in many cases that human disturbance will cause animals to relocate to a different habitat, even if it means occupying an alternative habitat that has less available resources (Frid and Dill 2002). Whether the animal is shifting its position in the canopy of the jungle, as can been seen with the neotropical Pigmy Marmoset (*Cebuella pygmaea*), avoiding heavily traveled roads that cross natural habitat, as is the case with the Woodland Caribou (*Rangifer*
*tarandus caribou*, or avoiding highly productive hunting grounds due to the sounds of motorboats, which occurs with Bottlenose Dolphins (*Tursiops truncates*), the indirect effects of nature-based tourism have the potential to displace wildlife from their preferred habitats (Gill et al. 1996, de la Torre et al. 2000, Dyer et al. 2001).

**Effects on mating**

On par with the need for quality habitat in order to obtain critical resources is the need to find suitable mates. The presence of ecotourists may disrupt an animal's ability to locate potential mates because they associate humans with predation risk. It is seen that mere human presence results in fewer calling events by animals such as frogs, birds, and mammals (Ryan 1985, Gutzwiller et al. 1994, de la Torre et al. 2000). It is commonplace in the animal kingdom for predators to use the sounds of calling prey as an advertisement of location, size, and suitability. The prey must therefore operate by balancing between the risk of predation and the potential reward of mating. However, when an animal detects a predator nearby, a threshold is crossed that causes the animal to quickly arrest any mate-attracting or territory-defending calling (Lima and Dill 1990, Magnhagen 1991, Lima 1998). Whether calling to defend territory against conspecifics, or to attract the attention of potential mates, the sudden interruption caused by an encroaching ecotourist could affect the ability of animals to mate and reproduce.

**Effects on parental investment**

When an ecotourist is perceived as a predation risk to both the parent and its offspring, the parent may be forced into adjusting its level of parental investment. The parent must choose between saving itself, in hopes of substantial fecundity in the future to produce more offspring, or putting itself in between the predator and offspring,
potentially sacrificing itself for the sake of the offspring’s survival. In the case of disturbance caused by ecotourism, the parent may mistakenly abandon their offspring due to a false predation risk. While encroachment by the ecotourist in no way requires such action on part of the parent, for no predation event is actually going to occur, the potential abandonment can increase the offspring’s vulnerability when separated from the parent. This is true even if the abandonment if momentary. As observed with Mountain Goats (Oreamnos americanus), Grizzly Bears (Ursus actos), Dall’s Sheep (Ovis dalli), Brown Pelicans (Pelecanus occidentalis), and several species of Night Herons, abandonment can open the offspring up to real predation (e.g., Wolves sensing an opportunity to ambush a young Dall’s lamb) or simply lead to death from physical factors or lack of provisioning (Tremblay and Ellison 1979, Nette et al. 1984, Anderson 1988, Piatt et al. 1990, Cote and Beaudoin 1997).

Habituation of wildlife to ecotourism

For high usage areas, such as within preserves, parks, and other ecotourism destinations, one would think that a certain degree of habituation would occur towards humans over time with most animals. Sometimes, this is the case and it can lead to unique and memorable ecotourism experiences, as is the case with African Lions (pers. obsv.). Those animals that are able to acknowledge the lack of real threat are at an advantage, for they increase their individual fitness by minimizing extraneous energy expenditures. However, this may take a substantial amount of time, not to mention that some animals simply will not adapt at all. Overestimating potential danger is an adaptive strategy. Should an animal underestimate a predation threat, that individual animal is in much greater danger of being predated upon, thus removing it from the population’s gene pool. By overreacting to stimuli, at the cost of reduced feeding,
increased metabolic output, or decreased mating success, the animal is in fact better off than if it repeatedly under-reacted (Bouskila and Blumstein 1992). While a certain degree of habituation is expected in nature, it is often limited and in many cases undetectable (Burger and Gochfeld 1981, 1990). It is simply maladaptive from an evolutionary viewpoint to habituate to an animal or behavior that so closely resembles true danger.

Effects on migration

Ecotourism can also have detrimental effects on wildlife by disrupting migratory routes and patterns. Each year, 5,700-23,000 Green Sea Turtles (*Chelonia mydas*) come ashore in Tortuguero National Park, Costa Rica, for breeding during their yearlong migration across the oceans of the world. Since the 1980s, tourism has been a major source of income for the local people living in Tortuguero, but has also proven difficult to manage at times due to steep increases in visitation levels (Brown 1991, Place 1991). Now a well-known ecotourism destination, Tortuguero National Park has programs in place to educate visitors and allow them to observe natural nesting behaviors of Green Sea Turtles in spectacular numbers. With the help of Jacobson and Robles (1992), ecotourism goals and policies were better outlined by the addition of guide training programs. Historically, ecotourism has been poorly regulated with regard to sea turtle observation, with many instances of disturbance on the wild turtle populations. Marred by the presence of ecotourists who were reported to use flashlights and camera flashes liberally, previous studies by experts such as Carr and Giovanolli (1957) suggested that bright lights and flashes were in fact nesting deterrents. Nevertheless, these early studies seemed to have no effect on managing ecotourism impacts.
Around the same time that the tour guide training program was initiated, Jacobson and Lopez (1994) conducted studies aimed at assessing the impacts of ecotourism on sea turtles. Somewhat surprisingly, it was found that typical ecotourism behaviors did not significantly alter turtle nesting activities. Specifically, the rate of nesting, false nesting, and non-nesting emergences did not change levels between times of high and low tourism rates (Jacobson and Lopez 1994). However, the total incidence of nesting did indeed differ markedly between high and low tourism rates. Although this is likely due to the fact that the high season is defined by seasons when larger numbers of turtles are present, evidence remains that ecotourists have targeted effects on individual turtles, but not necessarily entire populations. According to Jacobson and Lopez (1994), visitors were observed interacting with turtles, touching them, and blocking their routes to nesting sites, causing changes in individual behavior. Although this may not have immediate effects at a population level, clearly this situation is inappropriate and unacceptable. At the time of the study, Tortuguero National Park was witnessing a 24-fold increase in visitation over the preceding 10 years. Such pinpointed effects could easily expand to affect a larger proportion of migrating Green Sea Turtles. This would support Matheison and Wall’s (1982) generalization that as tourism increases, negative impacts on the environment and natural resources also increase. Fortunately, results from this study and similar studies have been the impetus for reform in the system, aimed at proving this generalization theory wrong.

Jacobson and Lopez (1994) report that shortly after the initial data collection period on visitor interactions with migrating Green Sea Turtles, new regulations, along with guide training programs, greatly reduced the number of lights and camera flashes
allowed on the beach. Closer monitoring of visitors also minimized the level of human contact with the turtles due to the grouping of ecotourists during each nighttime turtle walk. This grouping system functioned to reduce the total amount of time that ecotourists were present on the beach. It also permitted an effective watchdog system, where ecotourist activities and interactions were monitored not only by park officials, but also by guides and the ecotourists themselves (Jacobson and Lopez 1994). This model has been repeated in a variety of other ecotourism destinations with great success (e.g., the Galapagos Islands, pers. obsv.).

Effects of Artificial Light on Wildlife

The direct encroachment of ecotourists on sea turtles is a visible and measurable effect of ecotourism. One of the more pronounced indirect effects is light pollution, otherwise known as artificial night lighting. From beachside resorts to jungle lodges, artificial night lighting is a common occurrence that may have significant effects on wildlife.

Lighting effects on Sea Turtles

With sea turtles, we first see the problem as a female attempts to exit the water to come ashore and lay her eggs. Artificial lighting from beachside resorts and oceanfront restaurants has been shown to dramatically reduce the number of successful nesting events by females for both Loggerhead and Green Sea Turtles (Raymond 1984, Mattison et al. 1993, Mortimer 1982). Salmon et al. (1995) found that even trace amounts of lighting coming from streetlamps located behind beachfront buildings was enough to deter nesting. In cases where beachfront lighting deterred nesting and egg laying, turtles were found instead to choose beaches outside of their normal range,
often involving suboptimal conditions (Worth and Smith 1976, Murphy 1985). This result directly affects the fitness of the subsequent generations.

A second problem with artificial lighting occurs when the nesting turtle has completed egg laying and is ready to return to the ocean. Turtles rely heavily on their visual sense when navigating back to the ocean, as seen by work from Ehrenfeld (1968) and Caldwell and Caldwell (1962). Reacting directly to celestial light over the water, as they turn and orient towards the brighter night sky there on their way back to the ocean, they are a visually oriented organism. With excessive lights on beachfront property, or the glow from urban centers shining over the sand dunes, it is not surprising that some turtles will orient in the wrong direction by using false cues. What is surprising is the relative infrequency with which this actually occurs (Witherington 1992). Nevertheless, those few turtles that are misdirected by the light have little chance of ever finding the ocean, as they often turn up in parking lots and retention ponds well away from the water's edge (Witherington and Martin 2000). While this may not affect the fitness of entire populations yet, these are not isolated events. With increased lighting from new development in coastal communities comes increased impact at the population level.

A third problem associated with artificial night lighting involves the young hatchlings of sea turtles, just as they come into the world. Like their mothers, they must use light to navigate towards their new ocean home. Within a week of hatching, an entire nest of young turtles will emerge from their nest and begin a frenzied rush towards the ocean (Demmer 1981, Christians 1990). Occurring mostly at night, their survival from the time they hatch to the time they enter the water is based on the efficiency with which they locate the ocean. If they are delayed, or otherwise obscured,
the result is commonly death from exhaustion, dehydration, or predation (McFarlane 1963, Philibosian 1976, Mann 1978). Just as with adult turtles, juveniles use the light coming from the ocean via reflections on the water surface and horizon for orientation. Should competing light sources be coming from the opposite direction (i.e., lodges, street lighting, etc.), the turtles could become confused and vulnerable. Nevertheless, the process of navigation and the use of lighting are not simple, as can be seen by many historical studies on the matter.

**Lighting effects on animal navigation**

Throughout the past century, a great number of studies have been conducted on the navigating mechanisms employed by young hatchling turtles (Hooker 1907, 1908, 1911, Parker 1922, Daniel and Smith 1947, Carr and Ogren 1960, Carr et al. 1966). In these studies a great amount of data has been collected on sensitivity to lights and this provides useful information on minimizing impact, particularly from an ecotourism standpoint. First, Sea Turtles (Green, Hawksbill, Olive Ridley) have been found to be more sensitive to light (i.e., more apt to orient towards the light) in the blue part of the spectrum, when compared to the orange and red region. In fact, Granda and O’Shea (1972) found that red light must be 100 times more intense than blue light to elicit the same response from the sea turtle retina. Loggerheads were found to be weakly attracted to low levels of yellow light, yet at stronger intensities of yellow light, which were intended to simulate the moon or dawn horizon, they were actually repelled by it (Witherington and Bjorndall 1991a, Witherington 1992b). This was likely due to an inability to distinguish differences in the color spectrum at lower light levels. Ultimately, it is the ultraviolet part of the spectrum to which sea turtles are most sensitive. This comes as little surprise, seeing as how they spend the majority of their life underwater.
with a “blue ocean filter” over their eyes. This puts little priority on longer wavelengths of light at the red end of the spectrum, and on having greater visual acuity at shorter wavelengths of lights (i.e., blues, purples, UV light) (Witherington 2000). With these things considered, it would appear that if artificial light sources could be designed to minimize impact, they would be relatively harmless. However, the final point is perhaps the most important. The main problem with artificial lights is their proximity in space to the turtles, compared to the original navigating lights used by animals – celestial bodies. Because of the distant origin of celestial bodies, they are proportionately much less intense than any artificial light that illuminates a beach from much closer hotel or lodge. Celestial lights also provide both direct and indirect light, as their light is reflected off the atmosphere, earth, clouds, water, etc. Because these natural light sources are so distant, their lighting is relatively uniform, with no one direction being significantly brighter than others. Compare this with direct artificial lighting and immediately the observer recognizes how much more weighted the artificial lighting is compared to celestial lighting. Thus, artificial lighting creates a more localized impact, as it only affects its immediate source environment. When a hatchling is exposed to one of these “supernatural” lights, natural lighting from celestial bodies pales in comparison, offering little help in navigation at this point (Witherington 2000). Consequently, they are obligated to forgo these natural light sources and instead use artificial ones, which are far from helpful in most cases. Therefore, not only are artificial lights deceptive to wildlife, but they in fact override natural lighting, further adding to the confusion of the navigating animal.
**Lighting and insects**

The effects of artificial lighting on wildlife in general are certainly the most studied and comprehensive with sea turtles. Artificial lighting has also been seen to affect other taxa in other ecosystems. What is often termed “ecological light pollution”, unnatural artificial lighting leads to disruption of wildlife behaviors and can occur in a variety of ways (Longcore and Rich 2004). Disorientation, attraction, and repulsion are perhaps the most common ways for lighting to influence behaviors, whether in sea turtles or elsewhere in the Kingdom *Animalia*.

Lights are an attractive force for many nighttime animals found foraging around artificial lights. Often termed the “night light niche,” studies have documented a wide range of organisms, including birds, reptiles, amphibians, and fish that use artificial night lights as foraging areas (Schwartz and Henderson 1991, Hill 1990, Haymes et al. 1994, Munday et al 1998, Jaeger and Hailman 1973). In many cases, though, attraction to lights is documented but unsubstantiated, with little known about the ultimate cause for attraction or repulsion. Clearly a source of food would be the logical driving force for organisms higher in trophic level, but it is still unclear as to what might instigate prey items to congregate at these night lights. Insects present the best example, with moths being perhaps the most familiar, as anyone that has witnessed the stunning display of moths attracted to one ultraviolet light in the tropics can attest (Figure 4-1). Coupled with the unknown cause of light attraction seen with insects is the relatively unknown effect at both individual and population levels. Nevertheless, moths are relatively well studied regarding the physical effects of light on animals, perhaps providing critical insight to the effects on insects in general.
On an individual level, bright lights negatively affect moth vision. With as little as a 10-minute exposure to a bright light, the moth eye decreases in sensitivity by over 1,000 times (Bernhard and Ottson 1960a, Agee 1972, 1973, Eguchi and Horikoshi 1984). Full visual sensitivity may not return to the insect for up to 30 minutes (Bernhard and Ottson 1960b, Agee 1972). A moth flying toward a light and then flying away would effectively be blind until a given amount of time has passed, only then allowing its visual acuity to return. Given these facts, one would think that any lighting of a natural area is bad for the moths. The truth is that not all lights are equal in their effects on moth vision.

Moths have been shown to respond differently based on the spectral composition and spatial distribution of different types of lights (Frank 1988). Moths rarely fly toward the 589 nanometer wavelength of light seen in low-pressure sodium lights (Robinson 1952), suggesting that these lights may provide a less intrusive alternative to moth-attracting incandescent or mercury vapor lamps. In addition, the human eye is especially sensitive to light in the 589 nanometer wavelength range, showing in spectrograms as bright yellow-orange lines, making it very useful for illuminating areas where insect attraction in unwanted (Finch 1978).

In other cases, moth attraction to lights is affected by the arrangement and distribution of lights in a given area. Robinson and Robinson (1950a) found that lighting from an isolated phone booth was a stronger attractive force compared to larger clusters of more prominent urban lights. Other studies have shown that the diffuse light emitted by wide-scale lighting (i.e., of urban or large lighted complexes) parallels that of full moons. In these circumstances, the moth eye cannot properly “dark adapt” in order to separate, recognize, and be attracted by individual lights (Collins 1934, Bernhard and
Ottson 1964, Frank 1988). Perhaps there is a threshold of light intensity and distribution that effectively decreases the power of attraction and increases the repulsive properties of the source.

Artificial lighting is seen to disrupt moth behavior in several ways. The level of attraction and those qualities of light that elicit the most attraction is still debated today, but the obvious interference and change in behavior that lights induce in moths cannot be ignored. Acting as a diversion, due to its attractive nature, artificial lighting has been proposed to affect migratory behavior, oviposition, dispersal, feeding, and even mating among moths (Frank 1988). When resource use is a consideration, such as with oviposition and feeding, the density of moths in one single locality can be deleterious to the fitness of the individual moth, as well as the population. For instance, gravid female moths are often found at bright lights at night, which results in higher oviposition rates around such lighted locations in natural habitats (Gehring and Madsen 1963, Brown 1984, Martin and Houser 1941). In some cases, when suitable oviposition sites are not found within close proximity to the light source, egg-laying may occur on screens, lampposts, and buildings, thus lessening the chance of reproductive success (Martin and Houser 1941). In other cases, there is an overuse of suitable resources when host plants are in proximity. Gravid female moths may lay too many eggs on a single host plant, reducing the fitness of all eggs laid on the single plant. The fitness of the individual is decreased, as is the population’s fitness due to the “tragedy of the commons”.

While moth behavior may indeed be affected by artificial light, it is perhaps the behavior of moth predators that pose the greater risk to moths. The aggregations of
moths in concentrated areas, due to the attractive power of artificial lights, subjects them to predation by a wide range of taxa, including birds, bats, toads, spiders, and other insects (Turnbull 1964, Brower 1986). No generalizable data are available for measuring the effects of predators on insect populations due to night lighting, but as any observer at a productive moth light can attest, the sheer number of insects attracted is impressive. The ensuing feast that occurs during the early hours of the morning by incoming birds is perhaps even more so.

Given the wide range of hazards posed by artificial lighting, it would seem that moth populations are severely threatened by lights that encircle ecolodges and natural areas. However, many factors influence the numbers, diversity, and vulnerability of those moths subjected to artificial lighting. For instance, many species of moths are known to seasonally migrate, replenishing populations from losses due to both natural predation, as well as abnormal predation from night lighting (Williams et al. 1942, Johnson 1969, Ford 1972, Covell 1985). In addition, many moths navigate and migrate at levels high above the ground, limiting their exposure to night lighting (Mikkola 1986). Furthermore, typical Darwinian selective factors may be in place and serve to minimize effects of artificial lighting on moth populations. For example, moths that are more apt to be attracted to lights, thus potentially falling victim to the hazards of predation, loss of fitness, etc., may be removed from the population over a number of generations. This could result in a higher proportion of moths that are less likely to be strongly influenced by artificial lights. However, studies are lacking that attempt to measure the effects of population level disturbances on moths.
Lighting in ecotourism areas

As human societies progress and spread to new geographic areas, the total amount of light and radiant energy produced is changing the face of the nocturnal earth (Croft 1978). With ecotourism destinations often at the fringe of societal expansion and ecolodges intentionally seeking the seclusion and remoteness of natural areas, there is a risk that they represent the very first contributors to light pollution in virgin habitats. Because of the nature of ecotourism and its sustainable model, negative effects from artificial lighting around lodges should be minimized to promulgate their conservation-minded attitude. Nevertheless, from an ecotourism and educational standpoint, there is inherent value in the attraction of moths to lights.

Often underrepresented in daily ecotours and nature interpretation due to their temporal separation from most daytime tour activities, nocturnal insects are best seen through deliberate attempts to attract them to lights. Night lighting in ecotourism destinations offers the visitor a unique opportunity to observe incredible biodiversity. Not only does night lighting encourage ecotourists to familiarize themselves with the variety of organisms found in nature, but the display of thousands of moths, as well as other insects, is often regarded as one of the more memorable components to a jungle lodge or ecotourism experience (J. Adams, pers. comm.). Whereas artificial lighting should be curtailed in urban environments to reduce the impact on both humans and nocturnal insects, artificial lighting in ecotourism destinations should be managed to encourage sustainable levels of nocturnal entomological ecotourism. As seen in previous studies, arrangement and distribution of numerous artificial light sources may actually lessen the effects that any one particular light may have on the environment (Robinson and Robinson 1950, Bernhard and Ottson 1964, Frank 1988).
information can be highly useful in managing sustainable night lighting in both natural and urban environments.

Although intentional night lighting in ecotourism areas may yield still-unknown negative side effects, as described previously in this section, the intrinsic benefit of increasing awareness and exposure to insects by educating ecotourists may outweigh the potential harm. In all areas of the world, issues such as habitat destruction play a much more crucial role in the long-term survival of a species, making successful ecotourism and nature education all the more valuable and necessary. One may never know when the next great entomologist is visiting in his or her youth and is forever inspired by an extraordinary experience at a light sheet with thousands of insects in full brilliance.

Other Examples of the Effects of Ecotourism on Wildlife

In uncovering the effects of ecotourism on wildlife, many of the potential causes for disturbance are characteristic of man’s intervention into nature. As lodges and hotels penetrate remote areas, man brings with him certain baggage that invariably has an effect on wildlife and the ecosystem, such as the use of artificial lights, as seen in the previous section. However, ecotourism attempts to minimize this baggage, while still providing a unique and memorable experience for the travelers that partake in this unique brand of nature tourism. It is for this reason that those nuisance behaviors and unsustainable effects on wildlife be identified and better understood. Upon identification, it is then necessary to understand practical methods for reducing the impact. Exemplified by several studies, this is indeed possible and serves to improve the ecotourism experience for all involved parties.
Chimpanzees affected by ecotourism

A study by Johns (1996) provides an outline for a swift yet effective monitoring program aimed to identify and ameliorate the impacts of ecotourists on Chimpanzees. Conducted in Kibale Forest, Uganda, the study had the added incentive of attempting to understand the most effective way to promote habituation of Chimpanzees. Therefore, the study aspired to not only mitigate the ecotourism impact on Chimpanzees, but to maximize ecotourism potential. By ultimately striving to elicit a habituated response towards humans (i.e., Chimps either ignoring or being curious towards humans), the very same goal of the tourism enterprise becomes the goal of the conservationist. Then, you have not only sustainability, but also a neutral impact on the wildlife in question. This is highly desirable.

Johns (1996) took into account 10 variables when attempting to analyze the possibility of human-caused disturbance. These variables included: 1) human distance from the Chimpanzee, 2) distance from one Chimpanzee to another, 3) the activity that the Chimpanzee was engaged in prior to being encountered by humans, 4) location of the Chimpanzee when encountered (i.e., on the ground vs. in a tree), 5) number of human observers (i.e., ecotourists) present when encountered, 6) habitat type, 7) location method (i.e., how were the chimps found by the guide – vocalizations, feces, or by chance) 8) communicative impact (i.e., was an “alarm” sounded at first glimpse), 9) number of animals in the group, and 10) the age, sex, and social class of the Chimpanzee. Disturbance was then measured by observing the variety of response behaviors at the moment the Chimp became aware of human presence. These responses included behaviors such as charging, stealthy retreating, loud vocalization, soft vocalization, hiding, sitting and waiting for another Chimp, appearing curious, and
ignoring the observer. At the completion of the study, Johns (1996) found that there were several factors that impacted the Chimp behavior more negatively than others. First, it was determined that the distance between the Chimp and the observer significantly affected the Chimp’s propensity to flee or charge (as opposed to ignoring the observer – the ideal outcome). Secondly, the distance between the chimps significantly affected behavior. For instance, chimps within 5 meters of each other were far less likely to charge or flee than chimps with a distance 10 meters or more between each other. The activity that the chimp was engaged in just before the encounter also significantly affected the response from the animal. Those chimps engaged in eating plants were far more likely to charge or flee than those just resting. Furthermore, the method of locating the animals by guides strongly affected whether the chimp would elicit a “habituated” reaction. In fact, 74.3% of the total habituated reactions during the entire study, meaning the chimp would either ignore the researcher or exhibit curiosity, were the result of encounters during tree vigils (i.e., researchers waiting for chimps under a fruiting tree, or going directly to a fruiting tree in hopes of it being occupied by chimps). This was incredibly important information for the study, the Kibale Forest, and the Chimpanzees. As a result of this information, fruiting fig trees have subsequently been mapped out intensively and direct trails to them have been constructed for ecotourists. This has minimized unintentional contact elsewhere in the forest where habituated responses towards humans are more rare. It was also noted that larger group sizes of observers could be supported at fruiting figs compared to encounters elsewhere in the forest. This allows for more visitors and more income for the guides and Kibale Forest management and conservation. Johns (1996) also observed that
habituation responses increased with repeated exposure. With the majority of “first contact” between young chimps and ecotourists occurring at the fruiting figs, this serves as a favorable introduction between humans and young chimps. Should at some point unintentional contact between that chimp and an ecotourist group occur, such as on the trails connecting fig trees, the chimp will have already been introduced to the concept of human visitation and the encounter will result in less aggression towards the group.

**Asian Rhinos affected by ecotourism**

While Johns (1996) highlights the need for a proper method of approach to minimize tourism’s impact on Chimpanzees, as well as the context with which first encounters occur, other studies with other taxa concentrate more on the *distance* with which visitors approach animals in ecotourism destinations. For example, Lott and McCoy (1995) found that there are several distance thresholds that should be maintained with regards to visitation of Asian Rhinos (*Rhinoceros unicornis*). They found that when tourists approach Asian Rhinos from a distance of less than 10 meters, the Rhinos’ feeding habits are significantly affected. While all Rhinos spent less time feeding and more time on alert when visited, those that were given appropriate space during the visit returned to normal behavior within minutes after the tour group left. In fact, Lott and McCoy (1995) found that when visitors were 10 meters or less from the Rhino, the feeding rate was less than half as when they remained between 12-23 meters and one third as much as when visitors were 30 meters and beyond. In addition, Rhinos approached from less than 10 meters often fled, further obstructing their feeding behavior by stopping it completely.

The effects of tourism on the Asian Rhino are most pronounced when visitors approach them too closely. When appropriate distance is maintained (i.e., greater than
12 meters, but ideally at least 30 meters), the impact is minimal (Lott and McCoy 1995). While the feeding rate is reduced during the actual visit, principally because of the increased time spent being alert, normal feeding behavior resumes within minutes after the brief visitation ends (visits average approximately 20 minutes). Effects are further minimized due to the social structure of certain Rhino populations. As seen in Lott and McCoy (1995), Rhinos with large range sizes are apt to roam extensively while grazing, further reducing the impact of tourism by exposing the same Rhino to tourist groups infrequently and inconsistently (Laurie 1978, 1982). This, however, would not apply to Rhinos with more territorial behavior, and could result in disproportionate exposure to subsets of populations (Lott 1991). Unlike the example of the Chimpanzees, there is no evidence that repeated exposure to Asian Rhinos could result in habituation.

**Waterbirds affected by ecotourism**

For wildlife that forage and live near nature trails and wildlife observation areas, the impact of tourism could have the most pronounced effects. Aiming at ranking tourism behaviors that affect wildlife, Klein (1993) experimentally subjected waterbird populations to various degrees of ecotourism in the 2,000 hectare reserve known as “Ding” Darling National Wildlife Refuge (DDNWR), on Sanibel Island, Florida. The researcher targeted 15 species of waterbirds and exposed them to five different ecotourist disturbance regimes. On a scale from minimum to maximum disturbance, human disturbance treatments included the following: 1) Driving by the birds in a car and not stopping, 2) Stopping the vehicle within sight of the bird, but not getting out, 3) Stopping the vehicle within sight of bird and getting out for a look, but not approaching, 4) Stopping the vehicle within sight of bird, not getting out, but playing noisy tape recordings of human voices, and 5) Stopping the vehicle within sight, getting out and
slowly approaching the bird. Of the 15 species of birds studied, 11 were found to exhibit greater avoidance responses as the level of disturbance increased, suggesting a positive correlation between level of human interaction and wildlife disturbance. The specific avoidance behaviors exhibited by the bird species ranged from the bird simply looking up at the researcher, to fleeing. Ultimately, avoidance behavior among most birds appeared to increase in quality and quantity (both rate of avoidance behavior, and type of avoidance behavior – i.e., cautiously retreating vs. flying away) as treatment went from driving by a bird, to stopping and playing noise, to stopping and approaching. This suggests that noise plays a significant role in the disturbance caused by nature observers and waterbirds.

Similar effects have been reported in other studies. Noise has been seen to significantly alter the amount of time that birds spend foraging, the number of individual feeding events, and the number of feeding interruptions (Burger and Gochfeld 1998). Nevertheless, it is the physical act of approaching waterbirds that seems to elicit the strongest avoidance response. In an effort to examine the rate at which these behaviors are actually happening at DDNWR by visitors, Klein (1993) also observed incoming groups of visitors and recorded disturbance events based on their activity (categorized as: photography, nature observation, fishing, jogging, boating, and driving). Observing 622 visitor groups (1673 individuals) in all, it was found that 61 groups disturbed a total of 89 waterbirds. Photographers and nature observers contributed the most to disturbance, mostly from their tendency to approach wildlife to get better photos or views for identification. Joggers also disturbed wildlife, likely because of the close
placement of the trail to the habitat of the waterbirds. People driving on the road, boaters, and fishermen elicited the least response (Klein 1993).

This study raises interesting questions about the impact of ecotourists in natural areas. While the DDNWR is set up in a relatively unique way compared to many other ecotourism destinations, with roads and paths situated relatively close to wildlife habitat, the pronounced impact of noise stands out as a universal disturbance in ecotourism destinations. There exist relatively few other studies that examine the effect of noise on wildlife from an ecotourism standpoint. Nevertheless, there are several key studies that further examine the effect of noise on wildlife.

Effects of Noise and Flash Photography on Wildlife

Effects of Noise on Wildlife

Already discussed in this Chapter, noise has been seen to affect a range of wildlife, from helicopters eliciting avoidance behavior when approaching Dall’s sheep to waterbirds being disturbed and displaced by human noise. However, studies that examine the affects of noise on wildlife are not just restricted to terrestrial environments. Parijs and Corkerson (2001) showed that acoustic communication in Pacific Humpack Dolphins (Sousa chinensis) was altered as a result of noise from passing motorboat traffic. With ecotourism growing exponentially, further studies should look at the noise-related side effects of ecotourism. When natural areas are opened up to ecotourism, an increase in noise levels by humans is an expected result. Situations where cars are permitted to drive and boats are permitted to enter create perhaps the highest levels of noise, but this does not mean that the noises made from humans on simple walking trails have a benign effect.
We have seen in past studies that human noise elicits disturbance behavior from waterbirds in the Ding Darling National Wildlife Refuge (Klein 1993). Ranging from flying away to arresting feeding behavior, the behaviors that result from human noise could impact the fitness of wildlife, both as individuals and as populations. Other studies show that noises associated with ecotourism and human presence often drive wildlife from their habitats and affect feeding behaviors both in terrestrial and marine habitats (Stockwell et al. 1991, Frid 2001b, Parijs and Corkerson 2001). There are limited studies on the effects of ecotourism noise on invertebrates, but some studies do show that noise can affect invertebrate behavior. In honeybees, Frings and Little (1957) found that sustained noise caused worker bees in hives to slow their behavior and even stop movement in the presence of low frequency sounds. Frings and Frings (1959) reported that male swarms of the dipteran Pentaneura aspera would display startle reflexes in response to noise in a variety of frequency and sound pressure combinations. However, the total number of studies on invertebrates remain small, and the recent research is lacking. Of those few studies on invertebrates none covers Lepidoptera.

**Effects of Flash Photography on Wildlife**

It is evident that the mere presence of humans in wildlife habitat poses various threats, mostly in relation to the perception of humans as predators. However, ecotourists may pose threats other than simply resembling large predators when they encroach into wildlife habitat. The quintessential ecotourism adage to “take only pictures and leave only footprints” may allude to an additional danger. While certainly less intrusive than removing resources or animal products from natural areas, such as seashells, or bird feathers, and more benign than deliberately altering landscapes by
littering or carving names into tree trunks, it is evident that photos may in fact do more damage than originally thought.

Because of the intense nature of a photographic flash, it is not difficult to realize that camera flashes may elicit disturbance behaviors on wildlife. Just as with sound, these effects have been studied in both marine and terrestrial environments. Quiros (2007) found that the use of flash photography on Whale Sharks (*Rhincodon typus*) yielded responses similar to when the sharks were physically touched by humans. Also in response to camera flashes, Whale Sharks engage in avoidance behaviors such as diving, changing direction, and even violent shuddering (Quiros 2007). Heaslip and Hooker (2008) found that the presence of research monitoring cameras with flash systems attached to Antarctic Fur Seals (*Arctocephalus gazelle*) changed their behavior as well, specifically with regards to their diving behavior. During flash operation, the dive times of the seals were longer and deeper, with less time spent on the bottom feeding. In addition, use of flash was found to disrupt natural cycles of dive duration. Under normal circumstances, Fur Seals tend to oscillate between shorter and longer dives in a cyclic fashion. When subjected to flash, they no longer exhibited this predictable cycle and instead consistently engage in longer dives (Heaslip and Hooker 2008). Huang et al. (2011) found that when studying the response of the West Indian Anole (*Anolis cristatellus*) to flash photography, it was the noise of the flash and camera together that created a response. It was determined from this study that camera operation induced behavioral responses (i.e., avoidance, fleeing) by the anole that were similar to defensive reactions elicited by calls of their top predator, the American Kestrel.
(Falco sparverius). This details the complex assortment of stimuli that is produced by something as simple as taking a photograph.

Despite these interesting studies, there is a general paucity of previous research on the effects of flash photography on wildlife. Perhaps due to the recent advent of affordable digital cameras, it could be that the lower past prevalence of amateur and professional photographers was such that historically there was less cause for concern. Nevertheless, the significant results and negative impacts of flash photography on wildlife, as highlighted by the few existing studies, warrant further research. This is especially true regarding species not yet represented in the few studies that do exist. Invertebrates represent an entirely new group with which to conduct such studies.

**Effects of Ecotourism on Insects**

When looking at prior research on ecotourism’s effects on wildlife, invertebrate taxa are nearly non-existent in terms of being study subjects. This is true both for studies on the effects of noise and flash photography. The research reported in this Chapter is intended to study ecotourism’s effects on insects, specifically by examining the potential problems that occur in one of the best examples of entomological ecotourism – the Monarch butterfly overwintering phenomenon. Before going into the specific issues that ecotourism presents for the overwintering Monarch, it is appropriate to discuss this event in more detail.

**Ecotourism and the Monarch Butterfly**

One of nature’s greatest phenomena, the annual migration of the Monarch butterfly (Danaus plexippus), is a growing ecotourism attraction (Barkin 2003). Each year, approximately two billion Monarch butterflies migrate from across the eastern United States to a relatively localized area in southern Mexico, near the Transvolcanic
Range juncture of the Sierra Madre Oriental and Sierra Madre Occidental mountain ranges (Urquhart 1978, Brower 1995). Located 100 miles west of Mexico City, Mexico’s largest urban center, day and weekend trips to witness the colonies of millions of overwintering butterflies are becoming increasingly common, ever since the Monarchs’ winter home was discovered in 1975 by two Americans working with Dr. Fred Urquhart (Urquhart 1976). The Monarchs do not aggregate in just one colony, but rather in a dozen distinct sites throughout the Transvolcanic Range and reside there over the course of the North American winter (Calvert and Brower 1986, de la Maza and Calvert 1993). With first arrivals reaching the roosting sites in mid-November, the colonies grow in size until reaching their full potential roughly one month later, with three of the larger colony sites each routinely exhibiting over 100 million individual Monarchs throughout the overwintering period (pers. obsv.). Then, they will spend the remainder of the winter in reproductive diapause, a condition triggered prior to starting the southward migration by shortening day lengths, greater temperature fluctuations, host plant senescence, and lowered sun angles typical of the winter season (Goehring and Oberhauser 2002). At the end of their overwintering period and as the Spring equinox approaches in March, their reproductive diapause ends and the overwintering colonies begin to initiate their northward migration back to the U.S. (Herman, 1981, 1986, Herman et al. 1989). It is during these intervening four months of winter that the colony sites are open to ecotourism (five at present count, pers. obsv.) and will receive upwards of a quarter million visitors each year (Barkin 2003). Augmented by highway infrastructure between surrounding towns and man’s inherent desire to witness this spectacular event, a tourism culture has grown, with hotels, restaurants, and shops in Zitacuaro, Ocampo,
and, Angangueo. Infrastructure at each colony site has also grown throughout the years, with parking lots, vendors, small restaurants, guide services, and horse rentals abounding at the public entrances of each of the major publicly accessible colony sites (Figure 4-2, Figure 4-3). In most cases, after an hour’s walk or horse ride from the entrance station, visitors arrive at the Monarch colonies where tens of millions of Monarchs will be roosting, flying, and covering the vegetation (Figure 4-4).

As temperatures in the mountains warm from an early morning low of 32° Farenheit to a high typically in the high 60°s and low 70°s Farenheit (0° to 20° Celsius), the Monarchs become increasingly more active and take flight by the millions. The Monarchs that temporarily leave their roosting spots are doing so to cool down. Because of the incredible efficiency with which they fly and glide, the convection of air passing over their wings during flight cools the body and hemolymph compared remaining in sunlit positions and warm air within the colony, which may cause a deleteriously rapid metabolic utilization of their fat and lipid stores (Brown and Chippendale 1974, Masters et al. 1988, Alonso-Mejia et al. 1997). However, these brief periods of activity and movement to seek a cooler perch are a compromise and still use valuable energy from stored fats. The storage of fats and energy built up during the southward fall migration is vital to their survival, as only a small percentage of Monarchs are able to feed while in their overwintering grounds (Brower 1995). They must ensure that their stored nutrients and energy acquired during their southward migratory journey lasts for the entire overwintering period before powering them on their last leg of their great migration – their return northward in the Spring (Masters et al. 1988).
Just as the Monarchs are triggered in the fall to migrate southward by shortening day length, cooling temperatures, and a lowering of the sun’s zenith in the sky, the lengthening of the days, warming temperatures and raising of the sun’s zenith stimulate Monarchs to migrate northward in the spring (Goehring and Oberhauser 2002). These same cues also trigger internal hormones to conclude reproductive diapause, prompting the Monarch to mate and reproduce (Goehring and Oberhauser 2002, 2004). It is the southward migration from the eastern U.S. and southern Canada that receives most of the attention in terms of investigative research into the causes and factors involved in this 2,000 to 3,000-mile journey. However, the mechanisms behind their northward migration are even more of a mystery. As advances are made in uncovering the process of southward migration, we may also gain insight as to how it is possible for the rest of their great journey to be completed.

What makes the migration of the Monarch butterfly so unique is not just the fact that it occurs with such a simple organism, having a nervous system far less complex than in migrating vertebrates, but that the ability and proclivity to migrate is part of a genetic program (Reppert et al. 2010). Each migrating Monarch is participating in the journey for the very first time, without any benefit of parental imprinting or learning, and owing everything to heritable genes that are responsible for this impressive feat (Brower 1985, 1995). In fact, there are at least two generations of Monarchs between migrating generations each year (Malcolm 1993). Those intermediate generations are considerably shorter in lifespan and also have shown no tendency to migrate, even when subjected to environmental conditions comparable to those experienced by the migrating, or Methuselah, generation (Urquhart 1960, 1966, Brower 1961).
Monarch butterfly navigation techniques

In addition to genetic influences triggering a specific generation of Monarchs to migrate, there are also discrete navigational techniques that enable these butterflies to reach their overwintering grounds each year. Employing a variety of tactics, there are several levels of navigation that enable Monarchs to properly migrate to the same location year after year.

The first level of navigation is the use of a time-compensated sun compass (Reppert 2007). The sun is a relatively predictable orientation tool, as it has a predictable course throughout the day, rising in the east and setting in the west over a set trajectory. However, it is the motion of the sun that makes it somewhat challenging to use as an instrument of navigation, for it changes position in the sky by 15° hourly throughout the day. Its path, though, is indeed predictable and for this the Monarch employs a circadian clock that allows it to adjust for the movement of the sun by employing an internal timing device, effectively tracking the sun across the sky in relation to the time of day. Utilizing an internal compass, the Monarch may calibrate its compass continually as the sun moves across the sky. In order for these two components to be integrated and continue to work throughout the migration, both the circadian clock and sun compass must be adaptable to changes in environmental, atmospheric, and geographic conditions.

During the Monarch’s 3,000-mile journey, there are many challenges to performing effective navigation. When using the sun as a key navigational tool, the question comes up as to what the Monarchs do on cloudy days? Although not entirely understood, it is believed that Monarchs employ two tactics to maintain proper orientation, despite a lack of sun for proper compass use. The first is the use of polarized light from areas of the
sky where the sun may not be visible, but polarized light still shines through (Reppert et al. 2004). In an elegant experiment using directional flight simulators and polarization filters, Reppert et al. (2004) found that the use of polarized light disrupting filters significantly altered flight direction among migratory Monarchs when tested in a flight simulation cage. While not discounting the inherent value of the sun itself as a navigational tool, Reppert et al. (2004) concluded that polarized light is as useful to migrating Monarchs as other taxa such as honeybees and desert ants in facilitating proper navigation (Frisch 1967, Waterman 1981, Gould 1998, Wehrner 2001, Reppert et al. 2004).

The second tool that is employed by Monarchs to adjust for environmental and atmospheric changes while migrating is an internal magnetic compass (Jones and MacFadden 1982). Possessing magnetite, a magnetic iron-oxide metal, it is suggested that Monarchs may engage magnetic navigational tactics, as seen in a wide range of other taxa, from sharks to birds (Wiltschko and Wiltschko 1972, Kalmijin 1978, Jones and MacFadden 1982, Jungreis 1987). Although this would certainly help to explain the persistence of proper orientation on cloudy days when even polarized light may not be visible, there also exists evidence against this theory. As shown in novel flight simulating devices, Monarchs do not predictably follow magnetic paths or alter flight behavior in the presence of a shifting magnetic force (Mouritsen and Frost 2002). The possible use of magnetic poles in Monarch navigation theory remains controversial, with evidence both for and against it appearing in the literature.

Magnetism or no magnetism, there must be additional levels of navigation that Monarchs employ beyond the use of a time-compensated sun compass, which only
provides the Monarch with a south to southwesterly bearing. It is difficult to assume that this simple bearing is sufficient for the remarkably precise navigation ability observed when Monarchs roost in the same locations year after year, regardless of variations in environmental conditions. Monarch antennae have been shown to be critical in the navigation process when perceiving sunlight, and it is possible that they are further involved at the chemoreception level (Merlin et al. 2009). Although still a theory, many scientists working with Monarchs believe that olfactory cues, either from dead Monarchs, Monarch scales, or volatile chemicals from the Oyamel Firs, could be cues for locating appropriate colony sites. Additionally, distinct changes in barometric pressure or wind speed, as a result of crossing mountain passes or other geographic landmarks, could be perceived by Monarch antennae. This has already been shown to occur in other insect species and likely apply to Monarchs, too (Sane et al. 2007, Kamicouchi 2009, Yorozu et al. 2009). However, studies are lacking to make definitive conclusions on this ability.

Ultimately, the antennae have been shown to play their biggest part in ensuring the proper orientation for the first one to two thousand miles, as they cross through southern Canada and the United States. Being critical to the functioning of the time-compensated sun compass system, studies have shown that they may in fact be the key to proper time-compensation through the use of antennal clocks (Merlin et al. 2009, Reppert et al. 2010, Guerra et al. 2012). Originally postulated by Fred Urquhart as vital organs used in Monarch navigation, the antennae have proven to be one of the most critical components to the entire system of navigation and orientation (Reppert et al. 2010). Recent studies show that they are responsible for measuring light levels and
daylight length, both vital processes in the complicated time-compensated sun compass mechanism (Merlin et al. 2009). Through a series of intricate pathways from the antennae to the central complex of the brain to the dorsal rim and main retina of the eye, light perception is as complicated as it is necessary for a successful migration. While the pathways and efficacy of this suite of organs have been shown to play significant roles in Monarch migration, little has been done to measure the vulnerability of this system to unnatural disturbances or stimuli.

**Ecotourism at the Monarch overwintering sites**

Human visitation to sites exhibiting the climax of the annual migration and overwintering event is a prime example of entomological ecotourism. The main Monarch overwintering sites are popular destinations for Mexicans as well as international ecotourists. Currently there are five public colony sites that reside within a network of conservation areas, collectively making up the Monarch Butterfly Biosphere Reserve. These are the sites of Sierra Chincua, Cerro Pelon (El Capulin), El Rosario, Piedra Herrada, and La Mesa (Figure 4-5). Declared a UNESCO World Heritage site in 2008, the biosphere reserve and these protected areas receive nearly a quarter million ecotourists each year during the Monarch overwintering period from later November to early March (Barkin 2003). With this tremendous volume of visitation over the 135-day overwintering span comes great economic opportunity for the local communities, known as ejidos. These ejidos are composed of local Mexican citizens who inhabit the immediate areas surrounding the protected reserves. In most cases, the ejido is also the governing body for the management of forest conservation and ecotourism within the reserve. Each reserve has one ejido associated with it, and vise versa. As a result,
money is earned directly by each ejido, which then is distributed among the entire community as source of seasonal income (pers. obsv.).

The most direct way for these communities to earn money is by charging park entrance fees for visitation within the Monarch reserves. On average, these fees amount to the equivalent of five US dollars per person. Unlike many other national parks in other countries, there is no delineation between an international and national visitor in terms of entrance fee. This is likely due to the fact that the overwhelming majority of visitation comes from local nationals, who generally comprise over 95% of all ecotourists that visit the sanctuaries (Barkin 2003, pers. obsv.).

At the larger colonies, namely El Rosario and Sierra Chincua, there is an extensive network of vendor and restaurant stalls set up just outside the boundary of the reserve. Strategically, these are positioned in a way that all visitors must pass through them before reaching the ticketing booth and ultimately entering the reserve (Figure 4-2, Figure 4-3). As of February 2012, there were over 100 of these stalls in operation at El Rosario, and over 35 in operation at Sierra Chincua. Spending some time perusing the shops and enjoying the culinary delights of the local cooks is commonplace for both national and international ecotourists visiting the reserves.

Originally found only at Sierra Chincua, horses are now for hire to ride at El Rosario and Cerro Pelon, as well. These horses transport paying ecotourists from the entrance station to the general area in which the Monarch colonies are found. On an average year, the colony of Monarchs is about two miles from the entrance station, often requiring significant up and downhill hiking in high altitude conditions. Horses traditionally have been exclusive to the Sierra Chincua reserve, which exhibits the
largest support structure for such and has over 110 horses for hire as of 2012. Charging 75 to 100 Mexican pesos each way (approximately 5-10 U.S. dollars each way or 10-20 U.S. dollars round trip, to the colony and back to the parking lot later that day), the individual families that own these horses stand to make a significant wage. The owners routinely escort their horses and mounted ecotourists six to eight times on busy days (pers. obvs.).

Throughout the larger reserves (El Rosario, Sierra Chincua, and Cerro Pelon), park guards and rangers double as tourist guides. Helping both individuals and groups on their way to the colonies by showing the correct paths, carrying camera equipment, or providing interpretation along the way, these guides are paid by sharing in the entrance ticket proceeds, as well as tips from those ecotourists accepting their individualized service. In the largest of the reserve systems, at El Rosario preserve, there are 70 employed vigilantes, or park rangers/tourist guides, as of 2012.

Lastly, there are many more indirect ways for the local communities and cities to benefit from this ecotourism phenomenon. Larger towns in the area, such as Zitacuaro, Ocampo, Angangueo, and Morelia are often the staging areas and are hosts for international ecotourism, providing restaurants, hotels, stores filled with supplies, and transportation services. These examples serve to elucidate the many stakeholders in this one particular entomological ecotourism attraction (Figure 4-6, Figure 4-7). With larger ejidos comprised of over 10,000 total members, all depending directly on the success of ecotourism in the area, it is easy to understand why these local communities are also some of the greatest advocates for conservation and protection of the Monarch reserves. They very readily accept the indoctrinated idea that a healthy forest
ecosystem is vital to the Monarchs’ survival and return from year to year. It is also easy to realize the dependent economic relationship that these local communities have with the Monarchs and their great need to preserve the overwintering phenomenon.

Despite numerous threats to the persistence of the Monarch migration and the overwintering event, including transgenic corn and sorghum crops in North America, deforestation within the reserves in Mexico, and the ubiquitous issue of global climate change, these insects continue to display resilience year after year. Amidst occasional devastating news of winter storms in the immediate colony areas and reports of droughts in their breeding grounds, the Monarchs persevere. However, these very same threats reappear frequently and often bring into question the indefatigability of the migration event.

It is the belief of this author that ecotourism has provided solutions to some of the conservation problems that the Monarch butterfly faces. By creating significant economic incentives for preserving the forest and the Monarch habitat, the most immediate threat to the Monarch migration in Mexico, which is undoubtedly habitat destruction, is becoming less of an issue. Deforestation has historically been the foremost issue in whether or not the migration event would continue. As illegal logging infringed on the core of the reserve, there were serious concerns that the trees upon which the Monarchs depend would be cut down, leaving only unsuitable roosting locations. These unsuitable locations, in turn, would fail to protect the colony adequately from increasing winter temperatures, as well as winter storms that could sweep through open forests leaving a path of Monarch mortality behind. However, with the migration event increasing in popularity, and ecotourism surging, governmental
decrees are further protecting the forest by shutting down dozens of illegal saw mills and blocking logging roads with the help of the Mexican Army. In addition, local ejidos are as vigilant as ever, collectively regarding illegal logging as a catastrophic threat to their own economic stability.

**Effects of ecotourism in the Monarch reserves**

The virtues of ecotourism are very noticeable in the case of the overwintering Monarch colonies, as detailed in this Chapter. Ecotourism provides tremendous economic incentives to numerous stakeholders and has propelled the Monarch to serve as a flagship species, raising awareness about key conservation issues in Mexico, the U.S., and Canada. Ecotourism also functions as a tool to promote science education and create conservation-minded cultures that are capable of addressing environmental issues across the planet. With the intense promotion and escalating scope of ecotourism, one must ask whether there are unintended negative effects correlated with the growth of ecotourism in these reserves. As seen earlier in this Chapter, there are many possible impacts from ecotourism. However, no studies have been conducted on the effects of ecotourism on the Monarch butterfly. In the case of the Monarch overwintering phenomenon, two key actions on part of ecotourists have been identified as potential disturbances to the butterflies that overwinter there. These two actions have been seen throughout the literature to have effects on a wide array of other animals and are identified as noise and flash photography.

**Hearing in Butterflies**

Hearing organs have been identified in seven orders of insects, including Neuroptera, Orthoptera, Diptera, Dictyoptera, Coleoptera, Hymenoptera, and Lepidoptera (Hoy and Robert 1996). In some cases, the ability to hear is paired with the
ability to produce sound. This combination of hearing and sound production may be used in mate locating, predator avoidance, prey locating, and territorial behavior and is well studied (Bennet-Clark and Ewing 1970, Burk 1983, Adamo and Hoy 1994, Adamo et al. 1995, Alvarez et al. 2011). Among those insects capable of perceiving sound, the ability to do so is often vital to individual survival and the persistence of the species.

Despite the complexity inherent in the variety of insect hearing organs, they have not diverged from a common ancestor but instead have converged, meaning that they have evolved separately in each of the major insect orders that exhibit hearing organs. Furthermore, solely within the order Lepidoptera, sound perception has evolved independently at least 10 separate times, yielding a variety of forms and functions to insect “ears” (Scoble 1992). Contrast this with the fact that vertebrate hearing has evolved only once throughout evolutionary history, and it becomes clear that there is still much to learn about the ability of insects to perceive sounds and the hearing organs that facilitate this (Northcutt 1985, 2002).

Hearing organs differ within the Lepidoptera. This is especially true between groups of moths. In fact, tympanal ears have developed at least six different times within major moth superfamilies (Fullard 1998, Minet and Surlykke 2003). The mechanism for hearing in butterflies is rather different than that for moths, as butterflies, being mostly diurnal insects, are exposed to a completely different suite of predators for which sound perception is useful. While moths rely largely on the ability to perceive ultrasonic sound from bat echolocation calls, butterflies instead are tuned into frequencies in the lower range (<18kHz) where noises from their diurnal predators generally fall, such as calls from birds and some reptiles (Fullard et al. 1979, Mahony et
To perceive these mid-level and lower frequency sounds, some butterflies employ what is known as a Vogel’s organ (Vogel 1912, Otero 1990).

Vogel’s organ is a sound-perceiving organ located at the base of the subcostal and cubital veins (Vogel 1912). Consisting of a thinned region of exoskeleton, which represents the tympanal membrane, it is surrounded by a rigid chitinous ring (Yack et al. 2000). Attached interiorly to this membrane are three chordotonal sensory organs, with the largest of the three located at the center of the tympanal membrane and the two smaller ones located at the periphery. Together, the various components of the organ function like a vertebrate eardrum (Yack and Fullard 1993, Hoy and Robert 1996). Tests that directly enervate the tympanal organ have shown that this organ is indeed highly sensitive to sound. While frequencies at 18kHz appear to be at the upper end of the threshold for most butterflies exhibiting a Vogel’s organ, Lane et al. (2008) and Lucas et al. (2009) have found that the Vogel’s organ found in *Morpho peleides* (Nymphalidae) is most sensitive to sounds in the 2-4 kHz range at a median sound pressure level of 58 dB. Nevertheless, Vogel’s organ seems to be relatively adaptable to meet the needs of the organism, as Rydell et al. (2003) found that the Vogel’s organ of *Mantanaria maculate* (Nymphalidae) is able to perceive high-level frequencies (26kHz and above) as well. Because *M. maculata* has periods of crepuscular activity in the Costa Rican cloudforest where it occurs, it is believed that these extended abilities of the Vogel’s organ help prevent predation from bats by allowing the butterfly to perceive and avoid ultrasonic echolocation calls, as night approaches (Rydell et al. 2003). To date, studies have identified Vogel’s organ in several species of butterflies, so adaptations to specific frequency ranges are likely to differ. Different predators,
habitat characteristics, and mate-locating behaviors likely play a significant role in the functionality and evolution of each species' Vogel's organ.

Presence of a Vogel's organ appears to be inconsistent among butterflies. Nevertheless, there are several studies that have identified this butterfly “ear” in various families of Lepidoptera. *Hamadryas feronia* (Nymphalidae) is perhaps the most well studied butterfly, in terms of both sound perception and production, and is largely due to the extensive research reported by Swihart (1967), Monge-Nagera (1992), and Yack et al. (2000). Through their combined efforts, the morphology of the mesothorax has been thoroughly mapped and specific details on sound perception and production in *Hamadryas* revealed. Lane et al. (2008) and Lucas et al. (2009) have located a Vogel's organ in the Neotropical *Morpho peleides*, and Rydell et al. (2003) have found a Vogel's organ in *Manataria maculata*. Within the Satyrinae subfamily of Nymphalidae, Mahony et al. (2005) reported the presence and functionality of a Vogel’s organ in *Pararge aegeria*, and Murillo-Hiller (2006) suggests that *Yphthimoides castrensis*, which is found in Southern Brazil, is also capable of perceiving sound through a Vogel’s organ. Thus far, the Vogel’s organ has been identified and found only within Nymphalid butterflies. However, this is a vast family of insects comprised of over 6,000 species, and includes some of the most well studied butterflies in the world (Ackery et al. 1999). Thus the lack of studies on the presence/absence of Vogel’s organ in other Nymphalidae necessitates more research.

The Monarch butterfly is a particularly interesting butterfly to look at in terms of sound perception. The Monarch has certainly been the focus of extensive research across a variety of topics, but there is a general lack of research in the past literature
regarding the perception of sound by the butterfly. Although the Vogel’s organ has been found in butterflies within the same family as Monarchs, there is no literature that examines whether or not the Monarch shares these traits. However, sound perception is known to occur via other body parts in Lepidoptera as well. Sensilla located on the surface of the cuticle and subgenual organs, which are located intersegmentally on the legs of most insects, have been shown to function in sound perception at a range of frequencies in a variety of insects (Debaisieux 1938, Swihart 1967, Markl and Tautz 1975, Menzel and Tautz 1994, Devetak 1998, Vilhelmsen et al. 2001). Monarch larvae have been observed to react to sound, suggesting that they are able to perceive heightened noise levels, but little work has been done on adults (Rothschild 1997). The studies described in the Methods and Results sections of this Chapter serve to further our understanding of general sound perception in Monarch butterflies.

**Vision in Butterflies**

Butterfly vision may be broken down into various components, including the compound eyes, ocelli, and antennae. The compound eyes of butterflies are very similar to the eyes of most insects and are complex in form and function. Composed of numerous ommatidia, or optical facets (often several hundred to several thousand, depending on the species), insect compound eyes have optical components such as cones and rods (also known as rhabodmeres) that are adapted for efficient light perception, and lenses to regulate the focus and angle of view (Yagi and Koyama 1963, Scoble 1992). The primary receptor cells that integrate all information coming through the compound eyes are known as retinula cells. These sensitive cells are also connected to primary nerve fibers that deliver information to the insect nervous system, allowing the insect to react to external stimuli. Ultimately, the visual acuity of insects is
considerably advanced when compared to animals in general. Only two other phyla besides arthropods, namely the mollusks and the chordates, have image-resolving eyes that are composed of these advanced structures that can discern different light levels and perceive colors (Land and Fernald 1992).

Monarch butterflies have a rather complicated compound eye system, largely attributed to the need for long distance flight and navigation. In their case, the eye is divided into several different areas, each with specific microvillar alignments, rhabdomere lengths, and various pigment and accessory pigment cells optimized for discerning certain wavelengths (Frentiu et al. 2007, Blackiston et al. 2010). One practical reason for this is that the various areas seem to facilitate a higher degree of polarized light reception among insects (Nilsson et al. 1987, Reppert et al. 2004). For the Monarch, this ensures proper navigation along migratory routes regardless of the weather and amount of sunshine on a given day (Froy et al. 2003). Ocelli in Monarch butterflies are much simpler and in many ways do not appear to have a specific role compared to compound eyes. However, they do consist of a basic lens, retina, and retinula cells that deliver sensory information to the butterfly nervous system that ultimately aids in the total amount of visual data perceived (Scoble 1992). Ocelli have limited ability to focus and are believed to function in general orientation, as their limited ability to perceive specific surroundings (i.e., shapes such as leaves or flowers) allows for a more general perception of surroundings. This could help in orienting in a particular direction based on the horizon or light levels, while avoiding distraction from nearby objects (Land 1985).
Antennae are now proving to be rather important in the visual perception of Monarch butterflies, specifically regarding light perception. Merlin et al. (2009) demonstrated in a series of experiments that not only are antennae critical in the perception of changing light levels, but they are instrumental in governing the Monarch’s ability to navigate. Antennae are now proving to be the epicenter for the time-compensated sun compass used by the Monarch. Originally thought to be controlled by the insect brain, this novel research has proven that antennae are at the heart of the time-compensate sun compass mechanism and the navigation abilities it facilitates. At the time of writing this dissertation, research is being conducted on the Monarch antennae and their role in detecting light levels, but much was elucidated by Merlin et al. (2009) to suggest that the antennae are essential organs in the perception of light by Monarch butterflies. Undoubtedly more research will uncover novel findings in this area of study.

**Objectives and Hypotheses**

A byproduct of mere human presence, crowd noise has been seen to reach high volumes with almost no control against it within the overwintering colonies of Monarch butterflies. It has been shown in numerous other cases that animals respond to noise in a variety of ways, generally eliciting a behavior similar to that of predator avoidance (Stockwell et al. 1991, Berger 1998, Dyer et al. 2001, Frid 2001b, Huang et al. 2011). No study to date has examined the consequence of noise stimuli on the Monarch butterfly, especially with regards to ecotourism. For the sake of minimizing ecotourism’s impact on the Monarch overwintering phenomenon, there is a great need to understand what effects, if any, that ecotourism may have on Monarch butterflies. Should Monarchs behave similarly to those animals already documented as avoiding loud
noises resulting from ecotourism, the health of the migration event, as well as the viability of local communities, could face additional challenges as ecotourism grows.

I hypothesize that when subjected to crowd noise, Monarch butterflies will exhibit disturbance reactions in a range of behaviors. In addition, I hypothesize that when given a choice, Monarchs will prefer to spend more time in areas with lower noise levels. Furthermore, when exposed to increasing sound levels, Monarch butterflies will exhibit more frequent disturbance reactions, suggesting that louder noises are more disturbing to Monarchs. Sound perception in Nymphalid butterflies has been shown to rely extensively on the Vogel’s organ. In order to complement the applied studies on Monarch behavior and sound, I aim to determine if a Vogel’s organ is present in the Monarch, as has been shown with other butterflies in the family Nymphalidae.

A second ecotourism impact that has unknown consequences in Monarchs, but has well documented and pronounced effects with other wildlife, is flash photography. Studies have shown that the effects of lighting and flash photography are significant in eliciting disturbance behaviors in a diverse array of animals, including reptiles, fish and mammals (Carr and Giovanolli 1957, Quiros 2007, Heaslip and Hooker 2008). The incidence of flash photography is also widespread within the Monarch overwintering colonies. If Monarchs respond to flash photography in a way similar to that of other animals previously studied, there would be cause for concern. The predictability of annual Monarch roosting locations within each reserve is as essential to the ecotourism enterprises in local communities, as it is essential to the welfare of the Monarch and its migration event. Should flash photography cause Monarchs to be disturbed or displaced, their own welfare, as well as that of the local ejidos, could be in jeopardy.
I hypothesize that when subjected to flash photography, Monarch butterflies will exhibit disturbance reactions in a range of behaviors. Furthermore, with an increasing quantity of flash exposures, Monarch butterflies will exhibit proportionately more frequent disturbance reactions. While indirect effects of flash, such as disturbance and displacement, may have negative effects on the health of both the migration event and the individual Monarchs, I also aim to study the direct effects of flash on Monarch health, specifically with regards to butterfly longevity. I hypothesize that flash exposures will decrease longevity, and as the total number of flash exposures increase, longevity will decrease concomitantly. These objectives are primarily targeted at understanding the effects of ecotourism within the Monarch overwintering locations, but there are other instances where flash photography could affect the behavior and health of Monarch butterflies. Freshly emerged butterflies are often exposed to flash in enclosed butterfly exhibits. I aim to study these butterflies as well in order to test for any effects that flash may have on especially young adult butterflies. I hypothesize that freshly emerged butterflies exposed to flash will exhibit significantly shorter lifespans than those not exposed to flash.

Noise and flash photography have been shown to cause disturbances to wildlife throughout the animal kingdom. Most commonly, the reaction by the animal to such disturbances is to flee and simply avoid the stimuli. Should it be the case that the Monarch butterfly has the propensity to exhibit the same reactions, these components of ecotourism could have a pronounced impact on the annual overwintering event, particularly as ecotourism grows. Constant relocation is not only harmful to the butterfly, which has a very limited amount of stored energy, but could result in butterflies
choosing areas outside of the established reserves, which would cripple the local economies of the ejidos. The following sections detail experiments that were conducted in order to understand what effects ecotourism noise and flash photography may have on Monarch butterflies.

With ecotourism heralded as a solution to key conservation problems, it is imperative that any negative impacts resulting from ecotourism be identified. Once identified, impacts can be managed and controlled. Without understanding the possible negative effects of ecotourism on the Monarch butterfly, the highly promoted growth of ecotourism could be harmful to the wildlife and nature that it is inherently trying to protect.

**Experimental Methods**

**Punctuated Sound Experiments**

**Standard Frequency**

**Study organism.** At the start of the study, 40 adult Monarch Butterflies (*Danaus plexippus*) were purchased from Shady Oak Butterfly Farm in Brooker, Florida. All were less than 24 hours old when acquired and represented an even mix of male and female butterflies. The Monarchs were then divided equally among four screened cages in a temperature-controlled greenhouse (i.e., 10 Monarchs per cage) at the Department of Entomology and Nematology, University of Florida, Gainesville, Florida (Figure 4-8). Monarchs were allowed to acclimate for an average of 16 hours to the greenhouse conditions before beginning the experiments.

In order to test for Monarch age effects on a response to sound, testing was conducted on Monarchs at two age ranges: (1) 24-48 hours old, and (2) 12-14 days old. Using different age ranges served to test for the possibility that the age of the Monarch
may affect or determine the likelihood that they would exhibit a reaction to sound. Ages were defined in ranges, as these experiments often required several full days of testing to complete, meaning that part of the original group that was acquired when less than 24 hours old may not have been tested until they were 48 hours old. The same applies to Monarchs in the 12-14 day range.

**Location.** Two greenhouses were used at the University of Florida's Department of Entomology and Nematology as test sites in which to conduct this study (Figure 4-9). Research was conducted in June and July of 2011, in Gainesville, Florida. Temperatures inside the greenhouses were maintained between 21° Celsius and 27° Celsius throughout the days and nights in order to maintain stable environmental conditions. These temperatures were regulated through evaporative cooling units, which also ensured stable humidity levels throughout the course of the study. Each greenhouse was further subdivided into four separate screened cages that corresponded to the four sound treatment levels used, and housed the Monarchs during the study (Figure 4-10). In each cage, ample nectar plants (*Pentas* and *Agastache*) were provided for the Monarchs to feed upon between trials (while they aged from 24-48 hours to 12-14 days) and nectar plants were rotated out roughly every week with fresh ones in order to maintain nectar levels and to promote normal feeding. In addition, a small amount of Gatorade was provided in the form of a soaked sponge on a saucer, as an additional source of sugars, salts, and nutrients. Automated drip irrigation systems were attached to each potted plant in each cage in order to provide water for the butterflies, as well as the potted nectar plants (Figure 4-9).
Trials. To test for the effects of sound exposure on Monarch behavior, Monarchs were subjected to sound produced by a portable speaker (Altec Lansing, iM237 in Motion Portable Speaker) in three ranges of sound pressure levels or decibel levels (dB): (1) 65-80dB, (2) 80-95dB, (3) 95-110dB. A control of 40-55dB was tested, which represented nothing more than ambient noise. Ten Monarchs were subjected to each sound level at two ages in their life (Figure 4-10). A recording of human crowd noise with a frequency range of 200 Hz – 9000Hz was purchased on the Apple iTunes Store (Audio Environments & Co., Greatest Sound Effects, Crowd Noise #194) and used to simulate typical frequencies of human voices, as is a typical byproduct of ecotourism in the Monarch overwintering colonies (Figure 4-10). A sound testing cage was set up in the adjacent greenhouse. Within this testing cage, a single plant was provided as a natural substrate on which the Monarch was placed just before testing began (Figure 4-8). Along with the plant, the aforementioned portable speaker was placed in the cage and connected to an iPod, which was controlled by the researcher outside of the cage through the use of a two meter 1/8 inch mini-to-mini adapter cable (Figure 4-11).

Upon placing the individual Monarch onto the plant inside the testing cage, the butterfly was allowed to move about the plant and inside of the cage without any sound stimulus in order to adjust to being handled. Because they were being introduced to a new environment, it was the natural reaction for the butterflies to walk or fly briefly until finding a suitable part of the cage, screening, or plant on which to settle. Once the Monarch had settled, testing began. Testing occurred between 10:00am and 2:00pm EST. In order to maintain a set decibel level range (e.g, 65-80 dB) regardless of the Monarch’s exact location inside the cage, the testing cage was purposely small. This
allowed for a predictable distance between the Monarch and the sound-emitting speaker throughout the course of the treatments. The volume transmitted from the iPod to the speaker system was calibrated using a Scosche SPL1000 sound pressure meter, which was capable of detecting dB ranges of 30-140 dB (Figure 4-11). Decibel ranges rather than exact dB values were chosen due to the inevitable slight fluctuations and auditory attenuation that comes with variable distances between a sound-emitting device and a mobile test subject.

For each of the four sound pressure levels, five seconds of crowd noise sound was played and repeated 30 times per Monarch subject. Between each five second interval of sound was five seconds of silence (ambient noise). For each sound interval, Monarch behavior was recorded as one of six reactions to sound: 1) no response, 2) antennal twitch 3) body twitch 4) walk, 5) fly and land, and 6) fly away (Table 4-2). After the 30 individual sound exposures per Monarch were completed, each was returned randomly to one of the four holding cages. There they would remain until they reached the second age level (12-14 days) and the trials were conducted again. These holding cages would hold 10 Monarchs each and were provisioned with five nectar plants (a combination of Penta and Agastache plants), all connected to drip and spray irrigation hoses, as well as a small plate with Gatorade to act as an additional food/energy source should the nectar plants become depleated.

In summary, for each of four dB levels: (1) 40-55dB (control) (2) 65-80dB, (3) 80-95dB, and (4) 95-110dB, a total of 30 repetitions of punctuated sound exposures were conducted on 40 separate Monarchs at two points in their life: (1) 24-48 hours old and
(2) 12-14 days old (Figure 4-10). This resulted in a total of 2,400 events of punctuated sound exposure on the butterflies.

**Low Frequency Tests**

Twelve Monarch butterflies (*Danaus plexippus*) were acquired from Shady Oak Butterfly Farm and all were less than 24 hours old. On three separate days (August, 28-30, 2012), testing was conducted on 48, 72, and 96-hour-old butterflies in the same greenhouse as used in the standard frequency sound studies described in the previous section. Testing occurred between 10:00am and 2:00pm EST on each day that trials were scheduled. In order to test for Monarch butterfly reactions to low frequency sounds, two treatment categories were defined, dB level and sound frequency, with a total of two and three levels, respectively, for each category (58 and 85 dB, and 100, 150, and 200Hz). This randomized complete block design yielded a total of six different treatment combinations to which to subject Monarch butterflies (Figure 4-12). The application “Subwoofer Bass Tester” from Alkex Instruments was purchased from the Apple iTunes Store to produce consistent low frequency sounds at the appropriate decibel level and frequency combinations (Figure 4-13). The application was loaded onto an iPod, which was then connected to an Altec Lansing iM237 inMotion external speaker by a 1/8th inch mini-to-mini speaker cable.

The order and pairing of the treatment levels was randomized, with each combination of dB level and sound frequency repeated five times for each of the twelve butterflies, resulting in 30 events per Monarch (Figure 4-12). At the start of each trial, individual butterflies were taken from their holding cage and placed into a small screened cage. Once they had settled and ceased all movement, testing began by exposing them to three seconds of punctuated low frequency noise in a randomized
order of dB and frequency combinations. Response to sound was categorized as one of six possible reactions: 1) Antennal twitch, 2) Body twitch, 3) Walk, 4) Fly and land, 5) Fly away, and 6) No response (Figure 4-2). This study provided a total of 360 opportunities for datapoints on how Monarch butterflies respond to low frequency sound.

**Sustained Sound Study**

To test whether Monarchs are repelled by noise over the course of time, Monarchs were presented with a choice of nectar sources at different noise levels. More specifically, one nectar source was located next to a loud speaker and the other was located at the other side of the cage from the loud speaker, providing for a 25 dB gradient in noise (a 25 dB difference is comparable to the difference between a coffee grinder and a chainsaw) between each side of the cage. Then, their behavior was recorded over an eight-hour period.

In order to house this experiment, a large rectangular cage was constructed from four separate screened cages by cutting out the side panels of each small cage and connecting each cage end to end, creating a line (Figure 4-14). Individual cages were then connected to each other using binder clips, creating seamless transitions from cage to cage (i.e., no gaps), effectively creating one large rectangular cage measuring 3.0 meters in length, 1 meter in height and 0.75 meters in width (Figure 4-15). At each end of the cage, three small *Pentas* plants in full bloom were positioned and arranged into a tight cluster. At the “positive” end, a stereo speaker (Cambridge Soundworks Model TEAD-57-121500U) was placed directly in the middle of the cluster of *Pentas*, such that the speaker was in close contact with all flowering parts of the tight cluster of nectar plants. This speaker was connected via 1/8” speaker wire to an iPod loaded with
a pre-selected crowd noise simulator track purchased from Apple iTunes Store (Audio Environments & Co., Greatest Sound Effects, Crowd Noise #194). The volume and dB level of the speaker/iPod combination was calibrated using a Scosche SPL1000 sound pressure meter to put out an average level of 80 dB when measured from the distance of the Pentas flowers to the speaker. Frequency range of the sound was identical to the previous punctuated sound study, measuring 200Hz – 9,000Hz, as determined by Adobe Southbooth Pro software (Figure 4-11). At the “negative” end of the long cage, there was no speaker, only the plants, which allowed for a gradient to be created from the positive to negative end of the cage (Figure 4-14). Due to audio attenuation resulting from the distance between the two clusters of plants at opposite ends of the cage, dB levels were measured to be 55 dB at these “negative” plants. Because the large cage was made up of four smaller cages fastened together, the large cage was naturally subdivided into four distinct areas, or subcages. This allowed me to measure sound pressure levels in the subcages as follows: (1) 80 dB, (2) 72 dB, (3) 64 dB, and (4) 55 dB.

The Sample Size application was used in the statistical software package SAS JMP 10 to calculate the necessary sample size to achieve a high power and alpha level of $\beta=0.8$ and $\alpha=0.05$, respectively. With the program calculating a minimum of six Monarchs based on parameter estimates, I doubled this number to ultimately test a total of 12 Monarch butterflies to have extra assurance that I would be able to achieve $\beta=0.8$ and the ability to test for significance at an alpha level of 0.05. For each repetition of the experiment, two Monarchs were placed in the middle of the elongated cage at 10:00am each day. Then the crowd noise soundtrack was started, giving the butterflies a choice
of direction in which to move – toward the noise or away from the noise. For 24 hours prior to placing the Monarchs in the test cage, they were deprived of food (i.e., nectar plants), thus increasing the chance that they would move towards one of the sides of the cage in order to feed upon the nectar sources provided. The crowd noise soundtrack was looped into a playlist that allowed it to continue playing for the entire eight hours that the experiment was running. To test for any affect that sustained noise may have on Monarch behavior, the soundtrack was played from 10:00am to 6:00pm. A video camera was set up 2 meters from the cage so that the entire setup could be observed, along with the movements of the two Monarchs throughout the day and watched later to quantify the specific amounts of time each Monarch spent in each of the four subcages.

Data were recorded as the amount of time that an individual Monarch spent in each of the four subcages. Data were also recorded as the total time each Monarch spent in each cage by hour, in order to test for effects of noise duration (i.e., how long it had been playing prior to each reading) on Monarch behavior (Figure 4-16). After each eight-hour day of experiments, new Monarchs were used for each of the following trials. This generated 96 hours of data on choice behavior based on sustained noise levels. The data were analyzed using a multinomial logistic regression model and Poisson distribution, which allowed me to test for several things. First was the effect that the cage’s decibel level had on the chance a butterfly would remain in an individual cage, in order to determine if butterflies were repelled by louder noises. Second, it allowed me to determine if butterfly behavior (i.e., how long a butterfly remained in a particular
subcage) was based on the number of hours that the butterfly had already been exposed to noise.

**Vogel’s Organ Study**

To determine if Monarchs possess a Vogel’s organ similar to that of some other Nymphalid butterflies (Vogel 1912, Otero 1990, Yack et al. 2000, Rydell et al. 2003, Mahony et al. 2005, Murillo-Hiller 2006, Lane et al. 2008, Lucas et al. 2009), external morphology of the Monarch was examined and compared with new and existing depictions of external morphology for related species. Morpho (*Morpho peleides*), Forest Nymph (*Idea leuconoe*), Queen (*Danaus gilippus*), Viceroy (*Limenitus archippus*) and Monarch (*Danaus plexippus*) butterflies were obtained from the Florida Museum of Natural History’s Butterfly Rainforest and McGuire Center for Lepidoptera and Biodiversity collections as either freshly deceased specimens or mounted collection specimens. A Barska 7x – 45x Trinocular Zoom Stereo Microscope was used to examine each specimen. First, scales were carefully removed from the base of the cubital and subcostal veins of the butterfly’s forewing using a #1 insect pin (to isolate the scales) and a fine paintbrush (to brush them away). Then, wings and legs were positioned to allow for optimal visibility of the thorax and wing base. With help from images in Lane et al. (2008), *Morpho peleides* was the first to be examined in order to test for the ease with which the Vogel’s organ can be located and isolated on a butterfly already proven to have such organ. Once identified, photographs of the Vogel’s organ were taken using a Canon 7D digital camera (18mp) and 2x microscope adapter mounted to the optic tube of the stereo microscope. After initial studies of the Morpho were completed, the Monarch specimen was examined using the same techniques, by following the cubital and subcostal veins of the forewing down to the mesothorax in
search of a thinned tympanal membrane surrounded by a rigid chitinous ring. Then, these procedures were replicated on Forest Nymph, Queen, and Viceroy butterflies in order to examine other butterflies at various levels of relatedness to the Monarch (i.e., subfamilies Danainae, Nymphalinae, Morphinae, Limenitidinae). The Viceroy and Queen were chosen not only because of relatedness, but also because they occupy similar habitats and are part of a mimicry ring.

**Flash Study Experiments**

**Study organism**

From June 2011 to August 2012, 150 Monarch butterflies were acquired in batches of 30 at a time from Shady Oak Butterfly Farm in Brooker, Florida. Shady Oak is one of the largest suppliers of Monarchs in the eastern U.S. and provides consistently healthy butterflies to exhibits, classrooms, and researchers at all levels. Due to their meticulous breeding techniques and ability to yield high numbers of consistently healthy butterflies, they are the chosen group to work with by most University level researchers working on Monarchs today (e.g. S. Reppert, O. Taylor, C. Merlin, N. Miller). They routinely introduce new wild stock to their populations to minimize inbreeding depression and other genetic issues that could arise and negatively affect a captive breeding operation. During peak months from March to October, they are capable of producing over 1,000 Monarch butterflies per week. A full review of Shady Oak Butterfly Farm facilities and procedures may be found in Chapter 2 of this dissertation.

Composed of an even mix of females and males, all butterflies were less than 24 hours old when acquired, having emerged the previous day. Each group of 30 Monarchs was then divided equally among six screened cages, resulting in five Monarchs per cage. Ten butterflies (two cages) from each 30-Monarch group were
used immediately for testing (Figure 4-17). In order to test for a range of Monarch ages throughout the study, 20 of each group of 30 young Monarchs were not tested immediately, but remained untested until later ages in their life. A total of three treatment periods were scheduled for the course of each group of 30 Monarchs: (1) 24-48 hours old, (2) 12-14 days old, and (3) 22-24 days old.

Although it was the original intention to test the Monarchs at the advanced age of 22-24 days old, during the trials only a small number of Monarchs survived until this age. Thus, this group was not tested.

Location

Two greenhouses were used at the University of Florida’s Department of Entomology and Nematology as test sites in which to conduct these studies. Research was conducted from June 30 to November 27, 2011 and from August 15 to September 15, 2012. Temperatures inside the greenhouses were maintained between 21° and 27° Celsius throughout the day in order to maintain stable environmental conditions. These temperatures were regulated through evaporative cooling units that also ensured stable humidity levels throughout the course of the study. Both greenhouses were outfitted with large grated metal tables on which to place the smaller screened cages, which measured 0.75 x 0.75 x 1.0 meters each (Figure 4-18). Each of these separate cages provided ample space for five Monarchs and three nectar plants in bloom (a combination of *Penta* and *Agastache* species). Plants were rotated out with fresh blooming plants periodically in order to maintain adequate nectar supply. In addition to plant nectar, a small amount of Gatorade was provided in the form of a soaked sponge on a saucer, to provide another source of sugar and nutrients.
Trials

To test for the effect of flash photography on Monarchs, individual Monarchs were subjected to camera flashes in a controlled environment. Throughout the study, Monarchs of known ages were placed one at a time into an experimental enclosure (Figure 4-19). An external flash unit (Canon ex580II Speedlite) was synched with a Canon 7D camera body to act in tandem through wireless infrared communication (Figure 4-20). In addition, a Canon BGE7 Intervalometer was used to program the camera to take a set number of photos/flashes, with programmed intervals between each flash set to 10 seconds. With each flash exposure, 500,000 lumens were delivered for a duration of 1.0 millisecond at a viewing angle of 27° (i.e., roughly two million Lux, or lumens per square meter per second). This represents the typical flash power of a shoe-mounted consumer brand camera flash set on automatic settings. For consistency, though, a manual setting of f/4.0 at 1/60 of a second was used throughout the study, in order to disallow the camera from choosing different settings automatically (which could have affected consistent flash levels). Periodic testing of the flash output using a Sekonic L-508 Zoom Master Light Meter confirmed uniformity of flash output in terms of Lux delivered. Distance from the Monarch to the flash apparatus was maintained at one meter.

After programing the camera system, the trial began and observations on the behavior of each Monarch was recorded as a specific reaction to the flash exposure. Testing occurred between 9:30am and 3:00pm EST on each day that trials were scheduled. With each firing of the flash, I noted the response of the butterfly and recorded it as being in one of six categories: 1) no response, 2) antennal twitch, 3) body twitch, 4) walk, 5) fly and land and 6) fly away (Table 4-2). Careful observation was
needed in order to properly correlate the flash with the ensuing behavior. Actions and behaviors exhibited not immediately following the flash (i.e., not within 0.5 second) were not recorded as responses, for the typical reaction time for signals in butterflies is less than 3 milliseconds (Swihart 1967). Reaction data were recorded for each flash (e.g., for 120 flashes episodes, 120 reactions were recorded).

In addition to recording the Monarchs’ immediate reactions to flash exposures, Monarch longevity was tested in order to understand the long-term effects that flash may have on these organisms. After exposing each Monarch to flash individually, it was returned to its cage and monitored for longevity by checking daily for mortality among the group of experimental subjects. Data were recorded as the number of days after eclosion until the butterfly died.

For each of the groups of Monarchs, a separate flash treatment was used, which corresponded to the total number of flashes emitted. Flash treatments were as follows: 0, 30, 60, 90, and 120, with 0 acting as the control. For the control, Monarchs were handled in an identical fashion as with the experimental trials, and photos (without flash) were taken (75 per Monarch) in order to control for camera noise. Control testing was carried out throughout the study, concomitant with experimental treatments both as a single group of 30 controls and as multiple groups of 10 controls, which replaced the 22-24 day age group. Thus, consistent comparisons could be made between experimental and control treatments, since they were subjected to the same conditions throughout the study.

**Freshly Eclosed Adults**

Flash experiments were conducted in the same manner as the experiments described previously, but specifically to test for the effects of flash on butterflies that
have just emerged from their pupal cases. In order to do this, 30 Monarchs were acquired from Shady Oak Butterfly Farm as pupae. Pupae were chosen based on age so that they would all emerge within one day of each other. This was determined by the transparency of their pupal cases, such that highly transparent cases would indicate that they were most likely to eclose the following morning (Figure 4-21). As soon as they emerged, they would be subjected randomly to either zero, 60 or 120 flash treatments. Just as with the other flash experiments, reaction data and longevity data were recorded.

Statistics

Several different statistical tools were used to analyze the data from these experiments. Analysis of Variance (ANOVA) was used to compare mean reaction frequencies and longevities between flash treatment groups for both the longevity and reaction study. In addition, ANOVA was used to test for significance between age groups in these two studies, as well. Summary statistics would prove to be valuable for identifying mean longevities, median longevities, and 95% confidence intervals for these data. When testing for significance between mean longevities between two age groups or two treatment groups (e.g., 24-48 hour vs. 12-14 day or no flash vs. flash), T-tests were used with an alpha level of 0.05, allowing 95% confidence that we will not incorrectly reject a null hypothesis. Although more elaborate statistical models were fit to the data, the greatest significance came from these highly powerful tests. Bonferoni’s test was used in the reaction studies, allowing for comparisons to be made at a level of 97.5% confidence. Using this test, specific age group and treatment combinations could be compared with one another to analyze relative frequencies of specific reactions.
Multinomial logistic regression analyses were conducted during the sustained sound study to analyze the effects of noise on cage choice. This allowed for correlation equations to be calculated for the effects on individual cages, as well as analyses on interaction effects between hour and cage choice. A likelihood ratio test (LRT) was conducted to determine if cage choice was evenly distributed between the four subcages throughout the day based on the noise gradient level.

Results

Flash Studies

Effects on Monarch longevity

The experimentation with various flash treatments and their effects on Monarch butterfly longevity yielded unexpected results. Flash exposure was predicted to have a negative impact on Monarch longevity, but this was not observed. In fact, flash appeared to increase longevity (Table 4-3). There was a marked difference between longevities of Monarchs not exposed to flash and those that were. At zero flashes (control), the average longevity was 10.76 ± 2.27 days, with the 30, 60, 90, and 120 flash treatments exhibiting mean longevities of 17.67 ± 3.71, 17.60 ± 2.46, 15.54 ± 2.78, and 16.55 ± 3.67, respectively. These values were calculated to be within 95% confidence intervals to represent the true means of the data. Statistical analyses confirm that each flash treatment group was significantly different than the control group, suggesting that flash positively affected longevity (n=60, p<0.0001). Between flash treatment groups, there was a surprising lack of significant difference in longevities. It did not appear to make a difference as to which flash treatment Monarchs were exposed to in order to exhibit the pronounced increase in longevity, as long as they were exposed with a minimum of 30 flashes (n=120, p=0.80) (Figure 4-22).
Monarch age at time of flash exposure affected Monarch longevity. When comparing the longevity of Monarchs that were subjected to flash at the 24-48 hour period versus those subjected at the 12-14 day period, mean longevities were found to be 15.20 ± 2.31 and 19.36 ± 1.65, respectively, and a significant difference was detected (n=80, p<0.03) (Table 4-4). This suggests that the point in the Monarch life at which it was subjected to the flash affects its longevity.

In order to generalize the data into broader categories (i.e., flash vs. no flash), age groups and flash treatment groups were combined, so as to make a comparison that simply measures difference in longevity between all Monarchs that were either exposed to flash or were not. Monarchs that were not exposed to camera flash yielded a mean longevity of 10.03 ± 1.14, while those exposed to flash yielded a mean longevity of 16.84 ± 1.59. Statistical analyses show that across all ages and all treatments, longevity of Monarchs treated with flash were significantly greater than those not treated with flash (n=150, p<0.0001) (Table 4-6). This demonstrates that flash exposure does indeed have an effect on longevity, but very much the opposite of the original hypothesis.

**Longevity of freshly emerged Monarchs.**

Different levels of flash treatments were found to have no significant effects on the longevities of freshly emerged Monarchs (n=30, p=0.20) (Table 4-5). Variation appeared to be higher in freshly emerged Monarchs, as can be seen by the high 95% confidence intervals in Table 4-5. This suggests that while the effect that flash has on longevity does not seem to be as pronounced as with 24-28 hour and 12-14 day old
Monarchs, there could be more variation within this population due to the more fragile nature of freshly emerged butterflies.

**Reactions to flash by Monarchs**

With each individual flash exposures on Monarch butterflies in this experiment, immediate reactions to the flash were recorded as categorical data, representing either no reaction, or one of five disturbance reactions: 1) antennal twitch, 2) body twitch, 3) walk, 4) fly and land, or 5) fly away. Analyses were conducted to measure proportional frequencies of each reaction based on age, total number of flashes, and sex.

**Reactions based on age group.** Each age group of Monarchs was subjected to flash and then monitored for immediate reactions following each flash. When analyzing the data, first, flash treatment groups were combined (30, 60, 90, and 120 flashes per Monarch). This was done in order to group flash treatments together and test solely for the effect of age at time of flash exposure had on the probability of the Monarch exhibiting a disturbance reaction. The individual reactions were transformed from a count (e.g., 42 antennal twitches out of 120 flashes) to a percentage (e.g., 0.35) for analyses (Table 4-7). Comparing 24-48 hour to 12-14 day old adults, older Monarchs were more likely to respond to flash, as exhibited by the increase in probability values for the various reactions and concomitant decreasing probability value for no reaction (n=80, p<0.001) (Table 4-8). This result was heavily dependent upon the increase in body twitch behaviors, which were significantly different between the two age groups (n=80, p<0.0001). As far as age effects for the other reactions, there were none. In fact, for antennal twitches, which were one of the more significant reactions overall, there was no significant difference in reaction frequency between the two age groups. Figure 4-23 shows relative reaction frequencies for all reactions based on age group.
Comparisons of probabilities for individual treatment groups. The most noticeable change in reaction frequencies was between the 60 and 120 treatments. Using Bonferoni’s test, 97.5% confidence intervals were compared between these two treatment groups. This allowed for direct comparisons to be made about the probability of a reaction to occur based on age and treatment, which also tests for significance. When comparing the 60 and 120 flash treatment groups for the 12-14 day old Monarchs, we are 97.5% confident that Monarchs will exhibit no reaction to the flash between 84% and 90% of the time when exposed to 60 flashes. This interval drops significantly when the flash treatment increases to 120 flashes. At this treatment level, we are 97.5% confident that Monarchs will exhibit no reaction to flash between 34% and 41% of the time. Therefore, we can state with 95% confidence that when 12-14 day old Monarchs are exposed to 120 flashes versus 60 flashes, the relative frequency of their reactions increase by slightly over 100%.

Reactions based on total number of flashes. The correlation between increased flash and increased frequencies of disturbance reactions becomes less pronounced when we analyze all five treatment groups together (the control plus four experimental variables). As depicted in Figure 4-24, the frequencies of disturbance reactions have two spikes based on treatment level. The first is at the 30 flash treatment level, and the second is at the 120 flash treatment level. The frequency of disturbance reactions for the middle two flash treatments (60 and 90 flashes) is seen to be in the between these two frequencies. It appears that the lowest and highest number of flashes elicited the greatest number of disturbance reactions on part of the Monarchs. When analyzing these data using logistic regression at all levels, there is no
evidence of correlation. However, when the 30 flash treatment level data point is removed, the data become highly correlated ($R^2=0.9624, p<0.0001$) (Figure 4-24). Removing the 30 flash data point is not justified, though, and thus removing it may be forcing a correlation that simply does not exist. When examining the distribution of individual disturbance reactions throughout each trial, there was no evidence that reaction frequency increased as the total number of flashes increased. That is, the incidences of positive reactions were not weighted or clustered towards the initial or final flashes. The probability of individual reactions was evenly distributed throughout each trial. Nevertheless, it is worthwhile to acknowledge the potential high degree of correlation possible if the 30 flash treatment were removed and treated as an outlier.

There are significant differences in frequencies of antennal twitches and body twitches between the four experimental flash treatments ($n=80, p<0.0034$ and $n=80, p<0.0001$) (Table 4-9). In the case of antennal twitches, there is a sharp dichotomy between the lower number of flashes (30 and 60, with antennal twitch frequencies at 0.0444 and 0.0292 respectively) versus the higher number of flashes (90 and 120, with antennal twitch frequencies at 0.1265 and 0.1113 respectively). When grouped and compared using a T-test, there is a significant difference in antennal twitch frequency between low (30 and 60) and high (90 and 120) flash treatments ($n=40, p=0.004$). These data suggest that an increase in the number of flashes increases the frequency of Monarchs exhibiting antennal twitch disturbance reactions. In the case of body twitches, there was not the same sharp contrast between reaction frequencies when comparing low (30 and 60) and high (90 and 120) flash treatment levels. In fact, the 30 flash treatment level, which was the lowest treatment level tested in terms of total
flashes, exhibited the highest frequency of body twitches among the Monarchs. This was significantly higher than body twitch reactions in the next two levels of 60 and 90 flashes (n=60, p=0.019). In fact, approximately one out of every three flashes resulted in a body twitch reaction when subjected to the 30 flash treatment. Figure 4-25 shows mean reaction frequencies per flash treatment, broken down by individual reactions.

Reactions were simplified by grouping all reactions into one general positive reaction category. As seen in Table 4-10, there were significant differences between the treatment categories (n=100, p<0.0001). While significant differences were found amongst the treatment levels, a general trend was not observed.

**Reactions based on sex.** The sex of the Monarch was found to have little bearing on whether the Monarch reacted to flash or not. Table 4-11 illustrates the similarity in response frequencies. Statistical analyses confirm that there are no significant differences in these values.

**General reaction to flash.** To further simplify the data, Monarch ages (24-48 hr, and 12-14 day) and flash treatments (30, 60, 90, and 120) were combined and compared against the control (0). Among all ages and all flash treatments, antennal twitches (n=150, p=0.001) and body twitches (n=150, p<0.0001), proved to be significantly more frequent reactions to flash. The other three categories of reactions (walking, flying and landing, and flying away) were not found to be significant responses. Table 4-12 provides all average probabilities. In general, reactions were observed to increase noticeably when flash treatments were implemented. Figure 4-17 illustrates the mean reaction frequencies when combining all flash treatments at all ages.
Finally, as with the previous analyses, reactions were grouped into the simple positive response category and compared against the negative response category. Ultimately, it was found that over all treatments and all replications, Monarchs exhibited a reaction to flash 32.21% of the time (Table 4-13). Figure 4-27 illustrates the overall frequency of Monarch reactions to flash photography.

**Reactions to flash by freshly emerged Monarchs.** Monarchs that were subjected to one of three treatment categories (0, 60, or 120 flashes) exhibited identical results across all levels. Out of all 30 freshly emerged Monarchs tested, none exhibited any disturbance reaction in any category of response.

**Sound Studies**

**Standard Frequency**

Each punctuated sound event was an independent test for individual reactions. Thus, a total of 2,400 individual treatments occurred throughout the course of the study to provide analyses of behaviors (antennal twitch, body twitch, walk, etc.) in reaction to elevated sound levels. This figure of 2,400 sound events was divided into four separate sound level categories – 600 for sound in the 40-55 dB range (control), 600 for sound in the 65-80 dB range, 600 for sound the 80-95 dB range, and 600 for sound in the 95-110 dB range. For all trials and at all levels of sound range, no reactions of any kind were recorded for the Monarchs tested. While not all Monarchs remained perfectly still throughout the duration of each set of trials (meaning that they did walk or fly at certain points), such reactions could not be correlated with the delivery of punctuated sound. These movements were rare and occurred randomly within the five-second silent period between individual sound events. In summary, results from this experiment yielded a total of 2,400 instances of no reaction and zero instances of disturbance by Monarch
butterflies when subjected to simulated crowd noise at various levels of sound pressure in the 200 Hz – 9,000 Hz frequency range.

**Low Frequency**

Just as with the standard frequency study, data were to be represented by individual reactions by Monarch butterflies subjected to the various sound treatments. Also like the standard frequency study, not one treatment or replication yielded any correlated reaction on part of the Monarch butterflies. At three age ranges (24, 48, and 72 hours old) Monarchs were subjected to three low-frequency sounds at two sound levels, creating six distinct treatments and yielding a total of 360 potential data points. All treatments elicited the same “no reaction” response on part of the Monarch, once again questioning the real impact of sound exposure on the Monarch butterfly.

**Vogel’s Organ in Monarchs**

With punctuated sound seeming to have no effect on the Monarch butterfly, determining if the Vogel’s organ is present becomes even more interesting and more important to determine what effects sound truly have on Monarch butterflies. Examining the Morpho butterfly reinforced what Lane et al. (2008) reported, in that *Morpho peleides* exhibits a prominent Vogel’s organ. With the characteristic thinned tympanal membrane at the center of a sclerotized ring, the Vogel’s organ on *Morpho peleides* is unmistakable and is found exactly where it was expected to occur: at the base of the subcostal and cubital veins of the forewing (Figure 4-28). However, the same could not be said for the Monarch butterfly, nor for the Queen or Viceroy butterflies. After extensive examination, including more scale removal and more contortions of the wings and thorax than when examining the Morpho, the same tympanal membrane and rigid chitinous ring was absent for these three species (Figure 4-29, Figure 4-30, Figure 4-
While the thorax of these three related butterflies is indeed composed of chitinous exoskeleton, thoracic plates, and numerous musculature connections, there was no structure that compared at all to the Vogel’s organ found on the Morpho butterfly. Nor did anything similar occur that could have represented an adaptation to the traditional Vogel’s organ form. No prominent tympanal membrane, to which the chorodontal organs could connect, nor any sclerotized rigid ring encircling a sac-like membrane was found. A more detailed explanation of the structure and morphology for each butterfly may be found in Figures 4-29, 4-30, and 4-31.

Although the thorax of the Monarch is not drastically smaller than that of the Morpho butterfly (Figure 4-32), an additional butterfly was examined for the presence/absence of a Vogel’s organ that is closely related to Danaus, and is closer in body size to Morpho peleides (Ackery and Vane-Wright 1984, Brower 2010). After examining Idea leuconoe, the Forest Nymph butterfly, it also lacked a tympanal membrane surrounded by a chitinous ring characteristic of the Vogel’s organ (Figure 4-33). In these four cases where no prominent Vogel’s organ structures were found, it seems likely that the known sound-perceiving organ for butterflies in the family Nymphalidae, the Vogel’s organ, is either greatly reduced or completely absent in these cases.

**Sustained Sound**

A likelihood ratio test (LRT) determined that there was indeed a significant difference in the amount of time Monarch butterflies spent in each of the four subcages throughout the entire experiment (df=3, p<0.0001) (Table 4-14). The LRT test also showed that there was a significant interaction between cage and hour, meaning that cage choice was determined by the number of hours that the sound had been playing,
proving that Monarchs spent different amounts of time in some cages over time (df=3, p<0.0001) (Figure 4-34).

Mean minutes spent in each cage per day were plotted and analyzed for any significant correlation. Although a trend line was fitted to the data showed a slope of 21.86 (y = 21.86x + 65.35), meaning that from cage one to cage four, Monarchs spent approximately 21.86 minutes more in each cage, the R² value is low at R²=0.37705. This suggests that the correlation is not strong enough to accurately predict future outcomes of cage preference. This is likely caused by the sharp drop in mean total minutes per day in cage three (Figure 4-35).

A multinomial logistic regression model was then fit to a poisson distribution, which showed that Monarchs spent significantly less time in cage 1 with each passing hour (df=3, p<0.0001) (Figure 4-36). This is the most pertinent result of these trials, as it shows that Monarchs spent the least amount of time in the loudest subcage. What’s more is that this result became more pronounced over time, suggesting that Monarchs became less tolerant to being in areas with louder noises as the noise persisted over the course of the day. Conversely, Monarchs spent significantly more time in cage three with each passing hour (df=3, p<0.0001) (Figure 4-37). Figure 4-38 shows the mean number of minutes per hour spent in cage one versus cage three. The amount of time spent in cages 2 and 4 was not dependent on the number of hours the noise had been playing (Figure 4-39, Figure 4-40). Figure 4-34 shows the relationship between all cages and all hours.
Discussion

Punctuated Sound Studies

Standard Frequency

Results from this study show that Monarchs exhibit no reaction to crowd noise stimuli at various sound pressure levels. This is somewhat perplexing, as there exists a significant literature base showing that many families of Lepidoptera are able to perceive sound, with examples found in many of the major families (Swihart 1967, Lane et al. 2008). In these various families of Lepidoptera, there are documented examples of distinct reactions to sound, ranging from attraction to avoidance (Hoy and Robert 1996, Yack et al. 2000, Rydell et al. 2003). Classic examples are from *Hamadryas* butterflies, believed to both produce and detect sounds that are used in mate locating, as well as territoriality (Swihart 1967, Otero 1990, Yack et al. 2000, Fullard et al. 2003). New studies are showing that mute butterflies (i.e., those not producing sound) are also able to perceive sound, as exemplified by *Morpho peleides* (Lane et al. 2008, Lucas et al. 2009). Nevertheless, the vast majority of sound-perceiving Lepidoptera are found within the moths, which have evolved the ability to hear as a way to perceive ultrasonic echolocation calls from predatory bats (Fenton and Fullard 1981, Archarya 1998, Fullard 1998).

To date, morphological studies designed to identify and analyze possible tympanal structures on butterflies have targeted only individual species, and Monarchs had yet to become a subject of such tests. With the results of these studies, along with the apparent lack of pronounced Vogel's organ, it becomes highly unlikely that Monarchs rely upon a tympanal ear to perceive sounds in the treatments' frequency ranges. The ability of a Monarch to perceive sound is not necessarily reliant on a tympanal ear,
though, as a number of other studies suggest sound waves may be perceived via other apparatuses in insects. Studies show that the tympanal ear is adapted primarily to monitor ultrasonic frequencies rather than the lower frequencies typical of most human voices (Hoy and Robert 1996, Yack and Fullard 1999, Rydell et al. 2003). The ability to perceive ultrasonic sound suits moths and nocturnal insects quite well, having the need to detect high frequency sounds emitted by echolocating bats. But, for diurnal insects the need to perceive this upper range of frequencies is relatively unjustified. It is more likely that diurnal butterflies would prioritize sound perception in lower frequencies, for these lower frequencies are where most of their predators’ sounds fall, such as calls from birds and frogs. It has been shown that lower frequency sounds may, in fact, be perceived more effectively by simple hairs, or sensilla, on the body of insects, which the Monarchs do indeed exhibit. With many insects, butterflies included, substrate level vibration is an equally important sound-perceiving mechanism (Swihart 1967, Markl and Tautz 1975). Nevertheless, it is important to note that one of the more recent studies on butterfly hearing found that the Vogel’s organ of *Morpho peleides* was optimized for frequencies between 2,000 and 4,000 Hz, which falls right in the middle of the frequencies used in the experiments conducted in this Chapter (Lane et al. 2008, Lucas et al. 2009). Furthermore, another butterfly observed to have a Vogel’s organ, *Mantaria maculata*, has adapted to predation risks by employing a Vogel’s organ optimized for sound perception at higher frequencies (>18 kHz). Being a crepuscular species, it faces threats from a greater range of predators (i.e., bats and birds) and thus has been able to benefit from an expanded frequency perception range (Rydell et al. 2003).
Low Frequency

Monarch larvae have been seen to react strongly to low frequency sounds (Rothschild 1997). However, this does not appear to transcend to the adult stage, according to the results of this experiment. In fact, no reaction at all was observed when Monarchs were subjected to various low frequency levels. Higher frequency sounds are known to elicit reactions from adults of numerous moth species, as well as at least three species of butterflies (*Morpho peleides*, *Manataria maculata*, *Hamadryas feronia*) (Swihart 1967, Yack et al. 2000, Rydell et al. 2003, Lane et al. 2008). In the case of moths, there is significant evidence that they benefit greatly by being able to perceive ultrasonic noise from bat echolocation calls (Fenton and Fullard 1981, Archarya 1998, Fullard 1998). By evading predation, there is a significant selective advantage to this ability. Butterflies, though, are much less often the target of bat predation and thus, of those that do indeed "hear", have optimized sound perception in the lower frequencies where ranges of most bird calls are found. Nevertheless, as seen by the crepuscular butterfly *Manataria maculata*, there may still be advantages to perceiving higher frequencies, especially when opened up to bat predation for even a small window of the day (Rydell et al. 2003).

For those butterflies that are strictly diurnal and do not incur significant levels of predation from bats, "ears" of these Lepidopterans are optimized for the lower frequencies (<18kHz). However, there remains a paucity of studies that have sought to record reaction data at extremely low frequencies (<200Hz). The results of this study show that Monarchs do not react to noises in the low-level frequency range of 100Hz to 200Hz. This is perplexing, as previous studies have suggested that subgenual organs, located at intersegmental joins in nearly all pterygote insects, are indeed able to
perceive low frequency sounds through substrate vibrations (Debaisieux 1938, Menzel and Tautz 1994, Devetak 1998, Vilhelmsen et al. 2001). In these experiments, low frequency sounds were produced at both low and high decibel levels (58dB and 85dB, respectively). Vibrations were no doubt felt by the butterflies, as I myself could feel vibrations sitting several feet away from the experimental setup. This brings up a more cosmic question. If the Monarchs are indeed sensing certain noises and frequencies, even if nothing more than a slight vibration in their legs where the subgenual organs are located, why is it that they are not reacting to such sounds? The answer likely has to do with the frugality of expending excess energy in concert with their highly developed chemical defenses.

Reactions by the Monarchs would indicate that they feel threatened. Perhaps because they are chemically defended, their threshold for defensive action is relatively high. That is, no matter how odd or irregular a vibrating substrate may feel for the Monarch, it is employing an economy of resources by not expending energy when the threat is perceived as below a certain threshold. Although Monarchs do face predation from certain species of reptiles and birds, there exists the possibility that the noises such animals make (i.e., bird calls, chirps from lizards, etc.) are not naturally in these lower (<200Hz) frequency ranges. In addition, approach from these smaller animals (i.e., stalking or hunting) likely does not result in substrate level vibrations, as would a large mammal stomping through a forest. Simply put, there is no reason for there to be an evolutionary precedent for Monarchs needing to react defensively to substrate-level vibrations created from low frequency noises.
This is a positive result for the overwintering Monarchs from a conservation standpoint. Low frequency noises are made from humans and the horses which are common in the Monarch reserves throughout the winter. Nearby machinery can also fall into these low frequency ranges. Sounds of construction equipment when ejidos builds new stalls at the entrance of the reserves, or even from illegal logging operations that create noise from chainsaws may be less disturbing to Monarchs than initially thought.

The lack of reaction on part of the Monarch butterflies to the standard and low frequency sound stimuli demonstrates that crowd noise, common in the Monarch overwintering reserves, does not yield disturbance behavior, as was originally hypothesized. Whether noise is actually perceived to some degree remains unknown, but is less likely with the results of these punctuated sound experiments. The apparent lack of a pronounced Vogel’s organ further suggests that any sound perception that does occur in Monarchs is limited.

**Vogel’s Organ**

The ability to perceive sound has arisen a number of times in the Lepidoptera. Most research to date has been done on the sound organs of moths, for they evolved no fewer than six different times within the major moth superfamilies (Fullard 1998, Minet and Surlykke 2003). Furthermore, the incredible behavioral adaptations of moths to use sounds in communication and predator avoidance make them popular research subjects (Spangler 1988, Acharya 1998, Fullard 1998, Alvarez et al. 2011).

Hearing in butterflies has been a research topic for nearly two centuries, with Darwin positing some of the first questions on *Hamadryas* noise production and perception, and Vogel (1912) being the first to identify sound-perceiving organs in
butterflies (Barlow 1933). However, the overall scope has been limited compared to the acoustic research done on moths. Recent advances, though, have made great strides in not only the morphology and identification of sound-perceiving organs in species of butterflies, but also the physiology of the system, by identifying peak frequencies and sound pressure levels at which butterflies are able to effectively hear. Thus far, research on butterfly hearing has focused predominantly on *Hamadryas feronia*, perhaps because of its well developed Vogel’s organ and ability to produce sounds (Swihart 1967, Otero 1990, Yack et al. 2000). Current research by Lane et al. (2008) and Lucas et al. (2009) has highlighted another neotropical butterfly and its ability to perceive sound, *Morpho peleides*. The research conducted in this dissertation is the first to look at the Monarch butterfly (*Danaus plexippus*) for whether it too exhibits the tympanal membrane known to occur in other Nymphalid butterflies termed the Vogel’s organ.

Results are always less exciting when they come back negative, as was the case when examining the Monarch butterfly for the presence of a Vogel’s organ. In contrast to my hypothesis, there is no morphological evidence that the Vogel’s organ exists on the Monarch butterfly. This is also the case for the Viceroy, Queen, and Forest Nymph butterflies. Lepidoptera are known to exhibit a range of hearing organs, as has been previously described in this Chapter, but among those butterflies belonging to the family Nymphalidae, they are known to exhibit this characteristic chitinous ring surrounding a tympanal membrane, otherwise known as Vogel’s organ (Vogel 1912, Swihart 1967, Otero 1990, Fullard 1998, Yack et al. 2000, Rydell et al. 2003, Murillo-Hiller 2006, Lane et al. 2008, Lucas et al. 2009). However, judging by the obvious size, shape, color, and
structure of the Vogel’s organ for the Morpho butterfly, as was reported in Lane et al. (2008) and Lucas et al. (2009), and confirmed in these studies, one would expect that the Vogel’s organ for another mute butterfly belonging to the Nymphalidae family to be relatively homologous, should it occur in the first place.

This certainly has a bearing on the degree to which Monarchs can perceive sounds and is revealing as to why they elicted no reaction to the loud punctuated sounds used in other experiments of this dissertation. At this point, one must ask why some butterflies in the family Nymphalidae do possess a Vogel’s organ capable of sound perception while others do not? Unfortunately, there are no accounts in the literature of negative findings with regards to searching for a Vogel’s organ, so we must compare those that have been reported to positively have one versus the Monarch butterfly. The answer is relatively simple upon comparing the species studied thus far. The most obvious difference, and the one that this author believes is the primary driving force behind whether or not sound perception is prioritized in butterflies, is the type of defenses employed by the butterfly. In the case of *Morpho peleides*, *Pararge aegeria*, *Ypthimoides castrensis*, and *Hamadryas feronia*, they rely on crypsis and startle reflexes (e.g., the blue flash in the case of the Morpho, the wing-click in the case of the *Hamadryas*) to avoid predation. Therefore, they depend on avoiding predation by remaining undetectable by their predators, which in most cases are birds. Because crypsis works best when the organism remains still and motionless, there is a cost to being constantly undetectable. Remaining in one place limits mating, feeding, and egg laying opportunities. Because prey will generally employ a sense of economy when facing the choice of avoiding predation versus mating and/or feeding, it is best to remain
still and motionless (thereby maximizing their cryptic appearance) only when necessary. There is a massive evolutionary advantage for a butterfly that is able to perceive sounds made by their predators, for such sounds signal imminent danger and likely trigger the butterfly to engage in “maximizing cryptic behavior”, which is little more than remaining motionless. Nevertheless, the butterfly that is able to spend as much time as possible mating, feeding, and egg-laying until sensing an audible predation threat (and consequently avoiding predation by perching cryptically somewhere) has a significant evolutionary advantage.

The question now becomes, why wouldn’t the Monarch, Queen, Viceroy, and Forest Nymph benefit from being able to do the same? The answer likely lies in the fact that they employ an entirely different form of defense. Rather than being defended against predation only when motionless, these butterflies are defended through chemical means (Brower 1968, 1988, Ritland 1991, 1995). Feeding on plants with toxic chemical defenses as larvae, they sequester toxic chemicals that build up in their bodies and render them largely unpalatable by vertebrate predators (i.e., birds) (Brower 1968). This not only means that these butterflies do not need to limit their feeding, mating, or egg-laying in the presence of traditional predators of Lepidoptera, but it also means that they have no need to change their behavior when potential predators are nearby. Thus, for the sake of avoiding predation, there is no evolutionary advantage to being able to perceive predator sounds for those butterflies that are chemically defended and unpalatable. For an individual butterfly, there is no doubt that the evolution of a hearing organ is a complex and timely process. In order for something like a Vogel’s organ to provide sufficient benefit for a butterfly, it must be consistently
beneficial and contribute to survivability throughout thousands of generations. Although as humans we can clearly see the benefit of being able to communicate using acoustics, the same may simply not be true for Monarchs and the other butterflies tested alongside them. In fact, Monarchs have been shown to communicate very effectively through chemical communication, lessening the need to evolve acoustic perception (Boppre 1978, 1993, Malcolm and Zalucki 1993).

As discussed elsewhere in this Chapter, sound perception is not isolated to tympanal membranes and the Vogel’s organ in butterflies. Substrate-level vibrations have been shown to play a part in acoustic perception by butterflies (Swihart 1967, Markl and Tautz 1975, Yack et al. 2001). However, the ability to sense sound via vibrations is no doubt limiting to the range of frequencies and sound pressure levels able to be detected. While it is difficult to say that Monarchs are incapable of perceiving sound in general, the experiments conducted in this Chapter reveal that their ability is likely very limited. This is not to say that they are at an evolutionary disadvantage, however.

**A final consideration**

One final consideration should be made. Perhaps the lack of reaction by Monarchs to sound is not entirely benign. Although Monarchs did not physically appear disturbed during this sound study (i.e., exhibiting an increased propensity to move or relocate in reaction to sound), perhaps noise is actually the cause for remaining motionless on part of the Monarchs. Although unlikely, an early observation by Cecil (1877) noted that Sphinx moths (Sphinx ligustri and Metopsilus elepenor) arrested all movement the moment an adult human began talking within close range of these organisms. After being subjected to the stimulus of low frequency human voice, the
moths would then remain this way for some time. While this potentially opens the door for a lengthy and complicated discussion, Cecil (1877) raises an interesting question. What if “no reaction” is actually a reaction? Perhaps sound causes Monarchs to remain motionless, when otherwise they would be more mobile. Hypothetically, this could be a strong disturbance to the Monarchs in their overwintering colonies, as Monarchs need to leave their roosts periodically to drink water, to cool down by soaring, and to relocate to shadier areas of the mountain when temperatures rise (Calvert and Brower 1986, Brower 1995). Should human noise be confining them to their roosts, it could be harmful to the Monarchs, even though no empirical reaction can be observed. Although the sound experiments in this Chapter were not designed to test for these issues, no observations were made suggesting an inclination for a mobile Monarch to arrest all activity when subjected to sound events throughout the course of this study. In addition, out of 26 separate visits to overwintering colony sites by this researcher over eight years, never once did it appear that excessive noise prompted an arresting behavior on part of the Monarch butterflies.

**Sustained Sound Studies**

Results indicate that there was an effect that sustained noise has on subcage preference by the Monarch butterfly over the course of the day. Relating back to the original objective, which was to determine if noise functioned to repel Monarchs from otherwise suitable areas, there are several key points garnered from these experiments.

First, Monarchs do spend significantly different proportions of their day in areas with varying sound pressure levels (i.e. noise volumes). That is, they do not spend a uniform amount of time between areas of differing noise levels. Second, both noise levels and how long the noises have been playing for determine the areas in which
Monarchs spend most of their day. Third, Monarchs spend significantly less time over the course of the day in areas where noise is the loudest.

**Noise as a source of disturbance**

Noise generated from ecotourism has been shown to occur in a range of forms, from aircraft sounds, to passing hikers, to camera clicks (Stockwell et al. 1991, Frid 2001b, Papouchis et al. 2001, Huang et al. 2011). In most cases, noises resulting from these activities have been determined to disturb wildlife to one degree or another (Lott and McCoy 1995, Steidl and Anthony 1996, Burger and Gochfeld 1998, Burger 1998, Born et al. 1999, Delaney et al. 1999, Ward et al. 1999, Frid 2001, Lafferty 2001, Papouchis et al. 2001, Frid and Dill 2002). Because of the metabolic costs to the animal by avoiding prime foraging habitat, arresting mating behavior, or using excessive energy by fleeing areas with high noise levels, disturbance can be relatively harmful to wildlife (Ydenberg and Dill 1986, van Dyke et al. 1986).

In the present experiments, it was determined that Monarch butterflies avoided loud crowd noise in favor of other quieter areas, despite the presence of suitable food sources in the louder area. This represents one of the few studies to look at noise disturbance with invertebrates (and the first with Lepidoptera), but results are similar to studies conducted on well-known vertebrates. For example, Reijnen et al. (1995) have found that 60% of birds in Dutch grasslands occur in significantly lower densities near highways, where the sustained drone of motors persists throughout the day. Burger and Gochfeld (1998) found that noise affects the amount of time birds spend foraging, as well as the number of individual feeding events while searching for food. Klein (1993) found that as the level of human activity increases around waterbirds in Florida, the level of disturbance reactions exhibited by waterbirds increases. However, there
are other vertebrate groups that seem to be less affected by noise, such as frogs and
toads (Sun and Narins 2005, Lengagne 2008). In those two cases, their distributions,
diversity, and likelihood of displaying escape behavior in response to noise show little
connection to sound disturbance.

**Noise interference with the migration event**

Naturally, if Monarchs are known to avoid areas with the loudest noises, one
would expect the stationary clusters of overwintering Monarchs in Mexico to be under
threat. With upwards of 250,000 visitors a year to these overwintering areas, the
amount of human noise that overwintering Monarchs are exposed to is significant
(Barkin 2003). Although silence is encouraged for crowds of ecotourists within the
actual colony areas, from personal observation this is rarely enforced by park guards
and is left up to peer enforcement by fellow ecotourists. Monarchs must employ a
sense of economy when moving around during their overwintering period, for there are
insufficient food resources in the high mountains of southern Mexico to sustain the
entire population, should they all need to feed (Brower 1995). Instead, Monarchs
depend on the food that they consume prior to arrival to supply them with the necessary
amount of energy for the entire 135-day overwintering period (Alonso-Mejia 1997,
Masters et al. 1998). Thus, they may be less likely to avoid noises by fleeing or
relocating, for this would require daily movement away from visitor trails, as trails are cut
by park guards on an as-needed basis to provide colony access to ecotourists.
Conversely, if Monarchs are indeed moving in reaction to sound, it could prove costly to
their stores of energy and fats that they need for the remainder of the winter and
following spring.
Sustained noise as an additional threat

Punctuated noise did not elicit disturbance reactions, as was seen in the previous studies in this Chapter. This suggests that it is the sustained nature of the noise used in this study that made the difference. From hour one to hour eight, there was a significant correlation between the amount of time spent in each of the four subcages and the amount of time that the Monarch had been subjected to noise. This suggests that noise has an effect on butterfly behavior over time. This is particularly important when determining the effects of ecotourism noise on overwintering Monarchs. Although punctuated noise occurs by way of individuals yelling across the crowds, cheering, or children crying, the sustained hum of crowd noise is ever-present throughout the day.

The results of this study suggest that the duration of crowd noise may be more important than the frequency or volume. Other studies examining the effects of sustained noise on wildlife (mainly in response to vehicular traffic, boat traffic or air traffic) have found similar results. Including mammals like Dall’s Sheep and Humpback Dolphins, birds like Mexican Spotted Owls, and amphibians like European Tree Frogs, sustained noise from highways, airstrips, and flight routes cause a variety of disturbances. These can range from disrupting calling behavior to restricting habitat range (Stockwell et al. 1991, Delaney et al. 1999, Frid 2001a, Frid 2001b, Parijs and Corkerson 2001, Lengagne 2008). Cox et al. (2006) showed that sustained underwater sonar noise (from military communications programs) can actually be fatal for over 21 species of Beaked Whales (family Ziphiidae) because of what is known as gas-bubble disease. While the Monarch butterfly may not be that severely affected for now, there are valid conservation concerns derived as a result of these experiments.
Conservation implications

The implications of these results could be far-reaching. While the primary objective of this research was to study Monarch behavior in order to make inferences on the overwintering Monarch population, these results suggest that non-migratory summer populations of Monarchs could also be affected by sustained noise. Anthropogenic noise occurs all across North America, from farm machinery in rural areas to highway traffic and city noises in urban areas. There are few places in the world that are completely void of sustained noise at some point or another. Although the noise used in this study was termed “crowd noise”, it represented an even and consistent output of a wide range of frequencies in the 200 Hz – 9,000 Hz range, suggesting that general noises like vehicle traffic, machinery, and even loud music may produce similar results for Monarchs and perhaps other butterfly species, too.

There is no shortage of speculation that can arise from a study like this. This is especially true when dealing with the sensitivity of local ecotourism economics and the fight for the conservation of a widely-recognized cosmopolitan species of butterfly. It is easy but risky to come quickly to conclusions that just because Monarchs preferred subcages away from the loudest area in this study, overwintering Monarchs are likely to flee their ancestral overwintering grounds when loud ecotourists are present. This ignores the fact that a number of animals have proven to be very adaptable when dealing with sustained noise. For instance, species of whales, birds, and frogs have demonstrated great plasticity in response to sustained noise exposure by adapting their calling frequency, duration, and location to overcome noise interference (Lopez et al. 1988, Bee 2000, Miller et al. 2000, Rabin et al. 2003, Slabbekoorn and Peet 2003, Penna and Hamilton-West 2007). The Monarch butterfly undergoes a suite of
behavioral adaptations to help it better survive while overwintering. So acclimating to yet another environmental pressure, in this case noise, does not seem unlikely for an organism already known for its tremendous environmental plasticity (Masters et al. 1988, Brower 1995, Goehring and Oberhauser 2002).

**Management solutions**

The overwintering colonies of millions of butterflies are at the heart of these studies, for there is reason to believe that ecotourism, which is touted as a solution to a number of environmental issues, could have negative impacts on the butterflies it is designed to protect. To mitigate the potential disturbance that noise has on the Monarch colonies, pressure should be put on local ejidos, which are the communities in direct charge of protecting the Monarchs and their forested habitat. With the spread of education and awareness about the potential side effects of ecotourism noise, proper enforcement of quiet areas (i.e., those areas closest to the colony) should be in the hands of the park guards. With over 70 guards in the El Rosario colony alone, there is no question that the appropriate level of supervision exists. It is just a matter of taking the necessary actions to limit the steady hum of crowd noise that occurs when hundreds or thousands of people gather in one area.

Although this study does not suggest any cause for serious alarm, it does serve as an initial study on the effects of sustained crowd noise on the Monarch butterfly. In order to support a campaign to minimize noise in prominent and well-visited ecotourism areas, further research is warranted. Future experiments should focus on the transitional movement between areas of different sound levels to support these data. With more information on their movement, we can make further inferences on Monarch behavior to sustained sound and the possible consequences.
Flash Studies

Photographic flash has been proven to affect animals in a wide range of taxa, both terrestrial and marine (Witherington 1992, Jacobson and Lopez 1994, Quiros 2007, Heaslip and Hooker 2008, Huang et al. 2011) (Table 4-1). Previous studies have shown that some wildlife is physically disturbed by flash and exhibit disturbance reactions atypical of normal behavior. From Fur Seals changing their diving patterns, to Sea Turtles being deterred from nesting on beaches, a camera’s flash influences animal behavior to the point that it may be detrimental to their overall fitness.

We have seen from prior research that physical encroachment by humans can jeopardize the fitness of wildlife. When animals are disturbed and instigated to expend excess energy, abandon offspring, or refrain from feeding, they and their progeny are negatively affected (Nette et al 1984, Tremblay and Ellison 1979, Anderson 1988, Piatt et al 1990, Cote and Beaudoin 1997, Klein 1993, Lott and McCoy 1995). Flash photography may be another form of encroachment by humans, and we are only beginning to understand its effects on wildlife. The results reported in this Chapter are the first to examine the effects of flash on invertebrates and demonstrate intriguing consequences.

Effects of flash on longevity

The effect of flash photography on Monarch butterfly longevity failed to support the original hypothesis, which postulated that Monarch longevity would decrease when exposed to flash, and even more so as the total number of flash exposures increased for each butterfly. Surprisingly, the opposite was observed during the study. Monarch longevity actually increased significantly when subjected to flash.
Monarch longevity is affected by several key factors. While in nature, mortality is attributed to common biological cycles of predation, disease, parasitism, and rate of resource acquisition (Brower 1988, Oberhauser et al. 2007). However, when in captivity, physiological factors predominate, as natural pressures such as predation and the need to find food and water are removed as obstacles to survival. The physiological factors that govern longevity in captivity mostly have to do with metabolism, disease immunity, and somatic maintenance (Herman and Tatar 2001, Zhu et al. 2009). With insects, regulation of a thriving internal physiology is largely governed by heritable genetics and a flexible endocrine system. While the genetic code of species often changes over evolutionary time, in order to adapt to changing environmental conditions and interspecific and intraspecific interactions, genes and the total genetic coding system are less likely to change within a single lifespan. Instead, the flexibility of the insect endocrine system is responsible for the short-term adaptations that allow for flexibility and change on a near-constant basis (Brakefield 1997, Beldade et al. 2002, Zera and Harshman 2002, Brakefield et al. 2003, Zijlstra et al. 2004). Ranging from color patterns on butterflies to locust migrations, the endocrine system is as complex as it is vital to a considerable number of life processes in insects (Pener 1991, Koch et al. 1996). Within the complex endocrine system of Monarch butterflies, one particular hormone has a great deal to do with variance in longevity. This hormone is known as Juvenile Hormone (Herman and Tatar 2001, Zhu et al. 2009).

**The role of Juvenile Hormone on Monarch longevity.** Synthesis and release of Juvenile Hormone (JH) within the Monarch butterfly has different purposes between larval and adult stages (Nijhout 1994). While the presence of JH in a larval Monarch
functions to delay maturation, effectively prolonging the immature stage until ready for pupation, it has been seen to have a much different effect in adults. The presence of JH in adults facilitates oogenesis and vitellogenesis, key processes in the reproductive cycle of Monarch butterflies. However, an absence of JH in the adult stage not only induces reproductive diapause, but also enables migration by increasing the lifespan of the butterfly (Rankin et al. 1986, Dingle 1996, Herman and Tatar 2009). In fact, migratory Monarchs, typified by lifespans that are four to six times longer than those of non-migratory Monarchs, exhibit greatly reduced longevity when artificially treated with JH in laboratory conditions. Herman and Tatar (2009) proved that shorter lifespans can actually be induced through JH treatment. Similarly, by surgically removing the corpora allatum (the source of JH) in non-migratory Monarchs, longevity can be increased by 100% (Herman and Tatar 2009). In summary, the presence/absence of JH has been shown to be perhaps the most important cause for significant changes in Monarch butterfly longevity when other factors, such as parasitism and nutrient acquisition, are controlled.

Monarchs in this experiment exhibited on average a 70% increase in longevity when exposed to flash compared to the control group that were not exposed to flash. Environmental and biological factors, such as temperature, humidity, predators, and parasites, can easily cause such a large difference in longevity in natural conditions (Brower 1988, Masters et al. 1988, Oberhauser 2007). However, this experiment was conducted in a controlled greenhouse setting, suggesting that other physiological factors, such as variations in JH levels, may be the cause for the differences in mean
longevities between flash treatments. If this is the case, and JH is responsible, we must ask how variations in flash exposure could affect JH levels in a Monarch butterfly?

The perception of light has been shown to play a significant role in the life history of the Monarch butterfly (Barker and Herman 1976, Goehring and Oberhauser 2004). From providing cues to begin their migration, to affecting ovarian and testicular development, to assisting in navigation, the use of light by Monarchs is paramount when it comes to the maintenance of critical processes (Goehring and Oberhauser 2002, Reppert et al. 2010). With all other factors controlled in these experiments, the only difference between the experimental and the control groups was the use of flash. It is possible that the flashes acted in one of two ways. First, the amount of light over the course of each treatment could have functioned as a light stimulant, stimulating the Monarchs in the same way that natural light does. Second, the intensity of the photographic flash could have damaged or saturated the light-sensing receptors in the Monarch eyes and antennae, rendering them less able to accurately perceive light after the flash treatments. These two possibilities will be examined in the following sections.

**Flash as a natural stimulant.** Insects have been shown to change behaviorally and physiologically with varying light schedules. Studies on the wasp *Polistes metricus* reveal that longer photoperiods induce maturation of ovaries in female *Polistes* to the same degree as artificial treatment with Juvenile Hormone (Bohm 1972). Saunders and Gilbert (1990) found in *Drosophila melanogaster* that shortened photoperiods trigger reproductive diapause. Governed by significantly lower JH levels, ovaries become reduced and vitellogenin production significantly decreases, as the photoperiod is shortened (Saunders and Gilbert 1990). Monarchs are subject to similar
physiological changes. As photoperiods are lengthened, ovarian development and oogenesis increase. When photoperiods are shortened, Monarchs instead revert to a state of reproductive diapause, characterized by reduced ovaries and a cessation of vitellogenin production (Barker and Herman 1976, Herman and Tatar 2009). These things occur because reduced light levels trigger lowered JH production in Monarchs (Dingle 1996, Herman and Tatar 2009, Zhu et al. 2009). The importance of these examples lies in the fact that entering reproductive diapause has been shown to significantly increase Monarch longevity (Herman and Tatar 2009). By allocating fewer resources to the maintenance of the entire reproductive system, including the development of eggs and sperm, Monarchs age slower, thus increasing longevity. During reproductive diapause, resources are diverted away from normal reproductive maintenance and reallocated to somatic maintenance. By concentrating on cell growth, repair, and replication, the organism ages at a slower rate, and experiences increasing longevity (Tatar and Yin 2001).

In relation to this experiment, flash exposures could have an effect on the endocrine system, specifically with regard to the release of JH. A longer lifespan, as exhibited by Monarchs treated with flash, would suggest that an increase in light exposure reduces the amount of JH produced, thus instigating reproductive diapause and slowing the aging process. However, this would go against the fact that in nature, JH is reduced in response to decreasing photoperiods (i.e., less light), as days get shorter towards winter. This is the opposite of what happened in the experiment, where JH would have had to be reduced in response to increasing light levels. It is unclear how an increase in light perception, by way of flash exposure, would elicit a decrease in...
JH production. Nevertheless, because of the general relationship between light perception and the production of JH in Monarchs, there is still reason to believe that JH is involved.

**Flash as a disrupter of photoreception by Monarchs.** An alternative theory is that the light produced from flashes was so strong that it caused the Monarchs’ light perceiving organs to be damaged. This could result in the butterfly being less able to perceive light accurately after the flash treatments. It is widely known that exposure to high intensity light causes damage to the eyes of vertebrates and invertebrates (Noell et al. 1966, Anderson et al. 1972, Meyer-Rochow 1993). In the case of the Monarch butterfly, both the eyes and antennae play a critical role in light perception (Merlin et al. 2009, Guerra et al. 2012). While little is known about possible damaging effects of light on the Monarch butterfly, studies have shown that light plays a significant role in the premature degradation of visual organs in other invertebrates, including other Lepidoptera (Meyer-Rochow 1993, 2002). In the cases of *Papilio xuthus* and *Pieris napi*, retinula cells become damaged by excessive light treatments and in various species of crickets, their rhabdomeres were shown to be highly vulnerable to light (Meyer-Rochow 2002). Although it is presently unknown as to which visual component may be the most vulnerable in the case of the Monarch butterfly, past studies suggest that within insects, several possibilities exist.

Should flash exposure critically damage Monarch vision or the ability to perceive light, it is reasonable to believe that the butterfly would inaccurately perceive light for some amount of time after the treatment, or perhaps even permanently, as has been seen with various moth species (Bernhard and Ottson 1960a, 1960b, Agee 1972, 1973,
Eguchi and Horikoshi 1984). If this is true, then the Monarch’s perception of daily photoperiods could be affected by flash exposure, most likely resulting in less light perceived each day. This could initiate reproductive diapause. With this induction of reproductive diapause could come an increase in longevity, possibly explaining the 70% increase in longevity between those Monarchs not treated with flash and those that were.

This theory makes several assumptions that should be identified. For example, any pronounced damage to the Monarch’s sense of vision would also likely affect the butterfly’s ability to find food and water. While a decrease in JH levels may increase longevity, an impeded ability to find adequate nutrients may do just the opposite. This theory also assumes that reproductive diapause can be initiated and affect longevity within only a matter of weeks. Studies on Monarchs to test the response of reproductive diapause to changing environmental conditions have measured only reaction based on gradual changes in natural light cycles (Herman 1981). Because no studies have examined the initiation of diapause due to artificial conditions with somewhat rapid onset (especially with regards to punctuated light flashes), it is difficult to say whether or not it is reasonable to believe that diapause could be initiated within only a couple of weeks when normally it could take over a month (Goehring and Oberhauser 2002, 2004). Finally, an elegant study by Merlin (2009) showed that it is the antennae of Monarchs that are primarily responsible for perceiving changes in photoperiod and light levels. It is unknown as to whether butterfly antennae are vulnerable to excessive light in the same way that ocular systems are, but it is
interesting to note that in the flash reaction study (to be discussed later), antennal
twitches were one of the most common reactions by Monarchs when subjected to flash.

While the results of this experiment were significant, with longevity clearly
increasing when exposed to flash, more research is needed to definitively say that
Monarch longevity may be improved universally through photographic flash treatments.
In addition, research should be conducted to test for a correlation between flash
exposure and Juvenile Hormone synthesis in Monarch butterflies. The most important
point to take away from this research is that it does not appear that photographic flash,
as a result of ecotourism in Monarch overwintering colonies, would negatively affect the
longevity of overwintering Monarch butterflies. Does this mean that advisories and
warnings against the use of flash within colony sites be lifted? Definitely not, for follow-
up testings on the various issues addressed in this section are required.

Because these studies were not conducted within the Monarch overwintering
colonies, but instead were in controlled greenhouse conditions, we cannot be positive
that these results would be identical had they been conducted using overwintering
populations instead of captive Monarchs. However, when looking at the vulnerability of
young Monarchs compared to older Monarchs in these experiments (24-28 hour vs. 12-
14 day), we see increased resilience in the older population. In fact, older Monarchs
exhibited significantly longer lifespans than younger Monarchs when exposed to the
same flash treatment. Although the Monarchs inhabiting the overwintering sites are
much older than any Monarch used in this study, when we age them proportionately to
the non-migratory Monarchs that were used, they are actually well represented by 14-
day old Monarchs. Roughly halfway through their mean lifespans, they are not freshly
emerged, nor young, but are instead at an older midpoint of their lives. They have survived past the critical younger stages and have made it to a more stable phase of their lives. The fact that older Monarchs only increased in longevity is reassuring. Had it been the other way around, it would suggest that perhaps as Monarchs age, their sensitivity to light increases to the point that it becomes more harmful to their longevity. Fortunately, this was not the case.

**Onset of reproductive diapause and migration**

Monarch butterflies are unique in that not all generations undergo their characteristic migration each year. That is, several generations exist between migratory generations that actually do not migrate at all. These are often termed the “summer non-migrants” and have significantly shorter lifespans (Brower 1995). They also are reproductively active, in contrast to the diapausing Monarchs of the migratory generations.

The difference between a migratory and non-migratory Monarch is a topic that is receiving quite a bit of scientific attention currently. While complete understanding is far from achieved, researchers are finding differences in both the phenotypes and genotypes of Monarchs that determine whether they are likely to engage in migratory behavior or not. In fact, we now know that migratory behavior governed by a suite of 23 juvenile hormone-dependent genes found in their brain. Differential expression strongly separates these two types of Monarchs, and such genes have been shown to control fatty acid metabolism, longevity, and disease immunity, all of which are improved in non-reproductive migrant Monarchs (Herman 1975, Herman and Tatar 2001, Zhu et al. 2009). This means that the level of JH present in the Monarch has a great deal to do with the ability to migrate, allowing it to live a longer and healthier life. An additional 40
genes have been found in the Monarch brain that are not dependent on JH levels and play important roles in orientated flight behavior. As these are not JH-mediated, there is evidence that there could be a permanent molecular distinction between migratory and non-migratory Monarchs (Zhu et al. 2009). However, this is still to be conclusively determined and is a topic of much debate.

Although at the present time there is still much to learn from the processes that mediate differential expression, studies have identified a set of environmental cues that play key roles in the expression of migratory behaviors that are governed by JH. These are temperature, photoperiod, sun angle, and host plant senescence (Oberhauser and Hampton 1995, Herman and Tatar 2001, Goehring and Oberhauser 2002, Reppert et al. 2010). As temperatures begin to fluctuate in the fall, the ratio of light to dark hours each day decreases, the angle of the sun in relation to the horizon at noon approaches 55 degrees, and host plants (Asclepias sp.) begin to wither and senesce, Monarch butterflies undergo a change. While a single cue is not likely to elicit this change, according to Goehring and Oberhauser (2002), multiple cues occurring at the same time cause Monarchs to exhibit drastically lower levels of JH causing them to enter reproductive diapause (Goehring and Oberhauser 2002, Herman and Tatar 2001. It is this step that allows them to live longer and engage in migration.

In regards to these longevity experiments, there is a question as to whether tests conducted later in the season (August, September, October) yielded Monarchs with naturally longer longevities. Although this is a reasonable thought, analysis of the longevity data show that there was no main effect of time (i.e., the date at which each trial began) on the longevities of Monarchs. The environmental changes addressed
previously that cue Monarchs to enter the migratory phase (temperature fluctuations, photoperiod, sun angle, and hostplant quality) have significantly lessened effects when dealing with Monarchs in these experiments. This is because they were contained in a walled-in, opaque-windowed, temperature-controlled greenhouse, where they were not given hostplants. Within the greenhouses, the sun's zenith (less visible from opaque windows), temperature (as daily fluctuations are controlled via coolers), and host plant quality (because they are not permitted to search for oviposition sites in the wild) become non-issues. Furthermore, these tests were conducted in Florida, which also minimizes the effects of temperature and photoperiod variations, especially when compared to other summer breeding grounds in North America (e.g., Minnesota, Wisconsin, Michigan, Illinois, Indiana, New England) (Brower 1995, Goehring and Oberhauser 2002). Lastly, larvae were reared in a laboratory building with no windows and was temperature controlled to minimize any fluctuation from day and night. Lastly, the hostplants they were reared on were not naturally-growing Asclepias, which could exhibit signs of senescence later in the year, but instead were well maintained greenhouse-grown Asclepias clippings, showing no signs of sensescene throughout the season.

**Additional implications of flash study**

Understanding the implications of flash on overwintering Monarchs is paramount, but the results of this study can also be used to make inferences on another system – butterfly houses. Another popular type of entomological ecotourism, butterfly houses receive large numbers of visitors who frequently use flash when photographing the exhibited specimens. The results of this study are favorable when measuring the impact of visitors who do indeed use flash within live exhibits. Not only is longevity
important from an inherently conservation-minded perspective, but this is an economic concern, too. With the average butterfly house importing hundreds of butterflies each week, totaling thousands of dollars, a significant decrease in longevity could seriously affect the finances of such exhibits. The results of this study do not suggest that these houses should begin routine flash treatments on butterflies in order to increase their lifespans. Instead, this study shows that photographic flash is unlikely to be harmful to butterfly longevity.

Butterfly houses, as described elsewhere in this dissertation, typically have a live exhibit that showcases free butterflies flying in enclosed gardens, as well as a rearing facility where pupae are allowed to emerge for public viewing (Figure 4-41). At the start of this study, it was hypothesized that the pupal stage would be vulnerable to flash treatments, exhibiting high mortality at younger ages. While adult butterflies have the ability to avoid flash by walking or flying away, freshly emerged butterflies are relatively immobile in the first hour or two after emerging from their pupal cases. This was demonstrated in the flash reaction experiments, in which no reactions were recorded amongst all treatments on all freshly emerged Monarchs. However, longevities of those freshly emerged butterflies treated with flash exhibited no significant change in longevity. Again, from conservation-minded and economic perspective, this suggests that exhibiting freshly emerged butterflies as part of an exhibit and allowing them to be photographed with flash has no negative effects on their longevity. This also bodes well for entomological ecotourism, as there remains no evidence that flash exposure decreases longevity at any age of Monarch butterflies.
Reactions to flash by Monarchs

Although longevity was positively affected by flash in the experiments conducted in this Chapter, we cannot eliminate the possibility that other negative effects may result from flash exposure. The other part of this flash study was to measure Monarch reactions to individual flash exposures in order to examine the frequencies of various disturbance reactions, as exhibited by Monarchs. These data show several interesting things. First, among all five categories of disturbance reactions, two specific reactions predominated during the study – antennal twitches and body twitches. Across all trials, Monarchs exhibited each of the five types of disturbance reactions at one point or another, but these two were the most significant. Second, as Monarchs increase in age, they are more likely to exhibit a disturbance reaction to flash. Third, there is some correlation to suggest that Monarchs become more agitated as they are exposed to higher numbers of flash repetitions. Finally, when combining age groups and flash treatments, these data suggest that nearly one out of every three flash exposures (~33% frequency) will result in a Monarch exhibiting a disturbance reaction. Roughly 23% of the time this will be a body twitch, and 8% of the time it will be an antennal twitch.

In nature, Monarchs, as well as many other insect species, have evolved tactics to avoid threats from predation and parasitism (Tautz and Markl 1978, White et al. 1983, Rothschild and Bergstrom 1997, Koch 2003). When warranted, the twitch of a butterfly’s wing, or a quick burst into flight can make the difference between life and death, allowing escape from a potential predator or parasite. However, the quick decision to move or flee may still be costly to the organism’s health, even if it functions to avoid immediate harm. Animals must find a balance between expending excess energy and abandoning a suitable habitat with the need to avoid harm, which has been
a recurring topic in this Chapter (Ydenberg and Dill 1986). Should an animal take
evasive action each time a minimal threat is perceived, the animal would either spend
too much time exerting itself, or too little time engaging in other important life processes,
such as feeding or reproducing. A disturbance threshold must exist, below which there
is no reaction and beyond which the animal does whatever is necessary to avoid harm,
irrespective of the fitness cost (Ydenberg and Dill 1986). This is especially true with the
overwintering Monarch butterfly, as the conservation of energy while overwintering is
critical to the retention of limited lipid and nutrient stores (Brown and Chippendale
1974). The maintenance of these stores is vital in supplying the energy needed to
survive until the following spring and complete the migratory cycle. Without proper
amounts of energy stores remaining at the end of the winter, it may not be possible for
Monarchs to make the return trip to the U.S. and function to initiate the next generation
of Monarchs via mating and egg-laying. Thus, Monarchs should only exhibit
disturbance reactions to stimuli when a critical threshold is crossed and they truly feel
threatened.

Calvert (1994) was the first to examine causes for disturbance among
overwintering Monarchs. By subjecting them to various stimuli, including puffs of
human breath, clapping noises, and flaps of wind, the study aimed to examine possible
causes for what is termed “cascading” by Monarchs (Figure 4-42). This phenomenon of
en masse flight away from roosting positions in bursts of thousands of individual
Monarchs results in significant energy expenditures. It is thought to be primarily a
defensive reaction against predation within the colonies (Calvert 1994). Although
Monarchs are chemically defended and have few predators, there are some animals
that have succeeded in exploiting the colonies of quiescent Monarchs for predation purposes. Within the colonies, Blackheaded Grosbeaks (*Pheucticus melanocephalus*), Black-backed Orioles (*Icterus galbula abeillei*), and mice (*Peromyscus melanotis*) have been found to predate upon Monarchs at an estimated rate of 926,000 eaten per hectare in the 135-day overwintering period (Brower and Calvert 1985, Calvert et al. 1988, Glendinning et al. 1988). In an average year, this accounts for roughly 10% of the total population of overwintering Monarchs (Calvert et al. 1988). Cascading is believed to be a defensive reaction intended to confuse these predators with a burst of random and unpredictable activity. By disorienting and confusing the predator, reaction time for the prey is extended, therefore increasing the chance of survival (Humphries and Driver 1967). Calvert (1994) found that of the several different stimuli Monarchs were subjected to, only human breath, directed on Monarchs at close-range, elicited a significant effect on their propensity to cascade off from tree roosts. Loud claps and flaps of wind did little to instigate this phenomenon. It was suggested that perhaps the breath of predatory birds, just as they enter a cluster of butterflies, triggers the Monarchs to burst from the trees in reactionary response, instigating them to repeat this behavior when subjected to human breath (Calvert 1994).

While this mass flight has perhaps the most serious consequences for the conservation of energy by Monarchs, subtle reactions, when examined cumulatively, could have negative effects as well. The Monarch sanctuaries are open to ecotourism well over 100 days a year, exposing the overwintering sites to the presence of humans at a near-continuous rate through the winter. While stimuli such as close-range human breath may be rare but costly, photographic flashes may occur innocently hundreds of
times each day in each colony, and perhaps even more depending on the volume of visitors. Any resulting effects of flash are therefore multiplied by the sheer volume of users.

Photographic flash was seen to elicit reactions by Monarchs in all categories of disturbance, ranging from a simple antennal twitch, to flying away. However, the most common reactions across all age ranges were antennal twitches and body twitches. When coupled with this Chapter’s previous section on light perception, it becomes highly intriguing that antennal twitches were one of the more significant reactions to flash. If antennae are as critical to the perception of light as Merlin et al. (2009) and Guerra et al. (2012) show, an antennal twitch may be the insect equivalent of blinking, which we have all experienced when being photographed at one time or another. It is possible that just as we blink in defensive reaction to bright light, Monarchs twitch their antennae due to sensitivity as well. Monarch antennae have been previously studied to determine their role in chemoreception (Boppre 1993, Baur et al. 1998, Haribal and Renwick 1998) and navigation (Merlin et al. 2009, Reppert et al. 2010, Guerra et al. 2012), but little direct attention has been paid to the surface structure of the antennae with regards to light perception. From studies on Monarch navigation, we are realizing the importance of the antennae in general perception of light and landscape features. The following section details a study that I conducted as a follow-up to the antennal twitching results in order to investigate the surface of Monarch antennae and to make inferences on their role in light perception.

**Surface structure of Monarch antennae**

The importance of proper antennal functioning to the Monarch butterfly is being increasingly better understood through current research. It is now accepted that the
time-compensated sun compass system resides in the Monarch antennae and, although it is rather resilient, it has its vulnerabilities (Merlin et al. 2009, Guerra et al. 2012). For instance, Guerra et al. (2012) found that while a single antenna is enough to allow for proper orientation of migratory Monarchs (i.e., when the other antenna is removed), the system fails completely when both are present and one antenna is painted black, thus blocking light from being perceived. However, when the same Monarch had its black antenna removed, the single remaining antenna was enough to properly orient it on its migratory route, as if both antennae were properly functioning. The conclusion of their study was that conflicting antennal perception and timing disrupts sun compass orientation. Not only does this study underline the importance of antennae on the overall light perception by Monarchs, but it also shows that a disruption of only part of the system can have dramatic effects on the entire system’s functionality.

In an effort to determine exactly how the Monarch’s antennae were divided into functional components on the basis of an individual antenna, Guerra et al. (2012) looked at the two major parts of Monarch antennae, the club (i.e., distal bulb) and the filament (i.e., proximal flagellum) (Figure 4-43). Because the clubs of Monarch antennae are lighter in pigmentation than the filament, they postulated that perhaps it was the club area where the light-entrained antennal clocks resided (Guerra et al. 2012). By examining the temporal expression patterns of four clock-related genes (tim, per, cryptochrome1, and cryptochrome 2), they found all four to be expressed equally between the two antennal locations in both complete darkness, and in 12hr light/12hr dark cycles (which affect the temporal expression of various light-mediated genes).
Despite the recent advances in research that underline the importance of antennae to the Monarch butterfly, there is need for detailed accounts of the composition of the surface of the Monarch antennae with specific regards to potential light sensitive areas. As the studies in this Chapter mostly focus on the reaction of Monarchs to sound and light and the potential effects from these stimuli, there is reasonable evidence that Monarch antennae play a part in perceiving either or both. There exists little evidence thus far from the studies in this Chapter that sound is integral in the Monarch butterfly’s perceptive abilities, but it has been known for quite some time that the antennae of Lepidoptera function in chemoreception (i.e., perceiving smells) (Schneider 1964, Van Der Pers et al. 1980), and now new studies show that they play a part in the ability to perceive light (Merlin et al. 2009, Reppert et al. 2010, Guerra et al. 2012). In the flash reaction studies conducted in this Chapter, there was overwhelming evidence that antennal twitches are correlated with flashes of bright light. Although this twitching response was not recorded for every single flash output in the treatments, the overall frequency of twitches is worth more attention.

The correlated antennal twitching response to camera flashes seemed very much akin to the blinking of a human eye, in terms of the quick reaction time associated with the twitch (only a few milliseconds between the flash and the reaction). In order to examine this further, Monarch antennae were photographed using a scanning electron microscope. Scanning electron microscope (SEM) imaging was conducted on a Hitachi TM3000 microscope and images were taken at various magnifications at a 15kV observation condition. Figure 4-44 shows several magnification levels of the club of a Monarch antenna, which, from these photographs, are covered with large trichoid
sensilla measuring approximately 30 μm from base to tip. They are spaced apart unevenly from other sensilla anywhere from 50 μm to 150 μm. These sensilla appear on each segment of the antennal club, as do numerous clusters of small bristles that are arranged in a circle and protrude from the rest of the antennal surface at a height of approximately 10 μm. These protruding clusters are tightly spaced at distances of less than 20 μm from one another, but become less dense and virtually absent from areas proximal to the margins of the antennal club segments. These clusters represent a second type of sensilla present on the Monarch antennae termed coeloconic sensilla, where a single sensillum is located interior to these outer bristles (Figure 4-45) (Hallberg 1981, Zacharuk 1985, Scoble 1992, Hallberg et al. 1994). Lastly, patches of smaller trichoid sensilla are found in groups of approximately 20 individual sensilla and spread unevenly and in very low densities across both the antennal club and filament. These individual sensilla measured no more than 10 μm each, with the size of the patch covering an area of 100 μm by 100 μm.

The filament of Monarch antennae exhibits a different surface than that of the club (Figure 4-44). Whereas larger trichoid sensilla are abundant on the surface of the club, they are virtually absent on the filament (only one or two found on the entire antennal filament). Conversely, “cover” and “hair-like” scales (Downey and Allyn 1975) are abundant on the surface of the filament but absent from the club region (Figure 4-44). Upon examination of the entire club and filament, the only structures seen to be common and homologous between the two antennal regions are the clusters of coeloconic sensilla protruding from the antennal surface in a characteristic circular arrangement.
The functions of these antennal components are relatively unknown for the Monarch butterfly, but likely play significant parts in the various known abilities of Monarch antennae based on previous studies of other lepidopterans (Steinbrecht 1980, Keil 1989, Shields and Hildebrand 1999). There already exists sufficient evidence that these sensilla are indeed essential in the Monarch’s chemosensory ability, as reported by Baur et al. (1998). However, comparisons made between the antennal club and filament show that on the surface, these coeloconic sensilla are the only homologous structures between the two antennal regions in comparable abundances (Table 4-15). With the larger trichoid sensilla (Figure 4-44) mostly on the club, and already reported as being highly sensitive to chemoreception, it is reasonable to believe that their primary role is in perceiving chemicals rather than light levels (Baur et al. 1998). Similarly, the patches of small trichoid sensilla are randomly distributed and in very low abundances on both the club and filament. Guerra et al. (2012) reports that gene expression within Monarch antennae, as controlled by light levels, does not differ between the club and filament. Thus, it is also reasonable to think that any light sensitive structures should be found on both regions of the antennae.

Functions of coeloconic sensilla are unknown in butterflies, and are still not entirely understood in the moths. Most theories suggest that in Lepidoptera they play a part in chemoreception, just like other antennal sensilla. However, when searching for an antennal apparatus that functions to perceive light in all areas of the Monarch antennae, these small double-walled sensilla clusters may be key. Only with studies that directly enervate these coeloconic sensilla will we know for sure whether they interact with those genes responsible for the expression of time-compass mechanisms
in the Monarch antennae. Future research should focus on these structures to
determine their potential role in gene expression of the time-compensated sun compass
in the Monarch butterfly.

**Comparison with the Queen butterfly.** The structure of the Monarch antenna
closely resembles that of *Danaus gilippus*, the Queen butterfly (Myers 1968). This is
not entirely surprising, as the two butterflies are members of the the same genus, share
many of the same hostplants, and occur in the same habitats (Opler and Krizek 1984,
Judd et al. 1994, Ritland 1994). In addition, the Queen butterfly is known to migrate
north from Florida into central and northern U.S. areas each summer (Scott 1986,
Moranz and Brower 1998). Although untested, it is possible that Queens may share
similar navigation and orientation abilities with their Monarch cousins. Although Myers
(1968) examined the antennal structure of Queen butterflies in his research published in
1968, I conducted an additional study in order to make specific comparisons between
sensilla of the two closely related butterflies. Again using a Hitachi T3000 scanning
electron microscope under similar conditions, I looked at both the club and filament at a
range of magnification levels. What I found, which was supported by Myers (1968),
were similarities in the types of sensilla between the Queen and the Monarch butterfly
(Figure 4-47). First, both butterflies exhibit numerous large hair-like trichoid sensilla
projecting from pores on the surface of the antennal club. Also on the antennal club of
both species were clusters of circular bristles, representing the outer wall of coeloconic
sensilla. These were spaced approximately 20 μm apart, just as with the Monarch.
Also homologous between the two species were patches of smaller trichoid sensilla that
numbered approximately 15-20 sensilla per patch (the number of patches was variable).
On the filament of both the Queen and Monarch butterflies, the coeloconic sensilla were present in similar densities (Figure 4-46, Figure 4-48). The small patches of trichoid sensilla were also present in both species on the antennal filament, with roughly 15-20 sensilla per patch. One difference seen between these two species were the arrangement and abundance of the large solitary trichoid sensilla found on the antennal filament. Whereas these sensilla were extremely sparse on the Monarch antennal filament (i.e., only a few along the entire filament), they were common along the Queen’s filament (i.e., greater than 30 total). Another key difference between the two species was the overall abundance of the small trichoid sensilla patches, which were sparse on the Monarch antenna, but common across all areas of the Queen. Table 4-16 contains a comparative list of sensilla abundances between club and filament areas of the Queen antennae.

The vast majority of research conducted on sense organs found on insect antennae have focused on chemoreception. With new evidence in the Lepidoptera, specifically with the Monarch butterfly, that light perception can also occur on the antennae, there is need for further research. From Merlin et al. (2009), we have seen that Monarch antennae house the time-compensated sun compass and the genes that code for its proper expression, which are so very integral in the Monarch’s successful long-distance migration. Guerra et al. (2012) showed that these genes and the time-compensated sun compass mechanisms are found throughout the entire antennae, with no preference for light exposure on the club or filament for the proper functioning of the time compass. Guerra et al. (2012) also highlighted the vulnerability of Monarch navigation based on proper antennal functioning. The flash experiments in this Chapter
suggest that the antennae are sensitive to extreme light levels, as was exhibited by their twitching reaction. Upon examining the surface of Monarch antennae, it becomes clear that there are a number of structures projecting from the antennal wall that could play a part in light perception. When comparing the antennal morphology of the Queen butterfly, we saw a number of striking similarities, possibly suggesting that their antennal perceptive abilities are similar to that of the Monarch. While we know that for both species there is ample documentation that antennal sensilla function in chemoreception abilities, other pronounced and prominent structures (i.e., the coeloconic sensilla) have unknown function in Monarchs. Combined with the fact that they were some of the most abundant antennal sensilla seen for both species, they should be considered for future research, specifically with the possibility of functioning in light perception.

**Body twitch reactions**

More common than antennal twitching was body twitching in reaction to flash. This was defined by a flap, shudder, or twitch of the body and/or wings. Emmel and Benson (1973) show that twitching of wings and antennae, which overlap and touch in closely packed gregarious nocturnal roosts of up to 68 *Marpesia berania* (Nymphalidae) butterflies in the Osa Peninsula rainforest trees of Costa Rica, causes almost instantaneous communication throughout the roost. When one individual butterfly was disturbed, the entire roost would burst into flight immediately, as if signaled by the movement of the disturbed individual. These roosts occupy the same large leaf sites for many months and the individuals return nightly if not disturbed. Newly emerged adults replace adults that die to maintain consistent population structure and size, suggesting that there is selection for this kind of behavior that serves to protect the roosting
butterflies against nocturnal predator attacks. After several successive nightly disturbance events, from flash photography or touches, the original site is abandoned permanently, and the roosting individuals establish a new roost location the next night. There is reason to believe that Monarchs could have evolved a similar response behavior aimed at protecting the overwintering roosts against predation from birds.

It is clear from these data that photographic flash causes Monarchs to be disturbed, generally by initiating some sort of movement, such as twitching, walking, or flying. The risk of disturbance for overwintering Monarchs is that they are heavily dependent on remaining motionless throughout the winter, unless environmental conditions necessitate them to either shiver or to glide in the air (Masters et al. 1988). As Monarch survival depends on being within a critical temperature range of \(-2^\circ\text{C}\) and \(20^\circ\text{C}\), they will warm themselves by shivering and cool themselves by gliding in the brisk mountain air (Calvert 1983, James 1986). It is relatively common to see part of the colony exhibiting these thermoregulatory behaviors on a frequent basis (pers. obsv.). However, it is important to note that these Monarchs are not moving whimsically or playfully. Thermoregulation is a reaction that aims to ensure survival. Still, this energy expense has consequences on fitness, as all behaviors use energy. Excess movement functions to deplete their fat and lipid stores, which are critical to the Monarch’s well being (Brown and Chippendale 1974). This movement may be en masse, by cascading off of tree roosts, or it may be as simple as shivering to warm up. Either way, engaging in excess movement is taxing for the Monarch. The disturbance reactions, as exhibited in this experiment, may contribute to the depletion of energy stores.
The more costly reactions of walking and flying were not significantly frequent, and thus we instead focus on how the twitching reactions, which were highly significant, affect the Monarch butterfly. It is not the aim of this study to quantify the metabolic costs of the various disturbance reactions. However, it is reasonable to think that individual twitches, whether by the antennae or the body, deplete very little of the Monarch’s energy reserves on a per-event basis. As the muscles are not sustaining flight or functioning in walking, antennal and body twitches are the least consequential of all possible reactions tested for in this experiment. This serves to lessen any cause for alarm. Nevertheless, the small metabolic demand of individual reactions can become great with enough repetitions.

These data indicate that the probability that flash will elicit a disturbance reaction may increase as the total number of flashes is increased. On a day-to-day basis, or even on a flash-to-flash basis, the effects of flash are likely minimal, according to the results of this experiment. However, with the colony sites open to the public over 100 days each year, it is the cumulative effects of flash that cause the most concern. From personal observation, even with flash photography prohibited through signage along the trail to the colonies, a photographic flash is fired in the direction of the Monarch colonies roughly once every 10 minutes throughout the day. Extrapolating this out to full eight-hour days, and a conservative 100 days a year, this would produce 4,800 flashes each season. Even if the effects of flash did not increase in probability as the total number of flashes increase, this is still a large number of flashes. We are presently unaware of the probable increase in Monarch reaction frequency if such tests were repeated over the course of 100 days. This certainly warrants further research, for repeated flashes over
multiple days could have a multiplicative effect on the frequency of disturbance reactions.

Approximately 33% of flash events resulted in a disturbance reaction by Monarch butterflies in this study. If the conservative estimation of one flash every 10 minutes is correct, this means that during the course of the overwintering phenomenon, photographic flashes produce approximately 1,600 disturbance reactions among those Monarchs subjected to flashes. These reactions would mostly be in the form of body twitches and antennal twitches, according to this study, but some reactions would be in the form of relocation. However, this would likely occur only a handful of times throughout the colony each winter. If, instead, reactions increase in probability with an increase in total flash exposure (i.e., Monarchs become more sensitive to flash as they are exposed more), as was seen when going from 60 to 90 to 120 flashes (30 flashes seemed to be quite different), this number could multiply and become more significant and of more concern. Even if there is no reason to believe that Monarchs become more sensitive to flash with repeated exposure, there is still cause for concern when they are expending energy needlessly.

Reactions not resulting in relocation are certainly more benign, but not without impact. With every movement comes energy expenditure. The conservative estimate of 1,600 disturbance events can be viewed as little impact, even if this number is doubled, for Monarchs are naturally mobile throughout their overwintering phase. With the most common reaction to flash being a single body twitch, it is difficult to say that this has a pronounced negative effect in natural conditions. In the colonies, shivering Monarchs can be seen twitching perpetually by repetitive muscular contractions for
minutes at a time in order to warm themselves before flying or crawling up a tree to
regain their roosting position. When tallied, this could account for hundreds to
thousands of individual twitches on average. However, what we do not know is when a
shivering Monarch resumes flight and regains its position in the colony, if it retains the
same level of fitness and survival probability as those Monarchs not spending the
energy twitching. Most likely they do not, but we do not know. Without this key piece of
knowledge, it is unclear as to how serious these disturbance reactions could become.
For now, we must compare these reactions against the hundreds of thousands of
shivering Monarchs seen in Mexico each winter. If they are able to survive the winter
with reasonable similarity to other non-shivering Monarchs, then there is less cause for
concern about one or several thousand unnecessary twitches that were caused by
flash. The primary concern was whether flash would cause relocation events on part of
the Monarchs, which could have severe impacts on Monarch fitness, the migration
event, and the ecotourism enterprise that relies on the predictable locations of
overwintering Monarchs from year to year. This study suggests that significant
relocation events are unlikely to occur in reaction to flash.

**Age comparisons in extrapolation**

As with the study on Monarch longevity, this study benefits from using age
comparisons as a way to more accurately extrapolate these data to natural conditions.
Overwintering Monarchs, on a day-wise scale, are much older than any Monarchs used
in this study. Proportionately, though, overwintering Monarchs may be compared to the
non-migratory Monarchs used in this study by looking at the 12-14 day population. The
12-14 day population represents Monarch butterflies that are not freshly emerged, nor
young, but are in the middle to latter years of their life. These data suggest that
overwintering Monarchs may, in fact, be more susceptible to flash compared to non-migratory Monarchs due to their age. While on average, Monarchs exhibited a reaction to flash approximately 33% of the time, when we isolate 12-14 day old Monarchs, we see they reacted 44% of the time. When we isolate the data from the 24-48 hour old Monarchs, we see that they reacted approximately 23% of the time. It is difficult to surmise exactly why older Monarchs respond more often, but in comparison to the younger Monarchs studied, they were twice as likely to exhibit a disturbance reaction when exposed to flash. Generally speaking, the effect of increasing age on butterflies is complex. Depending on the process or behavior one is examining, in correlation with age, there are great differences in the literature.

Butterflies are positively and negatively affected by increasing in age. In males, older butterflies yield higher reproductive success and even outcompete younger conspecifics in territoriality contests (Kemp 2000, Fischer et al. 2008). With females, however, increasing age generally reduces fecundity and egg size (Begon and Parker 1986, Boggs 2008). Furthermore, effects on thermoregulation, nutrient acquisition and internal metabolism have yielded mixed results across the order Lepidoptera and even between males and females of the same species (Boggs 1988). While these data clearly indicate that older butterflies are more prone to react physically to flash, there is little prior work that may explain exactly why this should be. Further research on this topic is needed. The logical next step in research would be to compare total daily locomotion (i.e., quantify how often and to what degree these older butterflies move during the day), to see if there is a general increase in activity among older butterflies versus younger ones. It could be that with an increase in age comes a general increase
in activity, as well. Thus, older butterflies may be more likely to respond to stimuli more actively, too. Nevertheless, these studies show that older butterflies are more likely to demonstrate a disturbance reaction when subjected to flash. This indicates that they may have a lower threshold for responding to threats and disturbances and are more prone to take evasive action when presented with a predator-like stimulus.

**The importance of light attenuation**

There is still another significant consideration to make when analyzing the effects of flash. This is the issue of light attenuation. Light attenuates, or is reduced, by the law of inverse squares. That is, as the distance between the light source and the subject is doubled, the light intensity is quartered. In these experiments, a single level of light intensity was chosen at the beginning in order to maintain consistency between treatments, which measured roughly 2 million Lux (lumens per square meter) at slightly less than one millisecond. In order to properly calibrate the level of light delivered, light readings must be taken from the position of the subject, rather than a measurement directly from the flash emitting apparatus. This is because Lux is highly dependent on the distance from the flash to the subject. Therefore, in order to fully understand the implications of flash on Monarch butterflies, distance between the flash and the Monarch colony must be considered.

Throughout these experiments, approximately 500,000 lumens were emitted in a 1 millisecond burst at a distance of 1 meter. Within the Monarch’s overwintering colonies, visitors are generally discouraged from approaching within 10 meters of the primary Monarch clusters. If Monarchs are clustering especially low on the trees, guide ropes will be placed by park guards in the larger colony sites, ensuring that visitors do not approach too closely. Some Monarchs also occur higher in the trees and thus, even if
ecotourists are permitted to approach the same trees hosting the Monarchs, the clusters remain out of reach and high above ground. Table 4-17 shows the effect of light attenuation on percentage of Lux, as distance is increased between the flash and the subject. Immediately, we see that greater distances significantly lessen the intensity of flash. This would logically also lessen the effects it has on wildlife, too.

The primary concern is the use of flash at close proximity to Monarch butterflies. Although many Monarchs are located at or beyond 10 meters from camera-ready ecotourists, there are still many that can be found elsewhere in the colony sites and may be approached directly by ecotourists. On an average day in the colony sites, hundreds of thousands of Monarchs are commonly found on lower shrubs, on the ground, and puddling in wet grasses and streams. Because these have left the protected roosts, they are more difficult to monitor by park guards. Concentrated areas are easy to protect with boundary ropes, prohibiting close-up viewing and photography, but extended areas outside of the main clusters are not. In addition, Monarchs that have been displaced from the central colony area are already more vulnerable, since they have either fallen off of or been dislodged from the main clusters due to wind, rain, or predation. Alternatively, they could have been in an inopportune location prior to relocating and are attempting to cool down and conserve energy stores away from the protected colony center (Calvert and Brower 1986). When Monarchs are in more open areas or on the ground, they are more susceptible to harsh environmental conditions, as well as predation (Glendinning et al. 1988). Therefore, flash photography could be more distressing to these butterflies than to those securely within roosts.
Monarchs stay relatively mobile throughout the winter, despite their ultimate goal of conserving energy and remaining dormant. Often the entire colony will relocate multiple times each month, in order to adapt to changing environmental conditions (Calvert and Brower 1986, pers. obsv.). During these transitions, which may last for hours or days, colony sites are unprotected from encroaching visitors, as new areas have not yet been roped off. This represents another key opportunity for the use of close-range flash.

Monarchs are seen to react to flash photography in a number of ways. On average, Monarchs respond by twitching, which occurs at a rate of roughly one out of every three flashes. However, this statistic increases greatly as Monarch age is increased, and as the total number of flash exposures increases. This suggests that overwintering Monarchs, which may be exposed to flash photography hundreds to thousands of times each season and are more progressed in their age, are susceptible. Hence, there is reason to believe that when Monarchs are photographed using flash at close range, they may be negatively affected. This occurs primarily through the unnecessary expenditure of energy.

**Chapter Conclusions**

The promotion of ecotourism as a sustainable and environmentally responsible mode of travel necessitates an understanding of ecotourism’s impacts on wildlife, like those reviewed and analyzed in this Chapter. From this research, we are able to learn a great deal about behaviors and activities in which ecotourists engage. By understanding where vulnerabilities lie within each system, be it the overwintering Monarch butterfly phenomenon, or birdwatching in Costa Rica, we may make informed decisions on policies and procedures within the industry. Not only does this serve the
goal of conserving wildlife and the environment, but it also ensures that ecotourism attractions remain in good condition and continue to provide consistent economic incentives to local community stakeholders. Without the support of these local communities, environmental protection is jeopardized. Similarly, without proper environmental protection, the integrity and welfare of local communities is threatened. Both environmental protection and the promotion of community welfare must be at sustainable levels for ecotourism to function. When ecotourism functions properly, it is one of the most powerful conservation tools in the world today.

Ecotourism in the Monarch butterfly sanctuaries continues to grow. This is demonstrated by an increase in visitation at individual colonies, the opening of new colony sites to ecotourism in recent years, and new construction of infrastructure at existing colony sites. If we are to continue to promote Monarch ecotourism in an unrestricted manner (i.e., not setting visitation limits), negative impacts must be managed. However, the tolerance thresholds for negative impacts are subjective. While impacts from crowd noise and photography appear to be limited compared to the effects from things like deforestation or climate change, they are tremendously easier to control. Therefore, they should be prioritized. It is easy to make comparisons between the metabolic costs of body twitches and normal shivering behavior to say that Monarchs expend exponentially more energy on natural processes throughout their overwintering period. However, Monarchs need to be conservative and calculated in their energy expenditures. Therefore, any significant increase in activity could affect their fitness. The overall fitness effects that could result from flash photography are difficult to observe, as they are not likely to be expressed immediately, or even within
the colony sites. Instead, depletion of energy stores would have effects mostly on the total number of Monarchs that complete the journey to the U.S. and Canada each summer. If impacts are measured solely as resultant mortality or by observing low population levels the following season, rather than by studying individual reactions, as done in this study, such impacts could go relatively unnoticed until it is too late. Studies like this one are imperative to the health of ecotourism as an industry and conservation tool.

For the same reasons that this study does not recommend flash treatments to be used as a way to promote increased longevity in Monarchs, it is not advisable to ignore excessive crowd noise and flash photography in the colonies. In the case of flash photography, the problem does not lie with the impact of individual flashes. Rather, it is the high repetition of flash throughout the course of the winter that is more concerning. Should the extra movement exhibited by Monarchs in response to flash compete metabolically with other behaviors, especially those that ensure survival, problems could arise for these butterflies. The lack of negative impact that flash had on longevity is encouraging. However, because of the significant effects that flash exhibited on disturbance reactions, flash photography should be restricted in colony sites, especially in areas where flash is used at close range to the butterflies.
Figure 4-1. A moth light trap in the Chiriqui Highlands, Panama, attracts thousands of moths, beetles, and other insects at night. Photo courtesy of J. Court Whelan.
Table 4-1. List of ecotourism activities and their impacts on wildlife based on a review of previous studies.

<table>
<thead>
<tr>
<th>Ecotourism Activity</th>
<th>Wildlife Affected</th>
<th>Induced Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Encroachment/Aircraft</td>
<td>Ringed Seal ( Pusa hispida )</td>
<td>Escape behavior</td>
</tr>
<tr>
<td>Helicopter tourism</td>
<td>Dall’s Sheep ( Ovis dalli )</td>
<td>Feeding disruption and fleeing</td>
</tr>
<tr>
<td>Motorized watercraft tourism</td>
<td>Common Tern ( Sterna hirundo )</td>
<td>Increased disturbance and relocation</td>
</tr>
<tr>
<td>Helicopter tourism</td>
<td>Mexican Spotted Owl ( Strix occidentalis )</td>
<td>Flush responses increase with proximity</td>
</tr>
<tr>
<td>People walking</td>
<td>Snowy Plover ( Charadrius nivosus )</td>
<td>Moving and Flying Away from Disturbance</td>
</tr>
<tr>
<td>Encroachment/Aircraft</td>
<td>Pacific Brant ( Branta bernicla )</td>
<td>Fleeing and variation in route selection</td>
</tr>
<tr>
<td>Encroachment/Aircraft</td>
<td>Canadian Goose ( Branta canadensis )</td>
<td>Escape and disturbance behavior</td>
</tr>
<tr>
<td>Human presence/General ecotourism</td>
<td>Bald Eagle ( Haliaeetus leucocephalus )</td>
<td>Flush response of breeding and non-breeding individuals</td>
</tr>
<tr>
<td>Hikers, bikers, air traffic and road traffic</td>
<td>Big Horn Sheep ( Ovis canadensis )</td>
<td>Fleeing from habitat</td>
</tr>
<tr>
<td>Road traffic</td>
<td>Woodland Caribou ( Rangifer tarandus caribou )</td>
<td>Avoiding habitat near roadways</td>
</tr>
<tr>
<td>Proximal observation</td>
<td>Pigmy Marmoset ( Cebuella pygmaea )</td>
<td>Retreating to canopy</td>
</tr>
<tr>
<td>Sounds of motorboat traffic</td>
<td>Bottlenose Dolphin ( Tursiops truncatus )</td>
<td>Avoidance of feeding grounds</td>
</tr>
<tr>
<td>Proximal observation, encroachment</td>
<td>Sea Turtles</td>
<td>Insubstantial concealing of nests, misdirected movement towards nest and ocean</td>
</tr>
<tr>
<td>beachfront lighting</td>
<td></td>
<td>Negative effects on feeding behavior</td>
</tr>
<tr>
<td>Proximal observation</td>
<td>Asian Rhino ( Rhinocerous unicornis )</td>
<td></td>
</tr>
<tr>
<td>Ecotourism Activity</td>
<td>Wildlife Affected</td>
<td>Induced Behavior</td>
</tr>
<tr>
<td>----------------------------------------------------------</td>
<td>---------------------------------</td>
<td>--------------------------------------------</td>
</tr>
<tr>
<td>Proximal observation</td>
<td>Chimpanzee <em>Pan troglodytes</em></td>
<td>Fleeing or charging</td>
</tr>
<tr>
<td>Road Traffic, Walking, Jogging, Proximal Observation</td>
<td>Florida Waterbirds</td>
<td>Swimming or Flying Away</td>
</tr>
<tr>
<td>Sounds of motorboat traffic</td>
<td>Pacific Humpback Dolphin <em>Sousa chinensis</em></td>
<td>Disruption of acoustic communication</td>
</tr>
<tr>
<td>Flash photography</td>
<td>Whale Shark <em>Rhincodon typus</em></td>
<td>Diving, changing direction, and shuddering</td>
</tr>
<tr>
<td>Flash photography</td>
<td>Antarctic Fur Seal <em>Arctocephalus gazella</em></td>
<td>Change in dive frequency, depth, and duration</td>
</tr>
<tr>
<td>Flash photography</td>
<td>West Indian Anole <em>Anolis cristatellus</em></td>
<td>Defensive behavior akin to predator avoidance</td>
</tr>
</tbody>
</table>
Figure 4-3. Infrastructure at Sierra Chincua Monarch sanctuary and colony site. A) Original vendor structures at entrance of Sierra Chincua. B) Original restaurant building at Sierra Chincua. C) New renovations at Sierra Chincua to vendor and restaurant buildings. D) Solar panels were installed to promote sustainability. E) Park guards, known locally as Vigilantes, are present throughout the tourist crowds at colony sites. F) Fresh food vendors sell regional and seasonal fruit and vegetables to ecotourists. G) With new structures at Sierra Chincua come new welcome signs. F) An informational map describing the layout of the sanctuary and traditional colony sites. Photos courtesy of J. Court Whelan.
Figure 4-4. Examples of Monarch behavior and sights within the Monarch sanctuaries. A) As temperatures warm, Monarchs take flight by the millions. B) When cooler, or in shaded areas of the colony, Monarchs cluster to conserve energy. C) Periodically, Monarchs will leave the safety of the roosts to drink water at nearby streams. This is especially common when temperatures are warmer. D) Wildflowers, although in full bloom year-round, cannot support the entirety of the colony and only a fraction of the Monarchs will find nectar at flowers like these. E) Birds are commonly found in the Monarch sanctuaries, such as this Red Warbler (Ergaticus ruber). F) Monarchs will blanket bushes, tree trunks, and low shrubs to the extent that the vegetation is no longer visible beneath the butterflies. Photos courtesy of J. Court Whelan.
Figure 4-5. Map showing known overwintering colonies of Monarch butterflies in the Transvolcanic mountain range of southern Mexico (Journey North 2001: www.learner.org). Photo courtesy of Journey North.
Figure 4-6. Various stakeholders of the Monarch overwintering phenomenon. A) A young local Mexican boy enjoys the Monarch colonies for the first time. B) Crowds at the El Rosario colony can become quite large, sometimes taking away from the sanctity of the phenomenon. C) Horses are available for rent now at El Rosario, Cerro Pelon, and Sierra Chincua sanctuaries. D) Two young Mexican girls act as park guards to make sure that people do not cross into the field area. They will also help answer questions posed by visitors. E) For some, experiencing the Monarch migration event is highly spiritual. F) The Sierra Chincua colony is traditionally much less visited, allowing for more intimate experiences within the millions of Monarch butterflies. Photos courtesy of J. Court Whelan.
Figure 4-7. Stakeholders in Monarch ecotourism are also located in adjacent towns and benefit from the sale of goods and services. Angangueo is a predominant gateway for visiting the Monarch sanctuaries, as it lies between two of the major colonies. Townspeople actively maintain educational murals, street paintings, and other decorations featuring the Monarch butterfly. This not only serves the purpose of paying tribute to the organism and phenomenon that sustains their way of life, but also to encourage visitation from national and international tourists. These tourists will, in turn, stay in local hotels and purchase local goods. Photos courtesy of J. Court Whelan.
Table 4-2. Detailed descriptions of reaction behaviors exhibited by each categorical response. These categories remained the same for both flash and sound studies.

<table>
<thead>
<tr>
<th>Category of Reaction</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Response</td>
<td>No Response</td>
</tr>
<tr>
<td>Antennal Twitch</td>
<td>Movement of the antennae and/or head</td>
</tr>
<tr>
<td>Body Twitch</td>
<td>Movement of the wings and/or body</td>
</tr>
<tr>
<td>Walk</td>
<td>Walking around the plant or cage</td>
</tr>
<tr>
<td>Fly and Land</td>
<td>A burst of flight, followed by immediately landing elsewhere on the plant or cage</td>
</tr>
<tr>
<td>Fly Away</td>
<td>A burst of flight for a sustained period of 5 seconds or greater</td>
</tr>
</tbody>
</table>

Figure 4-8. Materials used for sound studies. A) One of the two greenhouses used at the University of Florida’s Department of Entomology and Nematology. B) Experimentation cage used in sound study, provisioned with one plant, as a substrate for the Monarch. C) One of the holding cages used to keep Monarchs in between sound treatments, provisioned with five nectar plants. The plants were rotated with fresh ones in order to maintain ample nectar supply. D) An outside view of holding cage used within the greenhouses. Photos courtesy of J. Court Whelan.
Figure 4-9. Greenhouses and sprinkler system used in sound and flash studies. A) Greenhouses used at the University of Florida’s Department of Entomology and Nematology. B) A drip irrigation system maintained adequate moisture levels for Monarchs and hydration for the potted plants. C) The drip irrigation system was also programmed to turn on at set intervals throughout each day. D) An evaporative cooling unit was used to maintain stable temperatures between 21° and 27°C. Photos courtesy of J. Court Whelan.

Figure 4-10. Monarchs were separated into four holding cages during the punctuated sound experiments. Each cage was designed to provide ample food and water to sustain the Monarchs until their next round of trials at the necessary age (24-28 hour and 12-14 day).
Figure 4-11. Audio materials used in sound study. A) iPod used to play simulated crowd noise recording. B) Decibel meter used to calibrate sound pressure levels. C) Portable speaker that was placed within test cage and attached to iPod via 6 foot 1/8” mini-speaker wire (not pictured). D) Graph of tested frequency range of audio. The yellow box shows that audio frequencies ranged from 200Hz and 9,000Hz. Photos courtesy of J. Court Whelan.
<table>
<thead>
<tr>
<th>Monarch Low Frequency Study</th>
<th>Time:</th>
<th>Date:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monarch #:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dB</td>
<td>Freq</td>
<td>NR</td>
</tr>
<tr>
<td>1</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>2</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>3</td>
<td>58</td>
<td>150</td>
</tr>
<tr>
<td>4</td>
<td>85</td>
<td>200</td>
</tr>
<tr>
<td>5</td>
<td>58</td>
<td>100</td>
</tr>
<tr>
<td>6</td>
<td>85</td>
<td>200</td>
</tr>
<tr>
<td>7</td>
<td>58</td>
<td>100</td>
</tr>
<tr>
<td>8</td>
<td>85</td>
<td>200</td>
</tr>
<tr>
<td>9</td>
<td>58</td>
<td>150</td>
</tr>
<tr>
<td>10</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>11</td>
<td>58</td>
<td>150</td>
</tr>
<tr>
<td>12</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>13</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>14</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>15</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>16</td>
<td>85</td>
<td>150</td>
</tr>
<tr>
<td>17</td>
<td>58</td>
<td>100</td>
</tr>
<tr>
<td>18</td>
<td>85</td>
<td>150</td>
</tr>
<tr>
<td>19</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>20</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>21</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>22</td>
<td>85</td>
<td>150</td>
</tr>
<tr>
<td>23</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>24</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>25</td>
<td>58</td>
<td>150</td>
</tr>
<tr>
<td>26</td>
<td>85</td>
<td>200</td>
</tr>
<tr>
<td>27</td>
<td>58</td>
<td>150</td>
</tr>
<tr>
<td>28</td>
<td>85</td>
<td>100</td>
</tr>
<tr>
<td>29</td>
<td>58</td>
<td>200</td>
</tr>
<tr>
<td>30</td>
<td>85</td>
<td>150</td>
</tr>
</tbody>
</table>

Figure 4-12. Data sheet showing various treatment combinations between the frequency and decibel levels that were used in the low frequency punctuated sound study.
Figure 4-13. Screen graphic of Subwoofer Bass Tester application (Alkek Instruments) used to generate low frequency sounds at set decibels in the low frequency punctuated sound study.

Figure 4-14. Schematic of sustained sound study. A single large cage was constructed from four smaller subcages, which allowed for complete mobility between the four subcages by the test subjects. Audio attenuation facilitated an even sound gradient from one end of the cage to the other.
Figure 4-15. Sustained sound study experimental setup. A) A single large cage was constructed using four smaller subcages. B) Subcages were fastened together via binderclips creating seamless margins between subcages. C) A videocamera with wideangle lens was positioned two meters away from the cage to allow for continuous observation during each 8-hour trial. D) At the positive end of the cage, a speaker was positioned in the middle of three *Pentas* plants so that it was evenly spaced from flowering parts and yielded an 80 dB level. E) At the negative end of the cage, only plants were present, creating a 25 dB differential between the positive and negative ends. Photos courtesy of J. Court Whelan.
<table>
<thead>
<tr>
<th>Butterfly</th>
<th>Hour</th>
<th>Cage</th>
<th>Time (min.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>7</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>7</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>7</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>7</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>

Figure 4-16. Data sheet for sustained sound study. Data were recorded as total minutes per hour that each Monarch spent in each subcage. This allowed for analyses both on cage choice, as well as any effect that hour had on cage choice over the course of each day.
Figure 4-17. Flash study cage grouping. Upon acquiring each group of 30 Monarchs, 10 were tested within the first two days of emergence. Ten were placed into holding cages to await testing until they reached the appropriate age. The final ten were treated as controls and not exposed to flash at all, but held in the cages under the same conditions as the Monarchs exposed to the experimental treatments. All cages were provisioned with food, water, and Gatorade.
Figure 4-18. Materials used for flash study. A and B) Pop-up screen cages were placed on tables. C) After placing plants, irrigation lines were connected and Gatorade was provided. D) Screened cages were kept moist to allow Monarchs to drink water as they pleased, and for plants to remain healthy. E) The inside of each cage contained three nectar plants, as well as a saucer of Gatorade. Photos courtesy of J. Court Whelan.
Figure 4-19. Test cage used for flash study. Distance from the flash unit to the cage was one meter. Photos courtesy of J. Court Whelan.

Figure 4-20. Materials used in flash study. A) Back view of Canon ex580II Speedlite camera flash. B) Canon BGE7 Intervalometer for automating flash exposures. C) Sekonic L-508 Zoom Master Light Meter for ensuring consistent flash output throughout multiple exposures. D) Front view of Canon ex580II Speedlite camera flash. Photos courtesy of J. Court Whelan.
Figure 4-21. Methods used for pupal flash exposure trials. A) Pupae were supplied in tissue-padded cups. B, C, and D) Pupae were removed from the protective padding and glued to a paper-towel substrate, allowing for 100% eclosion success. E and F) Pupae were identified and grouped together for proper timing of eclosion based on the transparency of their pupal cases. Photos courtesy of J. Court Whelan.

Table 4-3. Mean longevities (days) for each flash treatment, with 95% confidence intervals, and median longevity.

<table>
<thead>
<tr>
<th></th>
<th>0</th>
<th>30</th>
<th>60</th>
<th>90</th>
<th>120</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>10.03±1.14</td>
<td>17.67±3.71</td>
<td>17.60±2.46</td>
<td>15.54±2.78</td>
<td>16.55±3.67</td>
</tr>
<tr>
<td>Median Longevity</td>
<td>9</td>
<td>18</td>
<td>16</td>
<td>17</td>
<td>16</td>
</tr>
</tbody>
</table>

511
Figure 4-22. Monarch longevity increased significantly when Monarchs were exposed to flash treatments. However, there were no significant differences in longevities between experimental treatments.

Table 4-4. Mean longevities (days) across all flash treatments (30, 60, 90, and 120), with 95% confidence intervals

<table>
<thead>
<tr>
<th>Monarch Age</th>
<th>Mean Longevity</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-48 hour</td>
<td>15.20 ± 2.31</td>
</tr>
<tr>
<td>12-14 day</td>
<td>19.21 ± 1.65</td>
</tr>
</tbody>
</table>

p<0.03

Table 4-5. Mean longevities (days) between flash treatments for freshly emerged Monarchs, with 95% confidence intervals. No significant difference was found.

<table>
<thead>
<tr>
<th>Flash Treatment</th>
<th>Longevity</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>13.1 ± 6.79</td>
</tr>
<tr>
<td>60</td>
<td>17.0 ± 7.11</td>
</tr>
<tr>
<td>120</td>
<td>14.3 ± 5.21</td>
</tr>
</tbody>
</table>

Table 4-6. Mean longevities (days) across all ages between combined treatment groups.

<table>
<thead>
<tr>
<th>No Flash</th>
<th>With Flash</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Longevity</td>
<td>10.03 ± 1.14</td>
</tr>
<tr>
<td>T-test for difference</td>
<td>p&lt;0.0001</td>
</tr>
</tbody>
</table>
Table 4-7. Mean percentage of each response to flash by Monarch butterflies across all flash treatments (30, 60, 90, and 120 flashes), as determined by age.

<table>
<thead>
<tr>
<th></th>
<th>No Reaction</th>
<th>Ant. Twitch</th>
<th>Body Twitch</th>
<th>Walk and Land</th>
<th>Fly Away</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-48 hour</td>
<td>0.7757</td>
<td>0.0871</td>
<td>0.1273</td>
<td>0.0116</td>
<td>0.0052</td>
</tr>
<tr>
<td>12-14 day</td>
<td>0.5584</td>
<td>0.0584</td>
<td>0.3702</td>
<td>0.0018</td>
<td>0.0096</td>
</tr>
</tbody>
</table>

p<0.0001

Table 4-8. Mean percentage of reactions, as determined by increasing age categories. Positive indicates that a reaction was observed, whereas negative indicates that the Monarch did not react to the flash exposure.

<table>
<thead>
<tr>
<th></th>
<th>Negative</th>
<th>Positive</th>
</tr>
</thead>
<tbody>
<tr>
<td>24-48 hour</td>
<td>0.7757</td>
<td>0.2322</td>
</tr>
<tr>
<td>12-14 day</td>
<td>0.5584</td>
<td>0.4416</td>
</tr>
</tbody>
</table>

p<0.001

Figure 4-23. As the age of the Monarch progressed from 24-48 hour to 12-14 days old, the total incidence of reactions increased. Data from flash treatments were combined and percentages herein are based on frequencies of response per total number of flash exposures in the respective treatments. As depicted, the increase in total reactions is largely supported by the marked increase in body twitch reactions between the two ages.
Figure 4-24. Percentage of positive reactions for each flash treatment level when combining 24-48 hour and 12 to 14-day ages. No significant correlation was observed. Although it is unsubstantiated, if we remove the 30 flash data point, a strong correlation exists between the remaining data, as depicted by the trendline. This suggests that as total number of flash exposures increases, the frequency increases as well.

Table 4-9. Mean percentage of each response to flash by Monarch butterflies across all age groups, as determined by flash treatment.

<table>
<thead>
<tr>
<th>Flash Treatment Level</th>
<th>No Reaction</th>
<th>Ant. Twitch</th>
<th>Body Twitch</th>
<th>Walk and Land</th>
<th>Fly Away</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>30</td>
<td>0.6000</td>
<td>0.0444</td>
<td>0.3489</td>
<td>0.0000</td>
<td>0.0067</td>
</tr>
<tr>
<td>60</td>
<td>0.8592</td>
<td>0.0292</td>
<td>0.0917</td>
<td>0.0142</td>
<td>0.0050</td>
</tr>
<tr>
<td>90</td>
<td>0.6786</td>
<td>0.1265</td>
<td>0.1821</td>
<td>0.0043</td>
<td>0.0060</td>
</tr>
<tr>
<td>120</td>
<td>0.5829</td>
<td>0.1113</td>
<td>0.3013</td>
<td>0.0088</td>
<td>0.0100</td>
</tr>
</tbody>
</table>

p<0.0034  p<0.0001
Figure 4-25. As the total number of flashes increase from 0 to 120 per treatment, the frequency of reactions increased.

Table 4-10. The percentage of positive reactions based on flash treatment levels.

<table>
<thead>
<tr>
<th>% of Positive Reactions</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>30</td>
</tr>
<tr>
<td>60</td>
</tr>
<tr>
<td>90</td>
</tr>
<tr>
<td>120</td>
</tr>
</tbody>
</table>

Table 4-11. Mean percentage of reactions across all treatments and age groups, as determined by sex of the Monarch butterflies.

<table>
<thead>
<tr>
<th></th>
<th>No Reaction</th>
<th>Ant. Twitch</th>
<th>Body Twitch</th>
<th>Walk</th>
<th>Fly and Land</th>
<th>Fly Away</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>0.7471</td>
<td>0.0485</td>
<td>0.1931</td>
<td>0.0005</td>
<td>0.0088</td>
<td>0.0020</td>
</tr>
<tr>
<td>Female</td>
<td>0.7257</td>
<td>0.0793</td>
<td>0.1830</td>
<td>0.0180</td>
<td>0.0060</td>
<td>0.0007</td>
</tr>
</tbody>
</table>
Table 4-12. Mean percentage of reactions, across all age groups, as determined by flash. Data from all four flash treatments (30, 60, 90, 120) were combined into a single category, termed Flash.

<table>
<thead>
<tr>
<th>Reaction</th>
<th>Ant. Twitch</th>
<th>Body Twitch</th>
<th>Walk</th>
<th>Fly and Land</th>
<th>Fly Away</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Flash</td>
<td>1.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Flash</td>
<td>0.6802</td>
<td>0.0778</td>
<td>0.2310</td>
<td>0.0068</td>
<td>0.0055</td>
</tr>
</tbody>
</table>

p<0.001 p<0.0001

Figure 4-26. Mean percentages of reactions when combining all flash treatments at all ages. Body twitch reactions were the most common positive reaction at just over 23% of the time, followed by antennal twitches, which occurred over 7% of the time.

Table 4-13. Mean percentage of reactions by grouping all reaction categories into one, denoted by Positive Response.

<table>
<thead>
<tr>
<th></th>
<th>Negative</th>
<th>Positive</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Flash</td>
<td>1.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Flash</td>
<td>0.6802</td>
<td>0.3221</td>
</tr>
</tbody>
</table>
Figure 4-27. When subjected to flash, Monarch butterflies physically reacted nearly one out of every three times.
Figure 4-28. Vogel’s organ on *Morpho peleides*. The Vogel’s organ (Vo) found on *Morpho peleides* is a pronounced structure located at the base of the forewing (Fw) by following the subcostal (Sc) and cubital (Cu) veins towards the mesothorax. There is a prominent thinned portion of exoskeleton that forms the round tympanal membrane, which is surrounded by a chitinous ring. The lack of scales is natural, and no scales were removed in order to produce this clear photograph of Vogel’s organ. Photos courtesy of J. Court Whelan.
Figure 4-29. Lack of Vogel’s organ on Danaus plexippus. When following the cubital (Cu) and subcostal (Sc) veins of the Monarch butterfly’s forewing (Fw) down to the mesothorax, the area known to exhibit the Vogel’s organ for the Morpho (and other butterflies reviewed within this Chapter) does not exhibit the same round tympanic membrane and rigid chitinous ring. Instead, this area is composed primarily of integument, sclerotized plates, axillary sclerites, and musculature. In addition, the entire area was heavily covered with scales, which was not the case with Morphepeleides. Photos courtesy of J. Court Whelan.
Figure 4-30. Lack of Vogel's organ on *Danaus gilippus*. The region at the base of the forewing (Fw) where the subcostal (Sc) and cubital (Cu) veins terminate is heavily sclerotized and covered with scales, just as with the Monarch butterfly. No thinned tympanal membrane, nor chitinous ring is exhibited. Instead, the area is composed primarily of chitinous axillary sclerites underneath numerous scales. Photos courtesy of J. Court Whelan.
Figure 4-31. Lack of Vogel’s organ on *Limenitis archippus*. As with the Monarch, Forest Nymph, and Queen, the Viceroy exhibits no tympanal membrane with surrounding chitinous ring. The area at the base of the forewing (Fw) where the subcostal (Sc) and cubital veins (Cu) terminate has only axillary sclerites and musculature attachments. The lack of a thinned membrane and outer chitinous ring signifies that Vogel’s organ is not present. Photos courtesy of J. Court Whelan.
Figure 4-32. Although the Morpho is a larger butterfly, the size of the thorax is not drastically different between the Monarch and Morpho. Therefore, one would not expect the Vogel’s organ to be drastically different in size between the two species, such that it could be present but unobservable on the Monarch when using a high powered stereo microscope. Photo courtesy of J. Court Whelan.
Figure 4-33. Lack of Vogel's organ on *Idea leuconoe*. As with the Monarch butterfly, when following the cubital (Cu) and subcostal (Sc) veins of *Idea leuconoe* down to the mesothorax, the area is composed of rigid exoskeleton and attached muscle rather than the round tympanal membrane and rigid chitinous ring typical of Vogel's organ. Photos courtesy of J. Court Whelan.
Figure 4-34. Mean number of minutes per hour that Monarchs spent in all subcages during the sustained sound study.

Table 4-14. Mean minutes per day that Monarchs spent in each subcage with 95% confidence intervals that the population mean is within the value of the sample mean.

<table>
<thead>
<tr>
<th>Cage</th>
<th>Mean minutes per day</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>87.30 ± 4.95</td>
</tr>
<tr>
<td>2</td>
<td>134.60 ± 5.46</td>
</tr>
<tr>
<td>3</td>
<td>79.60 ± 4.49</td>
</tr>
<tr>
<td>4</td>
<td>178.50 ± 6.26</td>
</tr>
</tbody>
</table>
Figure 4-35. Mean total minutes per day spent in each of the four subcages of the experiment. Although the correlation between time spent in each cage is not strong, there is a trend exhibited by the regression line seen here.

Figure 4-36. Mean number of minutes per hour that Monarchs spent in cage one, where the speaker was located. The apparent repellant effect of the noise source in cage one is shown by the steady preference and/or movement of the butterflies away from cage one and in the direction of cages two, three, and four with increasing time of exposure.
Figure 4-37. Mean number of minutes per hour that Monarchs spent in cage three (third loudest cage). As the day progressed, Monarchs spent more time in cage three than at the beginning of the day. Although the r-squared number is not very strong, multinomial logistic regression analyses suggest that Monarchs spend significantly more time in cage three throughout the day (df=3, p<0.0001).
Figure 4-38. Comparing cage one and cage three, it is evident that the mean number of minutes per hour decreases for cage one, while increasing for cage three. According to multinomial logistic regression analyses, as time progressed, Monarchs spent significantly less time in cage one (df=3, p<0.001) and more time in cage three (df=3, p<0.0001).

Figure 4-39. Mean number of minutes per hour that Monarchs spent in cage two. Although the trendline indicates that there may be a slight correlation, both the r-squared value and logistic regression analyses suggest that Monarchs do not significantly change their preference for cage two with increasing time of exposure to noise.
Figure 4-40. Mean number of minutes per hour that Monarchs spent in cage four. There is a stronger r-squared value to match the apparent correlation, but multinomial logistic analyses indicate that this correlation is not strong enough to definitively prove correlation.
Figure 4-41. Examples of public exhibits displaying freshly emerged butterflies. A) The McGuire Center for Lepidoptera and Biodiversity, located in Gainesville, Florida, exhibits a large rearing facility that allows the public to view freshly emerged butterflies. B) Visitors may approach the glass directly, sometimes taking photos with flash. C and D) Although butterflies are removed periodically throughout the day, upon emergence, they often remain in the eclosion case for several hours for visitors to look at. E) All butterflies arrive as pupae, meaning that each butterfly exhibited in the live exhibit will pass through this eclosion case, entering as a pupa and exiting as a mature adult butterfly. Photos courtesy of J. Court Whelan.
Figure 4-42. Monarchs “cascading” from their roosts in the El Rosario Monarch Sanctuary in Mexico. Although the cause of this behavior is not entirely understood, many believe that such rapid bursts of thousands of butterflies into flight all at once may signify that they are being disturbed in some way. Only several predators exist within Monarch overwintering colonies, but they have been known to cause significant mortality, perhaps instigating these bursts as a defensive reaction to predation by birds. Photo courtesy of J. Court Whelan.

Figure 4-43. Monarch antennae are differentially pigmented with the base of the filament or flagellum darker than the bulb or club (Guerra et al. 2012).
Figure 4-44. Scanning Electron Microscope (SEM) photos of the Monarch butterfly antennal club. A) Segments of the club are void of sensilla. B) Larger trichoid sensilla measure approximately 30 μm from base to tip. C) The antennal club is covered with clusters of coeloconic sensilla that project from the surface of the antenna and are spaced less than 20 μm apart. These clusters may be involved with light perception, as they are the only homologous sensilla appearing in relative abundances between all antennal regions. The black circle shows a patch of smaller trichoid sensilla representing a third type of antennal sensilla present on Monarch antennae. Photos courtesy of J. Court Whelan.
Figure 4-45. Side and above views of the coeloconic sensilla described in Hallberg (1981).
Figure 4-46. Scanning Electron Microscope (SEM) photos of the Monarch butterfly antennal filament. A) Low magnification view of antennal filament. B) A closer look reveals that the visible surface of the Monarch antenna is comprised of cover scales. C) While no trichoid sensilla appear on the filament like they do on the club, there are indeed the same clusters of coeloconic sensilla. D) As with the club, coeloconic sensilla are spaced less than 20 μm apart. E) A broken scale is surrounded by numerous clusters of coeloconic sensilla. Photos courtesy of J. Court Whelan.
Table 4-15. Monarch antennae exhibit different structures on their club and filament. Of those structures that are homologous, they often differ markedly in abundance between the two antennal regions. Only one type of antennal sensilla was observed to be in relatively equal abundances between the two regions.

<table>
<thead>
<tr>
<th></th>
<th>Club</th>
<th>Filament</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Trichoid Sensilla</td>
<td>Common</td>
<td>Very limited</td>
</tr>
<tr>
<td>Small Trichoid Sensilla</td>
<td>Limited</td>
<td>Very limited</td>
</tr>
<tr>
<td>Coeloconic Sensilla</td>
<td>Common</td>
<td>Common</td>
</tr>
<tr>
<td>Scales</td>
<td>Absent</td>
<td>Common</td>
</tr>
</tbody>
</table>
Figure 4-47. Scanning Electron Microscope (SEM) photos of the Queen butterfly antennal club. A) Coeloconic sensilla are found on the surface of the antennal club and spaced less than 20 μm apart. B) Larger trichoid sensilla measure approximately 30 μm from base to tip and are present on the club. C) In addition to coeloconic sensilla on the club, small trichoid sensilla project from the antennal surface in patches measuring approximately 100 μm by 100 μm (within black circle). Photos courtesy of J. Court Whelan.
Figure 4-48. Scanning Electron Microscope (SEM) photos of the Queen butterfly antennal filament. A) Both large trichoid sensilla and coeloconic sensilla are present on the filament. B) In contrast to the club, the filament exhibits many scales protruding from pores in the antennal wall. C) Unlike the Monarch, trichoid sensilla are present on the filament of the antennae. Similar to the Monarch, coeloconic sensilla are present at all antennal regions, and spaced less than 20 μm apart. Photos courtesy of J. Court Whelan.
Table 4-16. Queen antennae exhibit different structures on their club and filament. Of those structures that are homologous, they often differ in abundance between the two antennal regions. Like the Monarch, coeloconic sensilla are common on both the antennal club and filament.

<table>
<thead>
<tr>
<th></th>
<th>Club</th>
<th>Filament</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Trichoid Sensilla</td>
<td>Common</td>
<td>Common</td>
</tr>
<tr>
<td>Small Trichoid Sensilla</td>
<td>Common</td>
<td>Limited</td>
</tr>
<tr>
<td>Coeloconic Sensilla</td>
<td>Common</td>
<td>Common</td>
</tr>
<tr>
<td>Scales</td>
<td>Absent</td>
<td>Common</td>
</tr>
</tbody>
</table>

Table 4-17. Light attenuation chart. As the distance between the light emitting device and the subject increases, light attenuates, or decreases in intensity dramatically. Known as the inverse squares law, as the distance is doubled between the light source and subject, the light intensity is quartered.

<table>
<thead>
<tr>
<th>Meters from Subject</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>% of Lux</td>
<td>1.0000</td>
<td>0.2500</td>
<td>0.1111</td>
<td>0.0625</td>
<td>0.0400</td>
<td>0.0278</td>
<td>0.0204</td>
<td>0.0156</td>
<td>0.0123</td>
<td>0.0100</td>
</tr>
</tbody>
</table>
The rise of entomological ecotourism has been an outcome of many centuries of rich tourism history. As motivations for travel expanded and tourism evolved throughout the early Egyptian, Greek, and Roman empires, we saw the first signs of travel for the sake of pleasure. Originally reserved for traders, businessmen, and armies, travel expanded throughout these early empires, particularly as new technologies in vehicle construction, road building, and ocean transport enabled faster, safer, and more comfortable transit. With greater levels of infrastructure came new attractions to serve as destinations for early tourists. During the last several millennia B.C., these attractions were largely festivals, games, and historic monuments. However, with the rise and domination of the Roman Empire, we began to see the formation of a true tourist culture and the birth of the modern day holiday concept. As travel and tourism expanded, natural wonders, such as raging rivers, volcanic fissures, and collections of exotic flora and fauna began to captivate the public, putting forth the natural world and the environment as a tourist destination. With unprecedented wealth and prosperity, an increasingly large percentage of society enjoyed tourism during the height of the Roman Empire. Seaside resorts, mountain vacation homes, and streets lined with restaurants, spas, and inns marked the firm establishment of what many view as the foundation for modern-day tourism.

With the rise of the Grand Tour era many centuries later, we saw another distinct shift in the motivations for travel. Whereas travel was historically reserved as a privilege for the wealthy elite, the Grand Tour era saw travel as a way to propel oneself into the wealthy elite. Tourism, for the first time, was used as a tool for acquiring skills,
experience, and education. At the start of the Grand Tour era, itineraries emphasized the cultural centers throughout Western Europe, concentrating on social betterment and learning about fashion, etiquette, and art. However, as the 18th century drew to a close, another distinct transition occurred in motivations for travel and tourism. The Grand Tour began to integrate nature as a core component to the tour itinerary and experience-building process. It was at this time that iconic figures emerged who would prove to shape the way we look at life and the natural world forever. While the word ecotourism would not evolve until several centuries later, the period in which Darwin, Bates, Wallace, and Humboldt would make their marks was perhaps the very beginning of our modern-day concept of ecotourism. They may have called themselves explorers, scientists, or naturalists, but their reverence and intrigue for natural areas, indigenous cultures, science, and conservation embodied much of the same beliefs and attitudes as found in today’s ecotourists.

Not only could these early naturalists be considered pioneers of ecotourism, but they could also be deemed pioneers of entomological ecotourism. Defined as nature-based tourism that incorporates insect education as a means to improve environmental and community welfare, entomological ecotourism may actually represent one of the earliest forms of ecotourism in general. As early as the 19th century, field clubs throughout Europe were formed for the purpose of assembling enthusiastic naturalists to share in their collective passion for insects and all things nature-related. However, they were not the sort of clubs that met solely within lecture halls and coffee houses to discuss current topics and publications like so many others at the time. The members of these clubs were dedicated to exploring the natural world through actively engaging
in excursions and expeditions to natural areas. In fact, these field excursions were the principal attraction of the clubs, and by 1873, over 100 of these organizations existed in Britain alone. The passion with which these early entomological ecotourists explored their world was not confined to Britain or Europe, or their individual field club and the concept of insects being featured in the ecotour would persist through to the present, only expanding as new entomological ecotour models would emerge.

Until now, entomological ecotourism was an all-encompassing term that was a model for integrating insects into the ecotour. This dissertation has taken the overall concept several steps further and identified a series of separate models within the greater realm of entomological ecotourism. Models were tested and a number of conclusions were made from case studies. Of particular importance was the overwhelming acceptance of such models by the ecotourism market and industry. These studies function as a baseline for future entomological ecotourism endeavors, from which new models and new variations within each model may be formed.

Entomological ecotourism has the ability to create a culture of conservation, both with the host communities/countries, as well as the visiting ecotourists. Details of this outcome will depend largely on the execution of the ecotour and the experience had by the ecotourists. Ecotourism guides are the ambassadors to a particular area or country and are the single most important factor determining the impact that ecotourism has on visitors. While the various models in Chapter 2 detail ecotours that focus on specific entomological attractions, be it the One Species/One Phenomenon Model, the Paired-Interest Model, or the Research Associate Model, there is no reason why insects should not be more involved in all ecotourism. For example, when visiting the Everglades of
Florida, alligator sightings will almost always invoke an enthusiastic response by a group’s tour guide, who may then initiate an interpretive discussion about alligator biology, behavior, or conservation. While charismatic megafauna may be the main attraction to such a tour, the sightings of a giant Belastomatid waterbug climbing on vegetation or a Monarch butterfly nectaring on a nearby flower offer similar opportunities for enthusiastic interpretation by the guide. This will ultimately serve to benefit the ecotour, the ecotour participants, and even the guide, when he/she appears more knowledgeable and experienced (and perhaps compensated better at the end of the tour!).

If insects are to be appropriately integrated into general ecotourism (i.e., ecotourism that focuses on general wildlife, landscapes, natural attractions, etc.), guides must be properly trained and confident with insect interpretation. Guides need not be versed at identifying every single insect encountered on an ecotour, for this could not only be a massive undertaking from a training standpoint, but general ecotourists are not likely to be interested in the exact scientific name of a fungus gnat that has landed on someone’s water bottle. Instead, training should prioritize the most charismatic insects that exhibit unique life histories, behaviors, appearances, or cultural traditions associated with them. Although only a few of such insects may be encountered on a typical ecotour, there are still general insect-related topics that may be initiated by the ecotour guide solely by encountering signs of insect presence. In order for entomological ecotourism to ascend to the next level, focused efforts should be made at properly training ecotour guides. Not only are they in charge of providing context to what is seen during a hike in the rainforest or a visit to a butterfly farm, but they also
represent key figures in the local communities. They are often paid well and highly respected. Conservation-minded guides create conservation-minded cultures.

The merits of ecotourism extend far and wide. Ecotourism is heralded as one of the more effective solutions to environmental conservation because of the fact that it adds value to a natural area. The philosophy behind ecotourism is that people want to visit pristine wilderness that is capable of supporting dramatic landscapes and charismatic flora and fauna. For this, ecotourists will pay entrance fees, they will stay at local lodges, eat at local restaurants, and employ local guides to spot wildlife and educate them on what they are seeing. However, as ecotourism continues to grow, concerns are raised about possible negative impacts that it may have on the environment. As seen in Chapter 4, studies have suggested that there are indeed negative side effects to ecotourism, although, these scientifically controlled studies are still few in number and need to be expanded. One of the goals of this dissertation was to research the possible negative effects of specific ecotourist behaviors that occur within the Monarch butterfly sanctuaries in Mexico. The results were surprising in several ways. Not only was it unexpected for Monarchs to exhibit absolutely no reaction to punctuated sound in a variety of decibel levels at both standard and low frequencies, but they also exhibited an increase in lifespan when subjected to camera flashes. Monarchs were seen to respond to flash frequently, with nearly one out of every three flashes resulting in a disturbance reaction of some kind. Reactions included antennal twitches, body twitches, walking, and flying. Two of these reactions predominated, and the frequency with which Monarchs responded by antennal twitches reinforces what Merline et al. (2009) and Guerra et al. (2012) have suggested, in that Monarch
antennae may be heavily involved in the perception of light. While Monarchs failed to respond at all to punctuated sound, they did appear to be repelled by sustained noise, as was indicated by their tendency to spend more time in quieter subcages. What is even more interesting is that this effect became even more pronounced with each hour in the eight-hour day. With overwintering Monarchs exposed to crowd noise for a similar duration each day for well over 100 days each year, there is reason to believe that unabated crowd noise levels within the colonies could affect the migration event.

These studies have certainly raised more questions than they have answered. For instance, the linkage between Juvenile Hormone (JH) and longevity is supported throughout the literature, but no prior studies have examined the effects of flash photography (i.e., punctuated high intensity light exposure) on the levels of JH produced by the insect endocrine system. Should there be a correlation, this finding could have wide-ranging impacts across many areas of study, from the management of pest insect populations via JH treatments, to basic insect physiology.

**Future Research**

The results from these tests on Monarch butterflies indicate that some side effects of ecotourism within the Monarch sanctuaries appear to have minimal impacts on the butterflies, while others may be more pronounced. These studies also serve to highlight the need for additional research, as other issues exist and necessitate further studies. Already discussed in Chapter 4, continuing these impact studies is essential. By measuring ecotourism effects on overwintering Monarchs over the entire season, and testing the effects of flash photography on Monarch navigational abilities and other activities, a more complete understanding of flash photography’s effects is possible.
More impact-based research on other aspects of Monarch ecotourism is also needed. One area that requires investigation is the impact of walking and introduction of horse trails created throughout the overwintering grounds. Although impacts are relatively confined to marked trails, these trails change throughout each season. As the colonies move, park guards modify trails in order to link the entrance station to the central colony areas. While Monarchs tend to roost in predictable locations from year to year, new trails must be made for the purposes of mitigating trail degradation and soil erosion. In addition, Monarchs will sometimes roost in areas not previously accessible via existing trails. For this, new ones must be made, at the expense of displacing native vegetation, which may be composed of nectar and food sources used by Monarchs and other wildlife. Studies that focus on trail use and the rate of new trail construction would provide critical information on forest usage by ecotourism. Obviously the hope is that these impacts are also benign, but with the potential displacement of native vegetation, as well as ongoing soil erosion problems, usage impacts must be more clearly understood in order to yield a responsible management plan for trail systems within the Monarch sanctuaries.

**The Future of Entomological Ecotourism**

**Poised for Growth**

The future of entomological ecotourism is promising. Ecotourism in general is an industry that is witnessing exponential growth that shows no signs of slowing. In fact, world ecotourism has been shown to grow an average of 20% to 34% from year to year, with landmark years exhibiting a 300% expansion compared to general tourism (Mastney 2001, World Tourism Organization 2004). This proliferation is tangible, with new hotels, lodges, restaurants, national parks, and transportation services being
developed to provide services to the increasing demand from ecotourists. There is also an intangible component, largely reflected by new opportunities for employment, education, and social mobility in developing nations. Ecotourism is estimated to be worth 500 billion U.S. dollars annually, with most of this exponential growth occurring in developing nations (The International Ecotourism Society 2006).

As ecotourism continues to expand in size, scope, and popularity, it is only natural for new niche markets to emerge within the greater realm of ecotourism. This dissertation serves to emphasize the very real potential that exists for entomological ecotourism by creating novel opportunities in a dynamic ecotourism market. During the five years of experimental case studies on various entomological ecotour models, consistently high participation levels in personally organized diverse entomological ecotours firmly document the viability of such programs. Using both conservative and innovative strategies for advertising and marketing, as detailed in Chapter 2, a total of 465 participants engaged in the One Species/One Phenomenon, Paired-Interest, and Research Associate models between 2007 and 2012. The possibility for expansion is evident, as new tour models are developed and new opportunities for existing tour models are discovered. In addition, with continuing research on marketing strategies that maximize awareness of these entomological ecotours, this number could quickly double several times over. This dissertation is intended to serve as a tool for others to utilize in creating additional entomological ecotour programs. The background, methodology, and strategies detailed within serve as a foundation for new students and professionals upon which to build. Should entomological ecotourism expand as rapidly as ecotourism currently is (which it likely will, given the documented parallel success),
the education and conservation implications could be tremendous for not only insects, but biodiversity in general.

Our knowledge of the natural world will only continue to grow. As new tools emerge that aid in learning, from electronic books, to smartphone and tablet applications, to websites and new guidebooks, they will serve to foster more appreciation for the natural world and further encourage ecotourism. This relationship is reciprocal, as it is often the eager ecotourist that is inspired by previous nature experiences to return home and create the next new iPhone application that helps to identify butterflies in state parks, or wildflowers on hiking trails. Thus, as new ecotourism opportunities emerge (i.e., entomological ecotourism), new resources will become available to perpetuate and expand the learning and discovery process. In fact, it is the intention of this author to use such tools to create and promulgate entomological ecotourism training materials. By using various parts of this dissertation immediately, a variety of extension booklets, guide training manuals, and journal publications will be produced to further serve the goals outlined in these chapters. In addition, the content of this dissertation will be used to create the first textbook on entomological ecotourism. This will serve to perpetuate the educational opportunities available to entomology and ecotourism scholars. The direction that future work takes is paramount in maintaining momentum and continuing to find novel ways to integrate insects in the ecotour as the field expands exponentially.

**Future Initiatives**

The linkage with academia is critical to the future of entomological ecotourism. Although the concept of entomological ecotourism stretches back for hundreds of years, it is still considered a young idea and an even younger academic discipline. We stand
at the front lines of securing a perpetual connection between the ecotourism industry, one which heavily relies upon education and sustainability, and one where higher education programs can serve many goals. This connection will facilitate the research initiatives necessary to ensure sustainability from both a social and environmental perspective. In addition, an academia-industry connection will promote training of students at all levels. These students may be naturalist guides interested in receiving higher education to enhance the content of their tour programs. Or, they may be researchers eager to learn about monitoring techniques and mitigation strategies for visitor impacts in natural areas. Programs intended to provide instruction on these fronts may be condensed into seminars or weekend workshops, or full semester-length courses for university students. This dissertation will serve as a template for many instructional initiatives capable of training new generations of entomological ecotour operators (Chapter 2), guides (Chapter 3), and researchers (Chapter 4).

**Importance of Entomological Ecotourism**

The promises of future expansion with entomological ecotourism are convincing, but why is this a good thing? The merits of this unique brand of nature travel have been discussed, but it is worthwhile to end this dissertation by summarizing the many answers to one key question. Why it is important to engage in, promote, and generally support entomological ecotourism? Before continuing, it should be restated that entomological ecotourism is defined as nature-based tourism that incorporates insect education as a means to improve environmental and community welfare.

Entomological ecotourism serves several purposes. The first, and most obvious, is that integrating insects into an educationally-based ecotour increases an individual ecotourist’s knowledge about insects. With greater knowledge comes greater
appreciation and greater awareness. Although this is inherently a good thing, it leads to an even more important benefit. Insects serve as a foundation for understanding the complexities of natural areas and the natural world in general. Insects function in many critical roles in ecosystems, such as pollination, nutrient cycling, decomposition, and many more. In addition, they are an important source of food for a great many other animals, and they themselves have tremendous impacts on plant and animal communities via their feeding habits in ecosystems around the world. Insects are indispensible, and by understanding their diversity, as well as the variety of roles that they play in the world, ecotourists and ecotourism guides will have more accurate views of nature in general. The promotion of environmental and scientific literacy is paramount in today's world.

An increase in one's understanding and awareness of insects also serves the goal of the conservationist. The world is losing richness in biological diversity at an alarming rate. With insects being one of the most numerous and species-rich groups of animals on earth, it is only logical to include them in conservation efforts. Many insects are keystone species in the environments where they live, making them all the more critical for the long-term health of our planet and its many diverse biomes. Nevertheless, insects are often over-looked and underrepresented when it comes to conservation work. By increasing our knowledge of insects, as well as promoting their awareness through entomological ecotourism, we may have a better grasp on global biodiversity threats and solutions. As the saying goes, you cannot save what you do not know.

Finally, entomological ecotourism serves to create new opportunities for ecotourism. The benefits of ecotourism have been addressed throughout this
dissertation, but center around the idea that ecotourism adds value to natural areas and wildlife. Whereas development may yield short-term gains through the sale of natural resources, ecotourism functions to keep wilderness areas pristine, as higher quality areas command higher prices for ecotourism services. Conversely, lower quality areas make less money. This is an easily translatable concept to local communities in both developed and developing nations. When new opportunities arise for which visiting ecotourists are willing to pay, local communities benefit directly. Those people who participate in an entomological ecotour are likely not to have visited a particular area, village, or country had it not been for a particular entomological attraction. They may not have even contributed to ecotourism in any way shape or form, had it not been for that particular butterfly-watching tour or Research Associate ecotour that they joined. More opportunities mean more growth for ecotourism.

Entomological ecotourism is not necessarily a panacea to all conservation concerns or social welfare problems, nor does it guarantee the perpetual preservation of wild areas. However, when local people realize the economic incentives behind conserving nature, there is tremendous justification for doing so. In addition, ecotourism dissuades destructive processes like deforestation and intensive development, which have historically been the most viable ways to yield significant monetary gains from natural areas. Now, a new tool exists and local communities are realizing its potential to transform their lives for the better. As entomological ecotourism continues to grow and provide novel opportunities for employment, conservation, and education, the world will listen and all will benefit.
LIST OF REFERENCES


Caldwell, M. C., and D. C. Caldwell. 1962. Factors in the ability of the northeastern pacific green turtle to orient toward the sea from the land a possible coordinate in long-range navigation. Contributions in Science 50:5–27.


Cambefort, Y. 1984. Etude ecologique des coleopteres Scarabaeidae de Cote d'Ivoire. Travaux des Chercherurs de la Station de LAMTO, 3, University of d'Abidjan, Abidjan, Cote d'Ivoire.


Casson, L. 1994. Travel in the ancient world. The Johns Hopkins University Press, Baltimore, Maryland, USA.


Ceballos–Lascurain, H. 1996. Tourism, ecotourism, and protected areas. IUCN Publication Services Unit, Gland, Switzerland.


Combe, G. 1850. The constitution of man. Silius Andrus and Son, Hartford, Connecticut, USA.


McAdam, J. L. 1863. Notes on practical road making and repairing for the information of surveyors, to be appointed by the new highway act of 1862. University of Michigan, Ann Arbor, Michigan, USA.


Murphy, T. 1985. Telemetric monitoring of nesting loggerhead sea turtles subjected to disturbance on the beach. Fifth Annual Workshop on Sea Turtle Biology and Conservation, Waverly, Georgia, USA.


Ritland, D. B. 1991. Revising a classic butterfly mimicry scenario: demonstration of Mullerian mimicry between Florida Viceroyos (Limenitis archippus floridensis) and Queens (Danaus gilippus berenice). Evolution 45:918–934.


turtles on an urban beach: correlates of nest placement. Journal of Herpetology 29:560–
567.

Books, Essex, UK.

Sands, W. A. 1973. Termites as pests of tropical food crops. Pest Articles and New

butterfly (Ornithoptera richmondia): a community conservation project. Memoirs of the

Sands, D. 2008. Conserving the Richmond birdwing butterfly over two decades: where


the baboons. Simon and Schuster, New York, New York, USA.

melanogaster by photoperiod and moderately low temperature. Journal of Insect


(Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae.

Schuurman, G. and J. M. Dangerfield. 1996. Mound dimensions, internal structure, and
potential colony size in the fungus growing termite Macrotermes michaelsensi (Isoptera:

of Biology 17:271–289.

descriptions, distributions, and natural history. University of Florida Press, Gainesville,
Florida, USA.

Scoble, M. J. 1992. The Lepidoptera: form, function, and diversity. Oxford University
Press, New York, New York, USA.


Whittaker, R. H. 1975. Communities and ecosystems. MacMillan, New York, New York, USA.


BIOGRAPHICAL SKETCH

Court Whelan was born in Clearwater, Florida. His love for nature and a passion for living things began early in his life through his participation in nature programs, ranging from summer camps to school field trips. His formal training in biology and entomology began with his undergraduate career at the University of Florida and completed a Bachelor of Science degree in entomology and nematology in May of 2005. That same year, he was awarded with a four-year Alumni Fellowship for Graduate Studies and accepted into the Ph.D. program at the University of Florida, which allowed him to pursue his passion for both entomology and ecotourism at the graduate level. With guidance from the chairman of the Department of Entomology and Nematology, Dr. John L. Capinera, Court began working with his advisors, Dr. Thomas C. Emmel, and Dr. Jaret C. Daniels on forming a new discipline with new research opportunities in the emerging field of ecotourism, while maintaining an entomology foundation. A new graduate degree, termed ecotourism entomology, was created within the Entomology Department at the University of Florida, thus permitting the previously uncoupled relationship between these two disciplines. Encompassing new goals and novel concentrations in the world of entomology, this program continues to make inroads towards a more interdisciplinary campus at the University of Florida. During his graduate studies, Court completed a Master of Science degree in this new discipline in August of 2008. Now having completed a Ph.D. in the studies of entomological ecotourism, it is his goal to continue his efforts in promoting the conservation of natural areas and cultures across the globe through sustainable ecotourism. By remaining heavily involved in both the academic and business sides of the entomological ecotourism world, he intends to continue to shape the industry, as well as the academic
component in order to foster new partnerships and promote higher conservation standards. With the industry modeled after sound academic research, these initiatives will create more opportunities for local community welfare, thus preserving our natural world by way of this unique niche of nature-based tourism.