EFFECTS OF MITES ON THE PHYSIOLOGY AND PERFORMANCE OF
THE FLORIDA SCRUB LIZARD (SCELOPORUS WOODI)

BY

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by

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Despite the emphasis on the individuality of research in our field, it is remarkable how collective an enterprise it is. I owe a great debt to my advisor Lou Guillette, who prodded me to think more mechanistically (no mean feat). Other committee members included Rich Kiltie, who was always available for statistical consultation; Carmine Lanciani who was a great source of information; Buzz Holling who taught me to think big and Jack Putz who supplied important perspective. I would also like to thank Roger Anderson who has been a remarkable collaborator, mentor and friend.

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TABLE OF CONTENTS

ACKNOWLEDGMENTS........................................................................................................ iii

LIST OF TABLES................................................................................................................ vii

LIST OF FIGURES............................................................................................................ viii

ABSTRACT........................................................................................................................ xi

CHAPTER 1 INTRODUCTION..............................................................................................1
  The Acarina and Reptiles.............................................................................................. 2
  Rationale for the Study................................................................................................. 5
  Study Animals............................................................................................................... 7
  Study Area.................................................................................................................... 9

CHAPTER 2 CHIGGER INFESTATIONS, EVAPORATIVE WATER LOSS AND THE POSSIBLE ADAPTIVE SIGNIFICANCE OF NUCHAL POCKETS................................................................................ 28
  Introduction................................................................................................................ 28
  Methods....................................................................................................................... 29
  Results......................................................................................................................... 32
  Discussion................................................................................................................... 33

CHAPTER 3 THE EFFECTS OF MITES ON THE MORPHOLOGY, PHYSIOLOGY AND PERFORMANCE OF THE FLORIDA SCRUB LIZARD, SCELORPORUS WOODI........................................................................ 42
  Introduction................................................................................................................ 42
  Methods....................................................................................................................... 45
  Results......................................................................................................................... 49
  Discussion................................................................................................................... 54

CHAPTER 4 EFFECTS OF ADULT MITES ON LIZARD METABOLIC RECOVERY FROM EXERCISE.................................................................................................................. 74
  Introduction................................................................................................................ 74
  Methods....................................................................................................................... 76
  Results......................................................................................................................... 77
  Discussion................................................................................................................... 77
LIST OF TABLES

Table 1.1. Aspects of acari-reptile relationships.................................21
Table 1.2. Duration of Eutrombicula alfrediuegesi life history stages...............................................................26
Table 1.3. Geckobiella texana life history stages........................................26
Table 1.4. A comparison of scrub and high pine......................................27
Table 3.1. Regressions of performance variables against hematocrit values for S. woodi.........................................................73
Table 3.2. Summary of average maximum performance values for male and female S. woodi in July and August...............................74
Table 3.3. Average intensity of Geckobiella texana on Sceloporus woodi during and after the reproductive season.................................74
Table 4.1. Effect of treatment with ivermecten on lizard performance measures........................................................................79
Table 5.1. Histories of sites in Ocala National Forest used to assess mite prevalence..........................................................98
Table 6.1. Variables that affect virulence (after Ewald 1994)......................121
LIST OF FIGURES

Figure 1.1. The life cycle of *Eutrombicula alfredugesi* (after R. Loomis, unpub. and Conant 1975).................................13

Figure 1.2. Distribution of scrub (filled in black) in Florida, with the Ocala National Forest and Big Scrub regions, where this study was conducted, labelled with larger type (after Myers 1990).
..................................................................................................................14

Figure 1.3. Average maximum and minimum monthly temperatures in Ocala, Florida (1961-1990)..............................................15

Figure 1.4. Average monthly precipitation in Ocala, Florida (1961-1990)..................................................................................16

Figure 1.5. Coefficient of variation of average precipitation (CVPPT) for Ocala, Florida.................................................................17

Figure 1.6 Marion County, Florida (shaded in black)................................18

Figure 1.7. Ocala National Forest within Marion County, Florida.................................................................................................19

Figure 2.1 Scanning electron micrograph (SEM) of a left nuchal pocket of *Sceloporus woodi* at 50X magnification..............................37

Figure 2.2. Dehydration chamber for small lizards........................................38

Figure 2.3. Stylostomes in longitudinal (left) and cross-section (right) in a nuchal pocket of a *Sceloporus woodi* (1 cm = 40 μm). .....39

Figure 2.4. *Eutrombicula alfredugesi* (chiggers) attached to the nuchal pocket of *Sceloporus woodi*. Extensive inflammation surrounds the stylostomes (1 cm = 40 μm).............................................39

Figure 2.5. Edge of nuchal pocket showing the localized inflammatory response to chigger infestation.............................................40
Figure 2.6. Regression of evaporative water loss on mite intensity

Figure 3.1. The morphology-performance-fitness paradigm (after Miles 1994 and Garland 1994).

Figure 3.2. Venn diagrams of model building strategies.

Figure 3.3. Stylostome (feeding tube) of an adult female Geckobiella texana into the thigh of Sceloporus woodi.

Figure 3.4. Inflammatory reaction from the attachment of adult Geckobiella texana behind the knees of Sceloporus woodi.

Figure 3.5. Inflammatory reaction from the attachment of adult Geckobiella texana behind the knees of Sceloporus woodi.

Figure 3.6. Hematocrit for parasite-laden lizards after being sprayed with a solution of ivermecten (mites-removed) or water (mites-retained).

Figure 3.7. Plasma osmolarity for parasite-laden lizards after being sprayed with a solution of ivermecten (mites-removed) or water (mites-retained).

Figure 3.8. Turn-around distance (m) regressed against hematocrit.

Figure 3.9. Fast-run distance (m) regressed against hematocrit.

Figure 3.10. Endurance, as indicated by total distance (m) covered by S. woodi individuals in a running trial, regressed against hematocrit.

Figure 3.11. The best performance of males in July as function of adult mite intensity. Maximum speed declines with increasing mite load.

Figure 3.12. Best performance (maximum speed m/s) of males in August.

Figure 3.13. Logistic regression of running tactic as a function of mite intensity (number of mites per lizard host).

Figure 3.14. Endurance of males in July as a function adult mite intensity.
Figure 3.15. Endurance of males in August as a function of adult mite intensity.........................................................71

Figure 3.16. Paired t-test of maximum speed in m/s before (pre-) and after (post-) mite removal with ivermecten..........................72

Figure 3.17. Paired t-test of total distance (endurance) before and after mite removal.........................................................73

Figure 3.18. The morphology-performance-fitness paradigm extended.................................................................73

Figure 4.1. Maximum endurance as a function of mite intensity........79

Figure 4.2. Minimum recovery time as a function of mite intensity..................................................................................80

Figure 5.1. Longleaf pine at Kerr Island, ONF in May 1994...........95

Figure 5.2. Turkey oak at Kerr Island, ONF in May 1994.............96

Figure 5.3. A typical edge between a young scrub and mature sand pine........................................................................97

Figure 5.4. Chigger intensity (number of chiggers per lizard) of Sceloporus woodi by habitat at Kerr Island in a) May, 1994...........99

Figure 5.5. Diel patterns of chigger activity, June 1997.................100

Figure 5.6. Monthly intensity of chiggers on male lizards, 1996......101

Figure 5.7. Monthly intensity of chiggers on female lizards, 1996.....102

Figure 5.8. Comparison of Geckobiella prevalence in roller-chopped (n = 4) and unchopped (n = 4) sites..................................103

Figure 5.9. Possible effects of roller-chopping on vegetation spacing..................................................................................104

Figure 6.1 Summary diagram.................................................................120
Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

EFFECTS OF MITES ON THE PHYSIOLOGY AND PERFORMANCE OF THE FLORIDA SCRUB LIZARD (*SELOPORUS WOODI*)

By

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May, 1999

Chairman: Dr. Louis J. Guillette, Jr.
Major Department: Zoology

Parasitology has enjoyed a renaissance in biology over the last decade under the aegis of modern evolutionary theory. Much of this reinvigoration is dependent on parasites causing measurable pathology, which until recently was thought to be relatively rare because group selectionist thinking predicted that parasites should evolve towards benignness. Ectoparasites are model organisms for studying effects on hosts because their intensities (number of parasites/host) are easily manipulated. Although pathologies of mites and ticks on reptiles are well documented, the mechanisms and implications of their non-lethal effects have not.
I found that chiggers (*Eutrombicula alfreddugesi*) increase the evaporative water loss of their lizard hosts, *Sceloporus woodi*, in north central Florida, by causing inflammation that probably disrupts the water impermeable lipid layer in their integument. The nuchal pockets of lizards may reduce water loss by localizing chigger infestations in areas of the skin that form enclosed spaces that become easily saturated with water vapor.

*Geckobiella texana* mites on *Sceloporus woodi* cause inflammation of muscles and nerves around the knees where they tend to attach. Adult females suck blood and appeared to increase the viscosity of the blood in the lizards by reducing fluid volume. Osmolarity did not seem to be affected. Both inflammation and blood loss may reduce host physiological performance. Maximum sprint speed and endurance were reduced when mites were present. Heavily infested lizards were more likely to turn evasively than run away from a threat. Mites also reduced the ability of lizards to recover from exhaustion.

Human activities affect chigger and mite populations. Fire suppression may result in high chigger populations. Chiggers are dense at ecotones, thus creating "edge" for deer may also create preferred habitat for chiggers. Lizards had higher mite prevalence in roller-chopped sites than burned or unchopped sites.

Habitat modification may select for high virulence of parasites by altering transmission rates among hosts. When combined with stress, loss of genetic variation, and decreased immunity from environmental contaminants, high virulence may have greater effects on host populations. By recognizing that virulence can evolve, we may be able to select for less virulent pathogens.
CHAPTER 1
INTRODUCTION

Over the last decade and a half, the study of parasites has enjoyed a renaissance in the ecological and evolutionary sciences (Lehmann 1993). Parasites have been linked to the evolution and maintenance of sex (Lively et al. 1990; Moritz et al. 1991), and many aspects of sexual selection (e.g., Hamilton and Zuk 1982; Møller 1990; Lefcort and Blaustein 1991; Folstad and Karter 1992). Careful application of individual selection theory has led to critical thinking on mode and frequency of pathogen transmission in the evolution of virulence (Ewald 1983, 1994). Parasites and disease that were once thought to evolve toward benignness "for the good of the species" can in fact evolve towards extreme virulence. The emergence of new diseases (e.g., HIV, Ebola, Hanta virus, and Lyme disease) and the reemergence of old ones (e.g., tuberculosis, cholera, and malaria) have biologists in many disciplines thinking seriously about pathogens and parasites again (Garrett 1994).

Ectoparasites are model systems for studying host-parasite interactions because they are relatively easy to study, can cause pathologies with ecological and evolutionary consequences, and have the potential to interact with other parasites by acting as vectors. Ectoparasites are also relatively amenable to experimental manipulation. The first part of this introduction is a review of what is known about acarine (i.e., tick and mite) interactions with reptiles. It is modeled after other reviews (Reichenbach-Klinke and Elkan 1965; Frank 1981), but rather than taking an acarine systematist's point of view, it focuses
on types of interactions among acari, reptiles and other parasites or pathogens. The second part of this introduction presents a rationale for this study by way of a "classification" of acarine-lizard studies that attempts to encapsulate what has been done and points to some gaps in our understanding. Finally, the third part of the introduction includes some background information on the species and landscape involved in this study.

The Acarina and Reptiles

The Acarina are found in nearly all habitats available to plants and animals. They can be found in terrestrial, aquatic (including hot springs) and marine habitats, living internally and externally on both vertebrates and invertebrates (Baker and Wharton 1952). Among the metazoa, perhaps only nematodes are more ubiquitous.

Within the reptilia, for example, ticks have been reported on marine iguanas (Amblyrhynchus cristatus), (Vercammen-Grandjean 1965) and sea snakes (Laticauda spp., Zann et al. 1975). Entonyssid mites are found in the lungs and trachea of snakes (Reichenbach-Klinke and Elkan 1965). The mite Mabuyonyssus parasitizes the nostrils of reptiles (Reichenbach-Klinke and Elkan 1965). The aptly named cloacaridae are found in the cloacal mucosa of turtles and are probably venereally transmitted (Frank 1981). The majority of ticks and mites on reptiles are found externally.

Some ectoparasitic mites are very host specific (e.g., Geckobiella mites have only been found on lizards of the genus Sceloporus). Others are generalists: e.g., the chigger, Trombicula batatas in the US infests about 100 species of vertebrates including reptiles and amphibians (Frank 1981). The chigger, Eutrombicula alfreddugesi, has been observed on 126 vertebrate species (Benton 1987). Different stages in the life cycle frequently specialize on
different foods. As juveniles and adults, ticks are blood feeders. As larvae and nymphs, mites are tissue feeders. As juveniles and adults, some are blood feeders, whereas others, like trombiculid mites, are free-living.

Table 1.1 summarizes the different kinds of relationships and pathologies attributed to mites and ticks on reptiles. Much of its content is outlined below.

**Direct Impacts**

Host dehydration, blood loss, anemia and even death by exsanguination (Mader et al. 1986) are common effects of ectoparasites (Frank 1981; Salvador et al. 1996; Dunlap and Mathies 1993). Ticks facilitate feeding by engaging in host manipulation with salivary secretions that include immunosuppressants, analgesics, anticoagulants and antiplatelet aggregatory compounds (Bowman et al. 1996). Because ticks are essentially giant mites, mite saliva probably has similar components with like effects. Heavy infestations of mites can present serious challenges to their hosts not only in terms of what is removed, but also in what is added.

Despite these manipulations by the ticks, inflammation, integumental lesions, dermatitis and granuloma formation do affect the reptilian host (Arnold 1986; Bauer et al. 1990; Goldberg and Bursey 1991a, 1993; Goldberg and Holshuh 1992). Tick saliva can cause paralysis in some reptiles (Frank 1981) and irritation caused by mite saliva of experimentally applied mites has even induced tail autotomy in geckos (Oliver and Shaw 1953). *Ixodes asanumai* ticks on the skink *Eumeces okadae* has been reported to cause limb muscle atrophy (Hayashi and Hasegawa 1984a).

Heavy infestations also lead to behavioral changes in the host. Anorexia has been documented (Klingenberg 1993; Mader et al. 1986; pers.
obs.). Effects may even be seen in the next generation. Sorci et al. (1994) found alterations of behavior and performance in offspring of infested females.

**Mites and Ticks as Vectors**

Mites and ticks are efficient vectors of disease. The bacteria *Aeromonas hydrophila*, which causes a fatal, hemorrhagic septicemia in snakes, is transmitted by *Ophionyssus* mites (Camin 1948). Ixodid and argasid ticks can transmit the spirochete that causes Q-fever (Frank 1981). Viruses and protozoans are also transmitted by mites and ticks (Sekevoya et al. 1970; Frank 1981). Klein (1985) was able to infect *Sceloporus undulatus* with the coccidium *Shellackia* by force feeding it *Geckobiella texana* mite vectors. *Leishmania* and *Hepatozoon sauromali*, a hemogregarine, can infect chuckwallas via *Hirstiella* mites (Lewis and Wagner 1964). The protozoan *Karyolysus* is transmitted by gamasid mites, *Sauronyssus saurarum* (Svahn, 1974), whereas *Leukocytozoon*, a hematozoon is transmitted by macronyssid mites (Frye 1981). Even parasitic worms can be transmitted; the argasid tick *Ornithodoros talaje* transmits the haemofilarian, *Macdonaldius oschei* (Reichenbach-Klinke and Elkan 1965; Frank 1981).

**Interactions with Other Variables**

Dunlap and Mathies (1993) found that nymphal ticks alone had little impact on hosts but when hosts also had malaria, their body condition declined significantly. Similarly, captive animals with heavy mite loads are more likely to develop bacterial infections (Klingenberg 1993; pers. obs). Stress can interact with immunity via hormones to affect the health of hosts (for review see, Guillette et al. 1995). The stresses resulting from parasitic infections and vice versa are not well understood.
In at least one case, the ectoparasite can benefit from its interaction with a host in a nontraditional manner; that is, its host actually eliminates a bacterial infection in the parasite. Lane and Quistad (1998) found that an unknown compound in lizard blood actually rids nymphal ticks of infections of *Borellia burgdorferi* bacteria, and argued that large populations of *Sceloporus* lizards limit the spread of Lyme disease in western North America.

Phoresy (passive attachment of a commensal to the host) has been documented between mites and reptiles. *Ophiomegistus* (Paramigistidae) can parasitize skinks and snakes but typically infests insects and myriapods. Reptiles may acquire these mites as they consume their insect hosts. Elkan reported a slow-worm (*Anguis fragilis*) infested by the sarcoptiform mite *Caloglyphus* sp. (Reichenbach-Klinke and Elkan 1965). Phoresy may be a minor cost entailed by feeding.

Mites can also be a source of food for lizards. Burrage (1966) found that *Uta stansburiana* ate *Ophionyssus* sp. mites from one another. One potential negative side-effect of this is the possible transmission of protozoans (see above).

**Rationale for the Study**

Between the extremes of death and phoresy, there are large holes in our understanding of the effects of ectoparasites on reptiles. To better appreciate these gaps, I will construct a crude classification of the types of studies that have been done. At the foundation of any biological study is proper identification of the organisms of interest. A large portion of the literature is devoted to α-taxonomy (e.g., Lawrence 1936; Cunliffe 1949; Powder and Loomis 1962; Loomis and Crossley 1963; Newell and Rykman
1964; Lucas and Loomis 1968; Loomis and Spath 1969; Loomis 1971; Bennett 1977; Bennett and Loomis 1981) and documenting the association of hosts and parasites (e.g., Jellison 1934; George 1960; Mather 1979; McAllister 1980; Simonsen and Sarda 1985). There is also some documentation of geographic and elevational variation in ectoparasite loads of different reptilian populations (e.g., Allred and Beck 1962; Spoecker 1967; Loomis and Stephens 1973; Gadsden 1988; Zippel et al. 1996). In addition to this spatial component, seasonal variation in parasite load has been recorded in some reptilian populations (Mohr et al. 1964; Spoecker 1967; Loomis and Stephens 1973). Additional studies describe where ticks and mites attach to their hosts (Powder and Loomis 1962; T. Auffenberg 1988; Auffenberg 1981, 1988, 1994; Pearson and Tamarind 1973; Hayashi and Hasegawa 1984b; Oliver et al. 1993), when mites attach in the life-cycle of the lizard (Goldberg and Bursey 1994) and the duration of this attachment (Jameson 1972; Goldberg and Bursey 1991b, 1993). Local pathology caused by mites and ticks has been examined histologically (Bauer et al. 1990; Goldberg and Bursey 1991a; Goldberg and Holshuh 1993). Finally, in recent years there has been some attention paid to the physiological (Dunlap and Mathies 1993) and performance effects of (Sorci et al. 1994) ectoparasitism.

A look at the dates of the studies cited in Table 1.1 reveals that the topics in this classification have developed in roughly chronological order. In as much as this time-line can be construed as a "phylogeny" of lizard-ectoparasite studies, the following chapters represent an ontogeny of my own thinking about these relationships. This study begins by recapitulating the phylogeny of lizard-ectoparasite studies and extends this descriptive work to an understanding of the implications of mite infestations for the physiology and whole-organism performance of the hosts. Finally, this study explores
some conservation oriented links among host populations, parasites and landscape-level modifications of habitat.

Study Animals

The Lizard Host

The Florida scrub lizard, *Sceloporus woodi*, is a small, grayish, spiny-scaled lizard (Figure 1.1) and is the only member of its genus not found west of the Mississippi River. It is a Florida endemic and is almost always restricted to sand pine scrub, a plant association with a highly disjunct distribution (see Figure 1.2). In addition to the Ocala National Forest-Big Scrub complex, where this study was conducted, *S. woodi* also occurs along the coast in isolated populations from Merritt Island south to Jonathan Dickinson State Park and Marco Island. Inland, there are populations at the Archbold Biological Station and the Lake Wales Ridge.

*Sceloporus woodi* is a forest edge species that prefers open, sandy areas adjacent to sand pine scrub and sandhill associations of long leaf pine and turkey oak (DeMarco 1992). Because of its narrow habitat requirements, the fragmented nature of scrub, and the rapid conversion of scrub into agricultural lands or housing developments, *Sceloporus woodi* is federally listed as threatened.

This species is sexually dimorphic for size and color (Figure 1.1). Adult females average 4-5 mm longer than males and retain dark undulating bands on the dorsum characteristic of juveniles, whereas males lose this pattern to achieve a uniform dorsal gray color. Males have bright blue patches on each side of the belly and black and blue patches under their throats. Some females
have faint blue patches in these areas, but generally tend to be light colored on the underside.

Females mature at about 47 mm SVL and can begin vitellogenesis as early as March, if they are in their second reproductive season (DeMarco 1992). Females in their first reproductive season typically yolk follicles in April or May. Courtship and mating occur from March - June. Females typically lay three clutches per season (DeMarco 1992) though some estimates are as high as five per season for larger individuals (Jackson and Telford 1974). Clutch size ranges from 2-8, averages 4, and increases with body size.

Reproduction is over by the end of August. Eggs take about 2.5 months to develop (depending on temperature) with hatchlings emerging from late June to early November at 20-25 mm SVL and around 0.40 gm mass (DeMarco 1992). Hatchlings reach maturity in as little as 6-10 months (Jackson and Telford 1974; DeMarco 1992; Hartmann 1993), depending on when they hatch.

Hartmann (1993) studied population demographics of a population of S. woodi on the Lake Wales Ridge and found that this species is essentially an annual species, with survivorship ranging from 2.5-22% depending on hatching date. DeMarco (1989) documented interannual variation of the seasonal shift in egg and clutch size.

The Parasitic Mites

To better understand how landscape level modifications could affect ectoparasite populations one must first understand the life cycles of the ectoparasites and how they interact with their hosts and habitat. Eutrombicula alfreddugesi is a trombiculid mite. Only the larval stage (commonly known as chiggers or red bugs) of mites in this family is parasitic on vertebrates. It
has been observed on 32 mammals (including humans), 52 birds, 39 reptiles and 3 amphibians (Benton 1987). The juveniles and adults are free-living in the soil and eat small arthropods and their eggs in the leaf litter (Figure 1.1). Duration of the life stages for *E. alfreddugesi* is shown in Table 1.2. In contrast, the pterygosomid mite *Geckobiella texana* lives its entire life cycle on its lizard host (Goodwin 1954; Table 1.3). *Geckobiella* has only been found on lizards of the genus *Sceloporus* (Lane 1954; Jack 1959). I have observed larvae, juveniles, and adults moving from one lizard host to another in captivity. *Geckobiella* can be involved in the transmission of disease. Bonorris and Ball (1955) implicated *Geckobiella* in the transmission of *Shellackia*. Klein (1985) experimentally infected *Sceloporus undulatus* by force feeding them *Geckobiella texana* infected with *Shellackia occidentalis*.

**Study Area**

This study was conducted in Ocala National Forest (ONF), Marion County, Florida (Figure 1.2). The Big Scrub complex, which lies within and around the ONF, is the largest inland scrub in Florida (Myers 1990). The Ocala region has an average minimum temperature of 14.8 °C, an average maximum temperature of 28.3 °C (Figure 1.3) and averages 1309 mm precipitation per year (Figure 1.4). The bulk of the precipitation falls between May and September (Southeastern Regional Climate Center 1998). Variation in precipitation from year to year is largely dependent on month. The coefficient of variation of average precipitation is highest in March and lowest in July (Figure 1.5).

The Ocala region is primarily a matrix of two upland ecosystems: scrub and high pine. The Florida scrub ecosystem is perhaps best summarized by (Myers 1990, p. 151) as "mature forests of tall, twisted leaning sand pines
*(Pinus clausa)* rising above an impenetrable mass of evergreen scrub oaks; rusty lyonia; rosemary; unusual varieties of holly, bay; and hickory; and an array of inconspicuous species, many with restricted distribution.” An estimated 40-60% of plant species are endemic. Scrub is pyrogenic and maintained by fires that occur every 15-100 years. The “varieties” of scrub patches seen today reflect their different fire histories (Myers 1990). Embedded in these extensive areas of scrub are islands of high pine consisting of open woodlands of longleaf pine (*Pinus palustris*) over a cover of wiregrass (*Aristida stricta*) and several hundred other species, and occasional clumps of turkey oak (*Quercus laevis*) or other oak species. High pine is maintained by fires recurring every 1-15 years. In the absence of fire, oaks and sand pine invade and begin to dominate.

Despite their physiognomic differences, scrub and high pine are strongly associated with one another as they both occur on dry, infertile uplands whose soils are derived from the same parent material, both are maintained by fire, and the ignition of scrub depends on flammable high pine (Myers 1990). A comparison of scrub versus high pine plant species composition and fire regimes is made in Table 1.4.

Unfortunately, both scrub and high pine ecosystems have been reduced to a fraction of their historic ranges. Longleaf pine has decreased from a nearly continuous expanse of 25 million hectares to a handful of sites that collectively contain less than 1000 hectares of old growth (Noss 1989). Much of Florida's historic sand pine scrub depicted in Figure 1.2 has been reduced or fragmented by development. The largest remaining tracts are in ONF, which like much of the managed xeric pineland in the southeastern coastal plain of the U.S., is oriented for timber production. Harvest schedules have been accelerated since the early 1980s with the result that uncut sand pine scrub
has been reduced to 25% of its original area within the ONF (Anderson and Tiebout 1993).

LANDSAT images are especially useful for characterizing large scale landscape changes over time (FGDL 1998) and can give some indication of the nature of management changes on the ONF. The LANDSAT series of satellites uses a Multi-Spectral Scanner (MSS) sensor with 60 m resolution. Three of the 4 spectral bands detected by the MSS are shown here to render a false color infrared image. Band 4 is near infrared, bands 2 and 1 correspond to the red and green portions of the visible spectrum. Multiple images were stitched together to form an image mosaic to cover the geographic extent of Marion County, Florida (Figure 1.6), the eastern half of which is depicted in Figure 1.7. The 3 different MSS images (Figures 1.7a, b, c) respectively, are from 1973, 1986 and 1991, plus or minus one year (FGDL 1998).

The patchwork nature of scrub and high pine habitats with various cut and burn histories on the ONF has created a series of what can be thought of as replicated plots of habitat. These are amenable to establishing patterns, and generating and testing hypotheses about the interactions among lizard hosts, their acarine parasites, and the landscape.

The first part of this thesis explores physiological effects of parasitism. If chiggers puncture the integument, can they increase evaporative water loss? Do the nuchal pockets of these lizards decrease the degree of water loss? Can blood-sucking mites affect the speed, endurance, behavior, and recovery ability of the lizards?

The second part of this thesis explores whether microhabitat and habitat affect chigger abundance. Does burn frequency affect chigger and other arthropod abundance? Does roller-chopping following clear-cutting of sand pine scrub alter the population biology of mites on lizards? Answers to these
questions will be addressed in an attempt to better understand the interactions among a host, its ectoparasites, and their landscapes.
Figure 1.1. The life cycle of *Eutrombicula alfreddugesi* (after R. Loomis, unpub. and Conant 1975).
Figure 1.2. Distribution of scrub (filled in black) in Florida, with the Ocala National Forest and Big Scrub regions, where this study was conducted, labelled with larger type (after Myers 1990).
Figure 1.3. Average maximum and minimum monthly temperatures in Ocala, Florida (1961-1990); (Southeastern Regional Climate Center 1998).
Figure 1.4. Average monthly precipitation in Ocala, Florida (1961-1990); (Southeastern Regional Climate Center 1998).
Figure 1.5. Coefficient of variation of average precipitation (CVPPT) for Ocala, Florida, where the coefficient of variation is the standard deviation of monthly precipitation divided by the average monthly precipitation (Winsberg, 1990).
Figure 1.6. Marion County, Florida (shaded in black). LANDSAT scenes in Figure 1.7 are of the eastern half of Marion County, which is primarily composed of sand pine scrub and long-leaf pine in Ocala National Forest.
Figure 1.7. Ocala National Forest within Marion County, Florida. The sigmoid towards the upper-left hand corner is the Ocklawaha River. The black U-shaped area in the upper right is Lake Kerr. The large undisturbed patch (in all scenes) in the middle of the eastern edge of the scene is the Juniper Wilderness. The circle that appears in Figures b and c in the lower right delineates the Naval bombing range.

Figure 1.7 a. Ocala National Forest, 1973. Much of the Forest appears dark red, which represents mature sand pine. Light colored areas have been recently clear cut, medium patches are several years old. The horizontal banded areas to the west of Lake Kerr on Kerr Island, and the vertical bands in Hughes Island to the south of Lake Kerr show the results of a Forest Service experiment to generate edge for deer with alternating bands of turkey oak and long-leaf pine.

Figure 1.7 b. Ocala National Forest, 1986. The once continuous blocks of mature blocks sand pine have been logged in sections of 8-25 ha (Greenberg 1993). The shading of patches gives some indication of the age of the cut with the lightest being the most recent.

Figure 1.7 c. Ocala National Forest, 1991. As before, shading gives some indication of the age of the cut with the lightest being the most recent. Careful inspection of the image from 1986, (Figure 1.7 b) can reveal the degree of regrowth in what were then young cuts.
## Table 1.1 Aspects of acari-reptile relationships

<table>
<thead>
<tr>
<th>Ectoparasite (Family)</th>
<th>Host</th>
<th>Pathology / Notes (duration of attachment)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pathologies</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hirstiella</em> sp.</td>
<td><em>Sceloporus jarrovi</em></td>
<td>acute dermatitis, death</td>
<td>Goldberg &amp; Holshuh 1993</td>
</tr>
<tr>
<td>(Pterygosomidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Neotrombicula californica</em></td>
<td><em>Uta stansburiana</em></td>
<td>epidermal necrosis integumental lesions (7 days)</td>
<td>Goldberg &amp; Bursey 1991a</td>
</tr>
<tr>
<td>(Trombiculidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Geckobiella texana</em></td>
<td><em>Uta stansburiana</em></td>
<td>(28 days) (5 days)</td>
<td>Goldberg &amp; Bursey 1991b</td>
</tr>
<tr>
<td>(Pterygosomidae)</td>
<td><em>Sceloporus gracius</em></td>
<td></td>
<td>Goldberg &amp; Bursey 1991b</td>
</tr>
<tr>
<td><em>Ixodes pacificus</em></td>
<td><em>Uta stansburiana</em></td>
<td>blood loss, acute fibrinoid reaction integumental lesions (16 days)</td>
<td>Goldberg &amp; Bursey 1991b</td>
</tr>
<tr>
<td>(Ixodidae)</td>
<td><em>Sceloporus gracius</em></td>
<td>(8 days)</td>
<td>Goldberg &amp; Bursey 1991b</td>
</tr>
<tr>
<td><em>Eutrombicula lipovskyana</em></td>
<td><em>Sceloporus jarrovi</em></td>
<td>focal ulcerative dermatitis inflammation granuloma formation (52 days in mite pockets, shorter elsewhere on lizard) tissue damage</td>
<td>Goldberg &amp; Holshuh 1992</td>
</tr>
<tr>
<td>(Trombiculidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;chiggers&quot;</td>
<td><em>Rhacodactylus</em> sp.</td>
<td>pruritis (=itching) and dermatitis</td>
<td>Bauer et al. 1990</td>
</tr>
<tr>
<td><em>Ophionyssus</em> serpentium</td>
<td></td>
<td></td>
<td>Mader et al. 1986</td>
</tr>
<tr>
<td>Ectoparasite (Family)</td>
<td>Host</td>
<td>Pathology / Notes</td>
<td>Reference</td>
</tr>
<tr>
<td>-----------------------</td>
<td>------</td>
<td>-------------------</td>
<td>-----------</td>
</tr>
<tr>
<td><em>Hirstiella trombidiformes</em> Sauromalus obesus (Pterygosomidae)</td>
<td>Gehyra mutilata</td>
<td>acariasis, anemia, death</td>
<td>Mader et al. 1986</td>
</tr>
<tr>
<td><strong>mites</strong></td>
<td></td>
<td>mites transferred from <em>Hemidactylus garnotti</em> caused tail autotomy</td>
<td>Oliver &amp; Shaw 1953</td>
</tr>
<tr>
<td><em>Ixodes asanumai</em> (Ixodidae)</td>
<td>Eumeces okadae</td>
<td>muscle atrophy</td>
<td>Hayashi &amp; Hasegawa 1984</td>
</tr>
<tr>
<td><strong>Physiology and Performance</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>mites</em> (Lealapidae)</td>
<td>Lacerta vivipara</td>
<td>altered performance &amp; dispersal in offspring</td>
<td>Sorci et al. 1995</td>
</tr>
<tr>
<td><em>Aponomma gervaisi</em> (Ixodidae)</td>
<td>Varanus sp.</td>
<td>suck blood</td>
<td>Auffenberg &amp; Auffenberg 1990</td>
</tr>
<tr>
<td><em>Ixodes pacificus</em> (Ixodidae)</td>
<td>Sceloporus occidentalis</td>
<td>reduced hematocrit, reduced &quot;condition&quot; in lizards also infected with malaria</td>
<td>Dunlap &amp; Mathies 1993</td>
</tr>
<tr>
<td><em>Ixodes ricinus</em> (Ixodidae)</td>
<td>Psammodromus algirus</td>
<td>lowered hematocrit and hemoglobin, increased intensity in T-implanted males</td>
<td>Salvador et al. 1996</td>
</tr>
<tr>
<td>Ectoparasite (Family)</td>
<td>Host</td>
<td>Pathology / Notes</td>
<td>Reference</td>
</tr>
<tr>
<td>----------------------</td>
<td>------</td>
<td>------------------</td>
<td>-----------</td>
</tr>
<tr>
<td><strong>Vectors</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacteria</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ophionyssus serpentium</em> (Macronyssidae)</td>
<td>snakes</td>
<td>vector of <em>Aeromonas hydrophila</em></td>
<td>Camin 1948</td>
</tr>
<tr>
<td><em>Ixodes pacificus</em> (Ixodidae)</td>
<td><em>Sceloporus occidentalis</em></td>
<td>reservoir host of <em>Borrelia burgdorferi</em></td>
<td>Lane 1989</td>
</tr>
<tr>
<td><em>Ixodes</em> (Ixodidae)</td>
<td></td>
<td>transmit spirochaete Q-fever</td>
<td>Frank 1981</td>
</tr>
<tr>
<td><em>Ornithodorus talaje</em> (Argasidae)</td>
<td></td>
<td>transmit spirochaete Q-fever</td>
<td></td>
</tr>
<tr>
<td><em>Hirstiella trombidiformes</em> <em>Sauromalus obesus</em></td>
<td></td>
<td>vector for Leishmania</td>
<td>Mader et al. 1986</td>
</tr>
<tr>
<td><strong>Protozoans</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hirstiella pyriformis</em> (Pterygosomatidae)</td>
<td><em>Sauromalus varius</em></td>
<td>vector of <em>Hepatozoon sauromali</em>, a hemogregarine</td>
<td>Lewis &amp; Wagner 1964; Newell &amp; Ryckman 1964</td>
</tr>
<tr>
<td><em>Geckobiella texana</em> (Pterygosomatidae)</td>
<td><em>Sceloporus occidentalis</em></td>
<td>transmits <em>Shellackia occidentalis</em>, via ingestion of mite, probably vectors of hemogregarine</td>
<td>Bonorris &amp; Ball 1955; Klein 1985</td>
</tr>
<tr>
<td><em>Ophionyssus natricis</em> (Macronyssidae)</td>
<td><em>S. undulatus</em></td>
<td></td>
<td>Frank 1981</td>
</tr>
<tr>
<td><em>Ophionyssus saurarum</em> (Macronyssidae)</td>
<td><em>Lacerta agilis</em></td>
<td>vector of protozoan <em>Karyolysus</em>; no symptoms</td>
<td>Svahn 1974</td>
</tr>
<tr>
<td>Ectoparasite (Family)</td>
<td>Host</td>
<td>Pathology / Notes</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>---------------------</td>
<td>--------------------------------------------------------</td>
<td>------------------------------------</td>
</tr>
<tr>
<td>Liponyssus saurarorum (Macronyssidae)</td>
<td>Lacerta muralis</td>
<td>vector of Karyolysus lacertarum</td>
<td>Grell, in Noble et al. 1989</td>
</tr>
<tr>
<td>Neoliponyssus saurarum (Macronyssidae)</td>
<td>lizards</td>
<td>transmit coccidia (Shellackia)</td>
<td>Frank 1981</td>
</tr>
<tr>
<td>Ophionyssus serpentium (Macronyssidae)</td>
<td>snakes</td>
<td>Leukocytozoon hematozoons</td>
<td>Frye 1981, Marcus 1981</td>
</tr>
<tr>
<td>Worms</td>
<td>Ornithodorus talaje (Argasidae)</td>
<td>transmit Haemofilaria (Macdonaldius oschei)</td>
<td>Reichenbach-Klinke 1965, Frank 1981</td>
</tr>
<tr>
<td>Phoresy</td>
<td>Caloglyphus sp. (Sarcoptiformes)</td>
<td>phoresy for non-feeding laveae</td>
<td>Elkan in Reichenbach-Klinke 1977</td>
</tr>
<tr>
<td>No Described Effect</td>
<td>Aponomma hydrosauri (Ixodidae)</td>
<td>none noted</td>
<td>Downes 1984</td>
</tr>
<tr>
<td>Ixodes ricinus (Ixodidae)</td>
<td>Lacerta agilis</td>
<td>finds host by its odor &amp; disturbance</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lacerta vivipara</td>
<td>no effects on host mortality</td>
<td>Bauwens et al. 1983</td>
</tr>
<tr>
<td>Ectoparasite (Family)</td>
<td>Host</td>
<td>Pathology / Notes</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------------------------------</td>
<td>-----------------------------</td>
<td>------------------------------------------------------------------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td><strong>Possible Benefit</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geckobiella texana (Pterygosiomidae)</td>
<td>Sceloporus jarrovi</td>
<td>none noted</td>
<td>Goldberg &amp; Holshuh 1992</td>
</tr>
<tr>
<td><strong>Ophionyssus nutrias</strong> (Macronyssidae)</td>
<td>Uta stansburiana, Sceloporus occidentalis</td>
<td>Uta ate mites off one another &amp; Sceloporus, which had lower incidence of disease</td>
<td>Burrage 1966</td>
</tr>
<tr>
<td>Ixodes asanumai (Ixodidae)</td>
<td>Eumeces okadae</td>
<td>deticking behavior</td>
<td>Hayashi &amp; Hasegawa 1984</td>
</tr>
</tbody>
</table>
Table 1.2. Duration of *Eutrombicula alfredugesii* life history stages.

<table>
<thead>
<tr>
<th>Stage</th>
<th>mean duration (days)</th>
<th>range in duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>egg</td>
<td>6</td>
<td>15-20 (egg + deutovum)</td>
</tr>
<tr>
<td>deutovum</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>unfed larva</td>
<td>1</td>
<td>up to 24</td>
</tr>
<tr>
<td>feeding</td>
<td>3</td>
<td>1-4</td>
</tr>
<tr>
<td>engorged larva</td>
<td>2</td>
<td>1-8</td>
</tr>
<tr>
<td>protonymph</td>
<td>6</td>
<td>9-10</td>
</tr>
<tr>
<td>nymph</td>
<td>11</td>
<td>12-32</td>
</tr>
<tr>
<td>tritonymph</td>
<td>17</td>
<td>5-10</td>
</tr>
<tr>
<td>adult</td>
<td>12</td>
<td>52</td>
</tr>
<tr>
<td>Total</td>
<td>55</td>
<td>67-98</td>
</tr>
<tr>
<td>Source</td>
<td>Jenkins 1947</td>
<td>Wolfenbarger 1952</td>
</tr>
</tbody>
</table>

Table 1.3. *Geckobiella texana* life history stages.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Female Duration (days)</th>
<th>Male Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>egg</td>
<td>6</td>
<td>6 days</td>
</tr>
<tr>
<td>deutovum</td>
<td>11-16</td>
<td>11-16</td>
</tr>
<tr>
<td>larva</td>
<td>feed 3-4 days posthatch, engorge 4-5 days</td>
<td>feed 3-4 days posthatch, engorge 4-5 days</td>
</tr>
<tr>
<td>nymphochrysalis</td>
<td>4-7 (small chrysalis)</td>
<td></td>
</tr>
<tr>
<td>nymph</td>
<td>engorge 7-15 days</td>
<td></td>
</tr>
<tr>
<td>imagochrysalis</td>
<td>4</td>
<td>7-10 (large chrysalis)</td>
</tr>
<tr>
<td>adult</td>
<td>engorge 7-10 days</td>
<td>engorge 7-10 days</td>
</tr>
<tr>
<td>Total</td>
<td>46-67</td>
<td>38-51</td>
</tr>
</tbody>
</table>

(after Goodwin 1954)

Note: Males skip the nymphochrysalis and nymph stages
Table 1.4. Comparison of scrub and high pine.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Scrub</th>
<th>High Pineland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pines</td>
<td><em>Pinus clausa</em> (Sand pine)</td>
<td><em>Pinus palustris</em> (Longleaf pine)</td>
</tr>
<tr>
<td>Hardwoods</td>
<td><em>Q. myrtifolia</em> (Myrtle oak)</td>
<td><em>Quercus laevis</em> (Turkey oak)</td>
</tr>
<tr>
<td></td>
<td><em>Q. geminata</em> (Sand live oak)</td>
<td><em>Q. incana</em> (Bluejack oak)</td>
</tr>
<tr>
<td></td>
<td><em>Q. chapmanni</em> (Chapman’s oak)</td>
<td><em>Q. falcata</em> (Southern red oak)</td>
</tr>
<tr>
<td></td>
<td><em>Lyonia ferruginea</em> (Rusty lyonia)</td>
<td><em>Q. margaretta</em> (Sand post oak)</td>
</tr>
<tr>
<td></td>
<td><em>Ceratolia ericoides</em> (Rosemary)</td>
<td><em>Q. marilandica</em> (Blackjack oak)</td>
</tr>
<tr>
<td>Foliage</td>
<td>evergreen</td>
<td>deciduous</td>
</tr>
<tr>
<td>Herbs</td>
<td>sparse</td>
<td>abundant</td>
</tr>
<tr>
<td>Ground cover</td>
<td>litter, lichens, bare sand</td>
<td>grasses, forbs</td>
</tr>
<tr>
<td>Aspect</td>
<td>dense thicket</td>
<td>open woodland</td>
</tr>
<tr>
<td>Fire Frequency</td>
<td>infrequent (15-100 years)</td>
<td>frequent (1-15 years)</td>
</tr>
<tr>
<td>Fire Intensity</td>
<td>high</td>
<td>low</td>
</tr>
</tbody>
</table>

after Myers, 1990
CHAPTER 2
CHIGGER INFESTATIONS, EVAPORATIVE WATER LOSS AND THE POSSIBLE ADAPTIVE SIGNIFICANCE OF NUCHAL POCKETS

Introduction

Reptiles are generally assumed to have impermeable integuments. Tight intercellular junctions, fibrous polymer layers of protein, and lipid layers in the integument all contribute to this impermeability (Lillywhite and Maderson 1988). The mesos layer just below the outer layer of β-keratin is of primary importance in creating a barrier to water (Lillywhite and Maderson 1982). Given the importance of this water-tight integument, one should not be surprised to see features and behaviors of reptiles that would serve to maintain its integrity. Likewise, dramatic effects as a result of compromising its integrity would be expected.

One issue in lizard biology is whether the small skin invaginations (integumentary pockets) in areas such as the neck, axilla, groin and postfemoral regions are adaptations to minimize the impacts of ectoparasites. Arnold (1986, 1993) and Benton (1987) argue that these pockets are adaptive features that benefit the host by concentrating mites in areas where their deleterious effects can be minimized. Bauer et al. (1990), and Bauer (1993) argue that pockets are merely facultatively exploited by mites.

If pockets are adaptations, then one prediction would be that parasitized animals with blocked pockets would have higher evaporative water loss than those with unblocked pockets because on animals with blocked pockets, ectoparasites would resort to using other locations on the body with a consequential increase in evaporative water loss. There are solid
biophysical reasons to predict this. Pockets, by creating a small enclosed space around the chiggers, should reduce evaporative water loss by creating a microenvironment that has a higher relative humidity than the surrounding environment. Some plants have a similar structure as well. Oleander (*Nerium* sp.), has stomatal crypts in which the stomata are sunk deeply into a thick "multiple epidermis" (Salisbury and Ross 1992).

Though the histopathology of mites on reptile integument has been well documented (Arnold 1986; Bauer et al. 1990; Goldberg and Bursey 1991a; Goldberg and Holshuh 1992, 1993), its implications for water balance, as well as other physiological and ecological aspects of the host, have not been examined. This paper will describe the histopathological effects of chiggers (*Eutrombicula alfredlagesi*) on the integument of the Florida scrub lizard (*Sceloporus woodi*) and link that pathology to increases in evaporative water loss. These results will then be extended to test if the prominent nuchal pockets on this species can reduce integumental water loss in parasitized animals.

**Methods**

**Scanning Electron Microscopy**

Scrub lizards were collected in Ocala National Forest (Marion County, Florida) in 1995-6. Three animals were euthanized with a 9:1 solution of water to sodium pentobarbitol (Nembutal® Sodium). Fresh tissue from the mite pockets was fixed in Bouin's alcoholic fluid for one week, followed by dehydration in an alcohol series and hexamethyldisilazane. A gold sputter coat was applied to the tissue which was then viewed with a Hitachi scanning electron microscope at 50X. Photographs were taken with Polaroid type 52 film which was then scanned at 300 dpi (see Figure 2.1).
Histology

Scrub lizards were collected in Ocala National Forest (Marion County, Florida) in 1995-6. Three animals were euthanized with a 9:1 solution of water to sodium pentobarbitol (Nembutal® Sodium). Fresh tissue from the mite pockets and behind the knees was fixed in Bouin's alcoholic fluid for one week. Tissue was embedded in paraffin following dehydration in an alcohol series and exposure to Hemo-D® (Fisher Scientific) for 2 h. Tissue was then sectioned at 7 μm and stained with a modified Masson's trichrome stain (Presnell and Schreibman 1997). Histopathology was examined using light and differential interference contrast (DIC) microscopy. Photographs were made at 200x magnification with slide film. Images were digitized with a slide scanner.

Evaporative Water Loss

Lizards were captured by noose in Ocala National Forest, Marion County, Florida. The number of chiggers on the lizards were counted under a dissecting microscope or with the aid of a hand lens. Lizards were placed in a 60 cc syringe that was fitted with a nylon exit valve. Air was pumped through the syringe after being dried by passage through a column of silica gel (Fisher Scientific); air was passed through a flowmeter to ensure a constant rate. A second column of silica gel was used to collect moisture lost by the lizard (Figure 2.2). Both the lizards and the collecting gel column were weighed before and after each 2 h run to the nearest 0.0001 g using a Mettler balance. All runs were done at 25 °C. From these data, evaporative water loss (EWL) in mg/g/h was derived. Lizard EWL was remeasured several days after the chiggers had finished feeding and dropped off. If an animal was actively
moving in the chamber during the measurement of EWL, that run was dropped from the analysis, in order to minimize the effects of activity level on the results. Linear regression was used to derive the relationship between EWL and chigger intensity (number of chiggers per lizard).

**Nuchal Pockets and EWL**

To test if nuchal pockets reduced evaporative water loss of parasitized hosts, 14 lizards (4 females, 10 males) were measured without mites (using the above techniques), and then remeasured following reinfestation with mites. The animals were divided into two groups of 7 lizards each. One group had its nuchal pockets blocked with Testors® enamel paint and the other had same-sized dots of paint applied just above the pockets on the back of the neck. The blocked group had 4 males and 3 females, while the unblocked group had 6 males and 1 female (this difference in sex ratio resulted from matching the animals for size). Lizards were reinfested with mites by being placed overnight in metal troughs that had been lined with freshly collected leaf litter from Ocala National Forest. I found that litter from forest edges that contained rosemary (*Ceratolia ericoides*) duff and lichens (*Cladina* sp. and *Cladonia* sp.) usually contained many chiggers. A repeated measures ANCOVA was performed with post-chigger EWL as the dependent variable, pre-chigger EWL, and pocket treatment (blocked or unblocked) as the independent variables, and intensity as the covariate. The assumption of homogeneity of slopes was checked using the treatment*pre-chigger EWL interaction term and supported ($F = 0.21, p = 0.66$), so it was valid to do a repeated measures ANCOVA.
Results

Scanning Electron Microscopy

The chiggers congregated in the nuchal pockets, which were not covered with scales (Figure 2.1). The skin in the pocket had a granular appearance.

Histology

Where the chigger attaches to the lizard, a stylostome (literally, feeding tube) is formed by the interaction of parasite saliva and host tissues (Figure 2.3). Pockets where chiggers attached showed marked inflammation with lymphocytic infiltration concentrated around the stylostome (Figure 2.4). The concentric layering of lizard cells around the stylostomes is consistent with early granuloma formation. Areas where chiggers had not attached showed no inflammation. Where infestation had occurred, the stratum corneum separated from the underlying stratum germinativum in 2 out of 3 cases. In uninfested areas it remained attached (Figure 2.5).

Evaporative Water Loss

Chigger intensity of wild caught lizards ranged from 8 - 454 chiggers/individual. The EWL ranged from 1.52 to 7.78 mg/g/h. The least-squares regression of EWL on intensity yielded the following relationship: \( \text{EWL} = 0.015 \times \text{intensity} + 1.52 \) and explained nearly 75% of the variation in EWL (Figure 2.6). After the chiggers reached repletion, they dropped off the lizards. Once the lizards had a few days to recover from the infestation, EWL
averaged 1.47mg/g/h, s.d. = 0.52, N=16, not significantly different than the y-intercept for the regression of EWL on intensity (p = 0.397).

**Nuchal Pockets and EWL**

Following reinestation, lizards with blocked pockets had higher evaporative water loss (1.66 mg/g/h) than those with unblocked pockets (1.22 mg/g/h), correcting for differences in intensity. The whole model explained 52% of the variation in EWL after chiggers attached (F = 5.74, p = 0.015). Intensity was the strongest predictor (F = 7.73, p = 0.019), followed by treatment (F = 3.68, p = 0.089) and pre-chigger EWL (F = 2.28, p = 0.13). Though males tended to have slightly higher evaporative water loss than females, gender, or interactions of gender with intensity did not contribute significantly when added to this model and, in fact, reduced the adjusted $r^2$ to 46%.

**Discussion**

**Histology**

The inflammatory response to chigger infestation in the nuchal pockets was distinct and localized around the stylostomes. Some have argued that the immune response is akin to host manipulation by the parasite, as the chiggers appear to feed on the mixture of lymph and cellular debris created by the reaction to their saliva (Hase et al. 1978; Arnold 1986).

The separation of the stratum corneum from the underlying connective tissue in infested areas could indicate that the compounds in mite saliva are capable of weakening the lipid-rich mesos layer (H.B. Lillywhite,
pers. comm.). This response could contribute to increased evaporative water loss through the areas of affected integument (Lillywhite and Maderson 1982).

On two occasions, when I noosed heavily infested animals, the 2 lb test monofilament line actually cut into the weakened integument in the nuchal pocket. The wound appeared to ooze lymph. This anecdotal evidence supports the histological observations.

**Evaporative Water Loss**

Evaporative water loss was strongly correlated with chigger intensity (numbers of chiggers per lizard). Increased EWL could significantly reduce the time it would take an animal to reach its vital limit of dessication in dry conditions. Crowley (1987) found that dessicated *Sceloporus undulatus* in enclosures selected significantly lower body temperatures than did hydrated lizards, chose body temperatures that were negatively correlated with degree of dessication, and showed decreased activity by remaining buried in the substrate. In a different study, Crowley (1985) found that sprint running performance of *S. undulatus* was relatively insensitive to the effects of dessication. In contrast, Wilson and Havel (1989) found that dehydration reduces the endurance running capacity of *Uta stansburiana*.

**Nuchal Pockets and EWL**

The one-tailed prediction that animals in the blocked pocket treatment group would have greater evaporative water loss was supported (p = 0.089, α=0.10). This result lends credence to the idea that the nuchal pockets could have adaptive value. Arnold (1986) has already suggested that nuchal pockets localize tissue damage and the immune response of swelling and
inflammation. Reduction in evaporative water loss is another potential benefit of pockets.

One other aspect of the chigger-concentrating effects of nuchal pockets is that they could create "badges" of status for the lizards. If home range size is correlated with intensity of infestation, then many chiggers would coalesce in the pockets to create a visually striking indicator of territory size. Males have home ranges that are about twice the size of females (G. Hokit, pers. comm., pers. obs.). Larger individuals tend to have more chiggers. In lieu of bright integument, males could use chiggers as indicators of territory quality. It would be interesting to manipulate chigger numbers and see if it affects mating success.

If nuchal pockets are an adaptive feature of lizards, it is worth asking what advantages chiggers gain from going into them. Chiggers tend to aggregate in the pockets where there might be an advantage of being in a "selfish herd" (Hamilton 1971), and they are better able to resist abrasion and shedding of skin. *S. woodi* routinely dive and shimmy into sand as part of their everyday activities (pers. obs.). Cyamid copepods ("whale lice"), are associated with the slits and pleats on whales apparently as a way of avoiding high velocity gradients (Vogel 1994). Chiggers may be doing the same thing by seeking out pockets on their sand-swimming lizard hosts. Multiple perforations of the lizard integument by the chigger mouthparts allow skin to slough off around groups of chiggers rather than pull them off as individuals (pers. obs.). The Allee Effect [positive density dependence (Ehrlich and Roughgarden 1987)], in which feeding efficiency increases with higher density (up to a point), may facilitate chigger growth and development. The trade-off here is whether the increased per capita feeding of grouped chiggers is still better than reduced per capita feeding over a wider area of the lizard. If
pockets create a "win-win" situation for both parasite and host, they could be an evolutionarily stable solution (Maynard Smith 1982) to the problems presented by ectoparasites.

Past studies have documented histopathology of lizards and their acarine parasites. This study was prompted by a need to place the pathology in a physiological and ecological context. In future studies it might be possible to reduce the response to infestation with anti-inflammatory agents and measure if evaporative water loss decreases. Testosterone has long been recognized as an immune suppressor. Are there qualitative differences in pathology between male and female hosts or juvenile and adult hosts?

This study was host-centered, but it could be profitable to examine the host-parasite relationship from the parasite's perspective. Hase et al. (1978) suggested that inflammation around the stylostome enhances feeding by breaking down tough dermal tissue. The administration of anti-inflammatories to the host would be expected to reduce the feeding efficiency and hence growth of the ectoparasites.

Finally, another way to explore the relationship between chiggers and nuchal pockets on lizards would be to use the comparative method. There is much variation in the depth of nuchal pockets within the genus Sceloporus (pers. obs.). Species found in arid western North America, tend to have deeper pockets than S. woodi, which is only found in Florida (pers. obs.). If nuchal pockets are a feature that has been selected to concentrate chiggers and create areas of high humidity and hence low evaporative water loss, then this pattern of pocket depth would be consistent with that adaptationist hypothesis. A study that measured pocket depth in several species of Sceloporus or a wide-ranging species like S. undulatus and attempted to
correlate it with climate in the areas where the animals were caught could be illuminating.

Figure 2.1 Scanning electron micrograph (SEM) of a left nuchal pocket of *Sceloporus woodi* at 50X magnification. The *Eutrombicula alfreddugesi* chiggers are clustered together towards the center of the pocket, which is devoid of scales.
Figure 2.2. Dehydration chamber for small lizards. Room air at 25 °C is passed by an aquarium pump through a column of dessicating silica gel, through a flow meter and over a lizard (head first). Moisture from the lizard chamber is collected in a second column of silica gel.
Figure 2.3. Stylostomes in longitudinal (left arrow) and cross-section (right arrow) in a nuchal pocket of a *Sceloporus woodi* (1 cm = 40 μm).

Figure 2.4. *Eutrombicula alfredi* (chiggers) attached to the nuchal pocket of *Sceloporus woodi*. Extensive inflammation surrounds the stylostomes (1 cm = 40 μm).
Figure 2.5. Edge of nuchal pocket showing the localized inflammatory response to chigger infestation. The stratum corneum has separated from the inflamed pocket on the left edge of the figure. There is no inflammation on the right side of the figure, where chiggers were not attached (1 cm = 40 μm).
Figure 2.6. Regression of evaporative water loss on mite intensity; \( y = 0.015x + 1.521; \text{Adj } r^2 = 0.75, F = 51.78, p = 0.0001 \). The adjusted \( r^2 \) of a 2nd order polynomial regression was actually lower (0.735) than for the linear regression model.
CHAPTER 3
THE EFFECTS OF MITES ON THE MORPHOLOGY, PHYSIOLOGY
AND PERFORMANCE OF THE FLORIDA SCRUB LIZARD,
SCELOPORUS WOODI

Introduction

Though relationships between morphology and behavior or ecology are well documented (e.g., Darwin's Finches), until recently they have largely neglected the intermediate step of organismal performance (Wainwright and Reilly 1994; Garland and Losos 1994). The conceptual framework for including performance in studies linking morphology to ecology was first laid down by (Arnold 1983) in a quantitative genetics context, and has been elaborated on by Miles (1994) and Garland and Losos (1994), (see Figure 3.1). Physiology and biochemistry, like morphology, can be considered as aspects of phenotype, as they are all sub-organismal in their level of biological organization. They can interact among one another. Behavior is seen as a potential filter between selection and performance in this expanded scheme (Garland et al. 1990a; Garland and Carter 1994). However, some workers prefer to view behavior as a category of morphology (Emerson and Arnold 1989).

From within the morphology-performance-fitness paradigm, a series of lizard indoor racetrack studies has emerged. Huey and Hertz (1982) and colleagues (Garland 1985) used computers to record light beams being occluded by lizards as they ran down the racetrack to make precise measurements of speed and acceleration. The results have been used to test repeatability of performance (Van Berkum et al. 1989), inter-familial variation in sprint speed (Van Berkum and Tsuji 1987), and to generate large
comparative data sets (Garland 1994; Bennett and Huey 1990) that have been used in phylogenetic analyses of performance. Though these studies have provided new insights into the evolution of performance, they have tended to favor precision over realism. Levins (1966) argued that models of the world can only emphasize two out of three components (precision, generality, and realism) at a time (Figure 3.2). Previous studies have been conducted in laboratory situations on small (2 m long), indoor tracks with unnatural substrates (see Huey and Hertz 1982; Garland 1985, 1994; Van Berkum and Tsuji 1987; Van Berkum et al. 1989). The result has been precise, repeatable measurements of performance over short distances, that do not, however, include complex behaviors.

In more realistic studies, precision and control over environmental parameters, such as temperature afforded by a laboratory-based investigation, are sacrificed. However, with a large track in the field on natural substrate, a more ecologically relevant environment is obtained. We hypothesized a more realistic situation would generate maximal performance data that more clearly reflects what the animals are capable of in situations where natural selection operates. We predicted that a more natural situation would allow collection of data that are usually difficult to obtain or analyse, e.g., behavioral decisions such as turning around. Previous studies have had difficulty dealing with such behavioral data and eliminated them from analysis (see Miles 1994).

Little attention has been paid to the effects of parasites within the morphology-performance-fitness paradigm. Sorci et al. (1994) found maternal mite load resulted in increased sprint speed of offspring in the viviparous lizard Lacerta vivipara. Schall (1990; Schall and Dearing 1987) has focused on malaria in Sceloporus occidentalis, and found both positive and negative
effects on male competition for mates. Infected males have darker ventral coloration and so appear older, an advantage for social displays. However they also suffer reduced stamina. This study documents the effects of ectoparasitic mites on the morphology, physiology and performance of a lizard.

The Florida scrub lizard, Sceloporus woodi, is a small, grayish, spiny-scaled lizard that is a Florida endemic and is almost always restricted to sand pine scrub, a plant association with a highly disjunct distribution. S. woodi is a forest edge species (like many of its congeners) that prefers open, sandy areas between sand pine scrub and sandhill associations of long leaf pine and turkey oak (DeMarco 1992). It has already been identified as a species that is unusually fast for its size (Miles 1994).

S. woodi is sexually dimorphic in size with adult females averaging 4 - 5 mm longer than males in snout-vent length (SVL). Females mature at about 47 mm SVL and can begin vitellogenesis as early as March. Courtship and mating occur from March-June. Females typically lay three clutches per season of 2 - 8 eggs (mean = 4). The reproductive season is over by late August (DeMarco 1992).

The pterygosomid mite Geckobiella texana lives its entire life cycle on its lizard host and larvae, nymphs and adults of both sexes feed on blood (Goodwin 1954). G. texana has only been found on lizards of the genus Sceloporus (Lane 1954; Jack 1959). Juveniles and adults can move from one lizard host to another in captivity (pers. obs.).

This study documents the effects of Geckobiella on the morphology, physiology, and several measures of performance of S. woodi, including maximum speed, endurance, and behavioral tactics. This study also describes
effects of reproductive season and gender on performance. All performance measures were made at a large outdoor racetrack on natural substrate.

Methods

Morphology/Histopathology

Scrub lizards were collected in Ocala National Forest (Marion County, Florida) in 1995-6. Three animals were euthanized with a 9:1 solution of sodium pentobarbital (Nembutal® Sodium). Fresh tissue from the mite pockets and behind the knees was fixed in Bouin's alcoholic fluid for one week. Tissue was embedded in paraffin following dehydration in an alcohol series and exposure to Hemo-D® (Fisher Scientific) for 2 h. Tissue was then sectioned at 7 µm and stained with a modified Masson's trichrome stain (Presnell and Schreibman 1997). Histopathology was examined under light microscopy using DIC microscopy. Photographs of histological sections were made onto slide film and images were digitized with a film scanner.

Physiology

To determine the effects of mites on hematocrit and osmolarity, lizards were maintained in aquaria and sprayed with a 1% sterile solution of ivermecten [(Ivomec®, Merck & Co., Inc., Rahway, NJ), 0.5 mL Ivomec®/liter H₂O, after Abrahams 1992] to remove mites or water as a control treatment. Blood was sampled from post-orbital sinuses (Frye 1981) with 10 µl capillary tubes (Drummond Scientific Co., Broomall, PA) and spun in a micro-centrifuge for 10 min to separate it into fractions of packed red blood cells and plasma. The lengths of the red blood cell (RBC) column and the entire
column (packed RBC’s + plasma) were measured to the nearest 0.5 mm and divided by one another to calculate hematocrit. Plasma osmolarity was measured with a Wescor 5100B vapor pressure osmometer (Wescor Inc., Logan, UT).

Data were analyzed with JMP In statistical software (SAS Institute 1996). Homogeneity of variance across groups was assessed with Levene's test, which compares the average absolute values of the within group residuals from the mean (Sall and Lehmann 1996). Data were checked for normality with the Shapiro-Wilk W test. Variables that violated assumptions of normality were compared with the Wilcoxon rank sum test. Relationships between hematocrit and performance were assessed with linear regression.

**Performance**

An outdoor racetrack was constructed in Ocala National Forest, near Ocala, Florida at the edge of a stand of mature sand pine (*Pinus clausa*) and a stand that burned and was cleared in 1989 (site YB in Anderson and Tiebout 1993). The track had sides composed of 24” wide aluminum flashing held in place by cable-ties wrapped around stakes driven into the ground. The surface of the track was made of packed sand available *in situ*. The track was 28.5 m long and 60 cm wide (wide enough for a researcher to run inside the track to chase the lizards). Vegetation (1 m high) was placed at 12 m from the starting line and at the far end of the track so as to provide a source of cover to encourage a subject to run quickly and continuously towards these landmarks. Lizards were caught at several sites in Ocala National Forest and brought to the track.

Lizards were weighed to the nearest 0.01 g and snout vent length was measured to the nearest 0.5 mm. We used the residual of mass over SVL as
an operational measure of "condition", assuming more robust individuals are healthier. Locations and intensities of *Eutrombicula alfreddugesi* (chiggers) and *Geckobiella texana* (mites) on the lizards were recorded. The lizards were housed in 50 mm diameter x 110 mm long plastic vials that were covered with tape so that they could not see out of them. Animals were post-absorptive but well hydrated. Approximately 0.5 h prior to the sprint-trials, the vials were placed in a portable, temperature-controlled chamber (Igloo Koolmate 36, Peltier-type cooler-heater) and heated to the active body temperature for these lizards (33-38 °C; R. A. Anderson, unpubl. data). Immediately before a sprint-trial, the cooler was opened, a vial removed, the lizard removed from the vial and its temperature taken with a Schultheis cloacal thermometer. Animals that struggled for more than 1 s were not run immediately and placed back into the cooler to be run at least 20 min later. A team of two researchers was required to run the lizards. One researcher chased the lizard and marked any critical locations, such as slow-down or turn-around points in the sand. The other researcher observed from beside the track, but behind the lizard and lizard-chaser, with 2 stopwatches (with split-time capabilities) in hand. Typically a run would proceed as follows: The chaser would hold the lizard in hand at the starting point and slowly show both eyes of the lizard the vegetation landmarks down the track, then would set the lizard down on the track and let it go. The lizard usually remained motionless for 1-2 s then would sprint away from the chaser towards the vegetation. In some trials, the lizard would double-back on itself and run through the legs of the chaser, who would mark the turn-around distance (TAD) and confirm with the timer that the turnaround had in fact occurred. Whether the lizard turned around it would eventually slow down. The slowdown point was distinctive and was identified as a rapid reduction in
stride frequency and running velocity, sometimes accompanied by exaggerated side-to-side movement of the anterior abdomen and forelimbs (wiggling). The chaser would mark this fast-run distance (FRD) which was also timed and then continue to chase the lizard until it could no longer move. This last interval was defined as the final distance/time. The turnaround (if applicable), slowdown and final distances and times were summed to determine a total distance (TD) and time for each run. Running rates for each interval and the entire run were calculated by dividing the distances by the appropriate durations. Nearly 100 lizards were run in this manner and 3-5 runs per individual were logged to obtain a reasonable estimate of maximum effort. Maximum speed was defined as the fastest leg of any of the runs. Animals that did not move at least 1 m/s were deleted from the analysis.

Animals were run during the breeding season (at the end of July) and post-breeding season (late August, early September) to determine if there were reproductive/seasonal effects on performance and interactions between seasonality, parasite load and performance. Animals were run with mites and then re-run several days after the mites had been removed with a spray application of ivermecten (Abrahams 1992).

Data sets were checked for normality with the Shapiro-Wilk W test and analyzed using JMP In software (SAS Institute 1996). Linear and multiple regression were used to assess relationships between mite load, body temperature, condition (residuals of body mass regressed on SVL), and the performance measures: maximum speed (MAXQUAL) and turnaround distance (TAD). Animals that turned around were labelled as “evaders”, whereas animals that ran continuously towards the end of the track were labelled “runners.” Logistic regression was used for predicting a categorical behavioral response (run or evade) from a continuous predictor, mite.
intensity (number of mites per lizard). A paired-t test was performed on the
data obtained in the mite removal experiment.

Results

Morphology/Histopathology

Adult *Geckobiella* tended to congregate behind the knees of the lizards. Occasionally, (< 10% of the time) 1 or 2 would attach in the nuchal pockets or the axilla. In the areas behind the knees, the *Geckobiella* mites made deep stylostomes (Figure 3.3). Inflammation in the form of lymphocytic infiltration extended into the thigh musculature, filling the interstices between muscle bundles (Figure 3.4). Inflammation also extended around the femoral nerve and layers of surrounding connective tissue (Figure 3.5).

Heavily infested lizards tended to push their feet along the surface of the sand rather than dig them into the substrate as they ran in performance trials (pers. obs.). Whether this "sliding" was due to discomfort, swelling, or mechanical interference by the mites is not known. It certainly could have contributed to decreased running performance.

Blood Parameters

The hematocrit and osmolarity data violated assumptions of normality, so a Wilcoxon rank sum test was used. The "mites-removed" lizards had significantly lower hematocrit than the "mites retained" lizards (Figure 3.6; $S = 85, Z = 2.65, P < 0.0081$). Plasma osmolarity was not significantly different between treatments (Figure 3.7; $S = 57, Z = -0.21, P < 0.83$). Total body water was not measured.
Turn-around distance range was 1.5 - 11.0 m (mean = 8.11 m, s.d. = 3.92), and was normally distributed (Shapiro-Wilk W = 0.97, P < 0.92). Fast-run distance (FRD), (distance until slowing) range was from 0 - 15.25 m (mean = 8.04, s.d. = 4.52), and was normally distributed (Shapiro-Wilk W = 0.97, P < 0.91). Total distance (TD) run by each lizard ranged from 12 - 31.5 m (mean = 20.0, s.d. = 6.41), and was normally distributed (Shapiro-Wilk W = 0.92, P < 0.29).

Performance measures were negatively correlated with increasing hematocrit (Figure 3.8 - 3.10). Least squares regression yielded the relationships in Table 3.1. After the Bonferroni adjustment for multiple comparisons ($\alpha = 0.05/3 = 0.017$), only fast-run distance (FRD) was significantly correlated (inversely) with hematocrit.

**Maximum Performance**

Average maximum speeds (2.08 ± 0.51 m/s) were similar to those recorded previously for this species (Miles 1994; i.e., ~2.25 m/s). However, highest maximum speeds were nearly 70% faster, (4 animals clustered around 3.0 ± 0.15 m/s). Our subjective impression is that lizards did not reach these high speeds until they had been running for > 5 m. For an average-sized (50 mm SVL) *S. woodi*, a speed of 3 m/s is about 60 body-lengths/s. The fastest run we recorded had a lizard averaging 3.8 m/s over the entire 28.5 m length of the track. This is 76 body-lengths/s, or 13.7 km/h!

**Male Speed**

Maximum speed of male lizards tended to decline with increasing mite levels. The maximum velocity (MAXQUAL) of males in July with no mites
averaged nearly 2.25 m/s (Figure 3.11). The best performing male ran nearly 3 m/s. A male with 21 mites ran less than 1 m/s. Collectively, body temperature, mite intensity, and the residual of mass regressed on SVL statistically accounted for nearly 70% of the variation in maximum running velocity (body temperature: $F = 15.86$, $P = 0.001$; adult mite intensity: $F = 16.98$, $P = 0.007$, resid. mass: 23.53, $P = 0.0001$; Adj. $R^2 = 0.69$, $F = 16.32$, $P<0.0001$). Mite intensity alone statistically accounted for 31% of the variation in maximum velocity in July.

Running performance among males in August showed a weak inverse relationship between mite load and maximum speed ($\text{maxrunqual} = 2.34 - 0.032 \times \text{mites}$; Adj. $R^2 = 0.048$, $F = 1.95$, $P = 0.18$), (Figure 3.12a). The residual of mass over SVL ("condition") and body temperature no longer contributed significantly to the regression equation, so they were dropped from the multiple regression. The range of body temperatures was narrow, therefore no correlation of running performance was expected. When the outlying point (indicated by the arrow in Figure 3.12b), was dropped from the analysis, mite intensity statistically accounted for nearly 23% of the variation in maximum running velocity in August and was the only significant predictor of performance, ($\text{maxrunqual} = 2.36 - 0.052 \times \text{mites}$, Adj. $R^2 = 0.23$, $F = 6.23$, $P = 0.023$, see discussion regarding the outlier).

**Female Speed**

Neither mite intensity nor temperature had any apparent effect on the maximum speed of females, which was $1.55 \pm 0.46$ m in July and $2.05 \pm 0.37$ m in August. The only significant correlate was the residual of mass on SVL (condition), which accounted for 15% of the variation in running speed in
July and 27% in August. Female sample size in July was n = 7 (most females were gravid and reluctant to run, hence they were not used), so it is difficult to assess the significance of the between month difference in speed.

**Turnaround Tactics**

There was a direct correlation between mite load and the tendency for males to turn around during running trials in July (n = 29). Probability of turnaround was about 30% with no mites and was nearly 100% with intensities greater than 10 mites (Figure 3.13). The logistic regression model was highly significant (p = 0.011, df = 1), and mite intensity statistically accounted for 17% of the tendency to turn around (p = 0.063, one-tailed test). There was no effect of mites on tendency for females to turn around in the July trials, but this may be an artifact of small sample size (n = 7). There was no trend in the probability of evading with increasing mite load in August for either males or females.

**Endurance**

The total distance (TD) the males ran in July was negatively correlated with mite intensity (TD = 23.77 - 0.56*mites; Adj. R² = 0.28, F = 8.04, p = 0.011). According to the regression equation, average TD was nearly 24 m with no mites but declined to < 12 m at intensities of 20 mites (Figure 3.14). Mite intensity explained 28% of the variation in total distance run. In July, the best performing male (i.e., fastest leg of either turnaround or fast-run distance) ran nearly 30 m before reaching exhaustion.

In August, the relationship between mite intensity and endurance was much weaker, with mites explaining only 3% of the variation in endurance (Adj. R² = 0.033, p < 0.23, df = 17). Four of the males in August ran farther
than the best performing male in July. In August, the best performing male ran nearly 45 m before reaching exhaustion (Figure 3.15).

The only strong predictor for endurance of July females was their residuals of mass/SVL which accounted for 47% of the variation in running distance ($p = 0.053$, df = 7). None of the variables measured were significant predictors for endurance of females tested in August.

Speed and endurance of males and females increased from July to August (Table 3.2). Both measures of performance are similar between the sexes in both months, with both sexes showing performance improvement in August, after the period of reproductive activity.

**Mite Intensity**

Table 3.3 shows that the average intensity (number of mites per lizard) was 4-5 mites per lizard. The average intensity of *G. texana* on *S. woodi* was not significantly different between males and females either during or after the reproductive period.

**Mite Removal**

If mites had no effect on performance, then upon re-running individuals after mite removal, 50% would be expected to run faster or farther and 50% would be expected to run slower or less far. In fact, 2-3 days after mite removal, all but three of the lizards ran faster and farther. Following removal of mites, the lizards ran an average of 0.73 m/s faster (Figure 3.16); ($t = 3.91$, df = 15, $p < 0.0014$) and 4.5 m farther (Figure 3.17); ($t = 2.16$, df = 17, $p < 0.046$).
Discussion

Morphology, physiological parameters and performance of lizards were all affected by mite infestation. The effects and their implications will be discussed below.

Morphology/Histopathology

Muscle tissue behind the knee joint was clearly inflamed. Goldberg and Bursey (1991a) also found that in response to mite infestation, skeletal muscle was infiltrated by an inflammatory response that included histiocytes, heterophils, fibroblasts, and lymphocytes. The proliferation of lymphoid cells into the leg musculature and nerves with the resulting myositis and neuritis could be painful and cause the observed decrease in running performance. Swelling could reduce the speed and angle of limb motion. The physical presence of the mites alone could interfere with flexion at the knee joint.

Hematocrit and Osmolarity

Lizards with mites had higher hematocrit than lizards for which the mites were removed with ivermecten. This result was not expected because host blood loss, anemia (Mader et al. 1986), and even exsanguination are common effects of ectoparasites (Frank 1981; Dunlap and Mathies 1993; Salvador et al. 1996). Mader et al. (1986) documented an extreme case of parasitism of captive chuckwallas (Sauromalus obesus) by the mite Hirstiella trombidiformes. The other cases involved ticks, which are much larger than mites and are capable of consuming more blood per individual parasite. In the case documented here, with levels of parasitism comparable to those observed in the field (pers. obs.), the lizards were apparently able to avoid
anemia. However, this story can be turned around. It may be that with mites attached, the lizards were unable to maintain plasma volume. This is contrary to studies of desert lizards in which homeostasis of plasma volume is achieved despite significant losses of body water to evaporation (Bradshaw and Shoemaker 1967; Nagy 1972; Lemire et al. 1982), and suggests that mites have an impact that is fundamentally different than dehydration due to evaporation. Perhaps under stressful conditions (like parasitism), lizards can, via the sympathetic nervous system release blood cells stored in the spleen or liver. In humans, release of blood cells from the spleen can raise hematocrit one to two per cent, and in so called lower animals, blood storage is even greater (Guyton 1991).

Despite the differences in hematocrit, there was no difference in plasma osmolarity between the experimental and control groups. If dehydration were an effect of ectoparasitism, then higher plasma osmolarity would be expected in the experimental group. Perhaps the lizards are able to respond to reduced blood volume and still maintain plasma osmolarity. Chuckwalla lizards (Sauromalus hispidus) on islands in the Gulf of California, were able to maintain osmotic homeostasis despite losing 20% of their total body water and consuming a high potassium diet (Smits 1985). Regardless, the probable major effect of higher hematocrit is increased viscosity of blood.

Performance and Hematocrit

Lizard performance was negatively correlated with hematocrit levels, with slow-down distance showing the strongest relationship. If blood viscosity is higher, then its flow must be lower because, according to Poiseuille's equation, fluid flow through a tube is inversely proportional to
its viscosity (Schmidt-Nielsen 1983). The rate of lactate clearance from muscles would be reduced proportionally with the decrease in blood flow. Lactate concentrations would rise faster in lizards with increased hematocrit, and this could account for the decrease in the slow-down distance. The weak negative correlation of turn-around distance with hematocrit is consistent with Crowley (1985) who found that sprinting performance of *Sceloporus undulatus* was relatively insensitive to the effects of dehydration. The strong negative correlation between slow-down distance and hematocrit is consistent with Wilson and Havel (1989), who found that dehydration (determined by % mass loss) reduced the endurance of *Uta stansburiana*. Thus, there is a compelling chain of causation from parasitism, increased hematocrit, increased blood viscosity, decreased lactate clearance, and decreased endurance. With a larger species it would be possible to measure lactate concentrations (e.g., Gleeson 1991).

**Maximum Performance**

The average maximum speeds we found were similar to those recorded in (Miles 1994); but the highest maximum speeds we observed were nearly 70% faster. These results are substantially higher than those obtained in the lab and illustrate the limitations of previous lizard racetrack studies. The relationships among speed, endurance, and mite loads were quite strong, but not consistently so (see below). The outlier in Figure 3.13b showed a phenomenal performance. We decided to eliminate that animal in one calculation of the regression relationship between maximum performance and mite load because it was so unusual. We suspect that its mites may have just all emerged as adults and attached. Another possibility is that particular individual was extremely agitated. This individual does force us to think
about "motivation" as a factor in performance studies. On the other hand, mites may simply not be as debilitating following the reproductive season when testosterone levels are lower, energy budgets are decreased, and relatively more energy is devoted to maintenance (see below).

**Seasonal Effects on Performance**

The strong negative correlations between mite intensity and performance (speed and endurance) during the breeding season decreased or disappeared as the breeding season ended. This is not surprising as reproductive activity has a huge energetic cost. A clutch of eggs represents about 8 kJ of energy (unpubl. data), which is equivalent to 2 weeks worth of a daily energy budget of 0.68 kJ/(animal day), with 88% converted to reproduction (from Nagy 1983). We expected tests of maximal performance during reproduction to be more likely to show effects of parasitism. Though mite intensities remained constant, average speed increased 12% for males and 25% for females, and average endurance increased by 5 m following the reproductive season. The seasonality of effects may be one explanation for why costs of parasitism have been difficult to measure consistently in the past.

**Condition**

Condition (the residual of mass regressed on SVL) consistently showed some predictive value for performance. Relatively heavy animals ran slower and for shorter distances. This type of relationship has been documented for pregnant female lizards (Shine 1980d; Bauwens and Thoen 1981), and recently fed snakes (Garland and Arnold 1983; Ford and Shuttlesworth 1986). This is not surprising either, as it takes more work to move more mass. However, its
implications for trade-offs in life histories are intriguing. Condition is generally assumed to be a monotonically increasing function, i.e., the fatter the better. This assumption may reflect evolutionary ecology's temperate-zone, homeotherm biases. The results of the current study suggest that rather than being a linear function, condition can asymptote or even decrease with respect to fitness. There are performance (i.e., speed and endurance) costs to being heavy and they may have some interesting implications for morphology (e.g., body shape and fat storage) and seasonality of reproductive strategies. Do animals have the ability to store more fat than they actually do? Is the risk of not having enough energy to overwinter balanced against the likelihood of being too heavy and slow? Detailed studies that examine trade-offs between condition and performance within individuals over time could be quite illuminating.

**Turn Tactics**

Changes in behavior may compensate for reduced locomotor ability (Garland and Losos 1994). If an animal is debilitated by parasites, it may be risky for it to attempt to run away from a predator. An evasive strategy could be more effective for avoiding capture. That the effect of mites on behavior was observed in males only during the breeding season is consistent with existing hypotheses about effects of testosterone (T) (see below). However, the lack of an effect in July females could be an artifact of small sample size or simply the swamping of any variation or correlation by the massive effects of gravidity.

Behavioral changes have been documented in response to other stressors besides parasites. Ectotherms tend to be more wary when they are below their optimal temperature (pers. obs.). Females reduce their cost of
reproduction by changing behavioral tactics. Gravid female skinks (*Eumeces laticeps*), for example, tend to be less active and less conspicuous on the surface than when they are post-reproductive (Cooper et al. 1990). Likewise, gravid female *Lacerta vivipara* allow closer approach by observers apparently as a way of increasing crypsis (Bauwens and Thoen 1981), as do gravid garter snakes (Brodie 1989).

**Sexual Dimorphism**

Testosterone is a well documented immune suppressor (Salvador et al. 1996; Saino et al. 1995), and could reduce the immune response in males, making damage from the mites worse. This could explain the decrease in effects of mites on male lizards between July and August. With reduced T in August, males could be healthier. Additionally, allocation of energy for maintenance could be reduced under the effects of T (Salvador et al. 1996). A male could devote so much energy to territoriality and reproductive behaviors that little energy remains for maintenance, repair, and immunity. Marler and Moore (1991) found that males with artificially elevated T could only be maintained in the field with dietary supplementation because their levels of reproductive activity were so high. More detailed studies of pathology that examine both adult male and female hosts and/or compared them to juveniles could be interesting, as could manipulations of T levels as in Salvador et al. (1996).

The lack of an effect of mites on female *Sceloporus* speed could reflect that they are not burdened by immunosuppressive effects of T. Also, female reproductive effort, particularly relative clutch mass (RCM = clutch mass/total female mass), could be so great as to overwhelm the effects of mites.
Extending the Paradigm

Maximal whole-animal performance abilities, defined as what animals can do when pushed to their limits, may in fact best be observed in natural or seminatural field environments (contra Garland and Losos 1994). Studies in which the scale of the observations allows subjects to reach their full potential and display behavioral options provide valuable information. Field observations also aid in the assessment of the relevance of lab studies to the field [see Schlesinger et al. (1993), which documents "lizard-fall" in the field with regard to the agility documented in a laboratory setting (Sinervo and Losos 1991)]. A trade-off with field studies vs. lab studies is that because of the increased variation in environmental variables in the field, sample sizes must be larger to achieve the necessary statistical power. This may be impractical for certain species or situations.

Another aspect of extending the paradigm of performance studies is the inclusion of parasitized animals. Lab studies in which animals have had parasites removed would not tell the full story of how traits related to performance evolve. Performance decrements can be directly caused by parasites or at least be correlated with their presence; therefore they should be included in the morphology-performance-paradigm (Figure 3.18). A caveat is that the inclusion of parasites in these studies also increases variation in the measured sample populations (see comments about sample size and statistical power above).

Variation in a trait is a necessary precondition for natural selection to result in evolution (Endler 1986). If there is a heritable component in susceptibility to parasitism (e.g., Møller 1990), then including parasites in performance studies could be important. Even if there is no heritable
component to likelihood of parasitism, there could be heritable rules for behavioral tactics when parasitized or faced with any conditional stressor (see turning tactics above). There are obvious implications of the effects of parasitism for studies of natural selection and both components of sexual selection: mate choice and male-male competition. Links between performance and social dominance in reptiles have already been made (Garland et al. 1990b). Adding parasites to these studies will take longer and require more effort; however because of their emphasis on realism and variation, they should be quite rewarding.

![Diagram](Morphology ➔ Physiology ➔ PERFORMANCE ➔ Behavior ➔ Fitness)

Figure 3.1. The morphology-performance-fitness paradigm (after Miles 1994 and Garland 1994).
Figure 3.2. Venn diagrams of model building strategies (after Levins 1966). Models may simultaneously possess only two of the three properties of realism, generality and precision.

a) this model sacrifices realism for precision.

b) this model sacrifices precision for realism.
Figure 3.3. Stylostome (feeding tube) of an adult female *Geckobiella texana* into the thigh of *Sceloporus woodi*. Only female mites are blood feeders (Goodwin 1954); (1 cm = 40 μm).
Figure 3.4. Inflammatory reaction from the attachment of adult *Geckobiella texana* behind the knees of *Sceloporus woodi*. Lymphocytes extend well into the thigh musculature, filling the interstices between muscle bundles on the left side of the figure (1 cm = 40 μm).
Figure 3.5. Inflammatory reaction from the attachment of adult *Geckobiella texana* behind the knees of *Sceloporus woodi*. Lymphocytes surround and extend into the femoral nerve (see arrow); (1 cm = 40 μm).
Figure 3.6. Hematocrit for parasite-laden lizards after being sprayed with a solution of ivermecten (mites-removed) or water (mites-retained). Symbols represent means (large dots) with standard error bars.

Figure 3.7. Plasma osmolarity for parasite-laden lizards after being sprayed with a solution of ivermecten (mites-removed) or water (mites-retained). Symbols represent means (large dots) with standard error bars.
Figure 3.8. Turn-around distance (m) regressed against hematocrit. As hematocrit increases, the distance covered by the lizard before it turns around decreases.

Figure 3.9. Fast-run distance (m) regressed against hematocrit. As hematocrit increases, the distance covered by the lizard at a fast run decreases.
Figure 3.10. Endurance, as indicated by total distance (m) covered by *S. woodi* individuals in a running trial, regressed against hematocrit.

Figure 3.11. The best performance of males in July as function of adult mite intensity. Maximum speed declines with increasing mite load.
Figure 3.12. Best performance (maximum speed m/s) of males in August with the outlier (indicated by arrow) a) included and b) removed from regression calculation.
Figure 3.13. Logistic regression of running tactic as a function of mite intensity (number of mites per lizard host). The curve represents the probability of the lizard trying to evade capture. With no mites, lizards are likely to evade about 40% of the time (and run, 60% of the time). With 20 mites, lizards are likely to evade nearly 100% of the time. Highly infested animals are more likely to evade rather than run away from a perceived threat.
Figure 3.14. Endurance of males in July as a function of adult mite intensity.

Figure 3.15. Endurance of males in August as a function of adult mite intensity.
Figure 3.16. Paired t-test of maximum speed in m/s before (pre-) and after (post-) mite removal with ivermecten. The heavy line represents the null hypothesis of no difference. The thin line represents the line of fit through the sample. The dashed lines around the thin line represent the 95% confidence intervals for the difference in means. Because the heavy line lies outside the confidence interval, there is a significant difference between the speeds before and after mite removal. Following removal of mites, the lizards ran an average of 0.73 m/s faster, (t = 3.91, df = 15, p < 0.0014).
Figure 3.17. Paired t-test of total distance (endurance) before and after mite removal. For interpretation, see above. Following the removal of mites, the lizards ran 4.5 m farther \((t = 2.16, \text{df} = 17, p < 0.046)\).

Figure 3.18. The morphology-performance-fitness paradigm extended.
Table 3.1. Regressions of performance variables against hematocrit values for *S. woodi*.

<table>
<thead>
<tr>
<th>performance variable</th>
<th>regression equation</th>
<th>Adj. $R^2$</th>
<th>F-statistic</th>
<th>$p^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAD</td>
<td>$= 11.97 - 15.54 \times \text{Hct}$</td>
<td>0.069</td>
<td>0.55</td>
<td>0.49</td>
</tr>
<tr>
<td>FRD</td>
<td>$= 24.12 - 52.90 \times \text{Hct}$</td>
<td>0.52</td>
<td>11.81</td>
<td>0.0074</td>
</tr>
<tr>
<td>TD</td>
<td>$= 38.24 - 66.48 \times \text{Hct}$</td>
<td>0.39</td>
<td>7.35</td>
<td>0.024</td>
</tr>
</tbody>
</table>

a. TAD is turnaround distance; FRD is fast-run distance; TD is total distance

b. $P_\alpha = 0.017$, due to Bonferroni correction

Table 3.2. Summary of average maximum performance values for male and female *S. woodi* in July and August.

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>maxqual (m/s)</td>
<td>Total Dist. (m)</td>
</tr>
<tr>
<td>sex</td>
<td></td>
<td></td>
</tr>
<tr>
<td>male</td>
<td>1.89 ± .68</td>
<td>21.43 ± 6.94</td>
</tr>
<tr>
<td>female</td>
<td>1.55 ± .46</td>
<td>20.14 ± 9.82</td>
</tr>
</tbody>
</table>

Table 3.3. Average intensity of *Geckobiella texana* on *Sceloporus woodi* during and after the reproductive season.

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>sex</td>
<td>mite intensity</td>
<td>mite intensity</td>
</tr>
<tr>
<td>male</td>
<td>4.39 ± 1.28 (n = 26)</td>
<td>3.96 ± 0.99 (n = 24)</td>
</tr>
<tr>
<td>female</td>
<td>5.57 ± 2.46 (n = 7)</td>
<td>4.33 ± 0.99 (n = 24)</td>
</tr>
<tr>
<td>P</td>
<td>0.67</td>
<td>0.79</td>
</tr>
</tbody>
</table>
CHAPTER 4
EFFECTS OF ADULT MITES ON LIZARD METABOLIC RECOVERY FROM EXERCISE

Introduction

Mites are commonly found on free-living reptiles and they frequently become a problem for captive animals because they can reach high intensities and enjoy increased transmission rates among stressed hosts with decreased immunity. Histopathological response to mites (Goldberg and Bursey 1991a; Goldberg and Holshuh 1992), and mite prevalence in both space (Allred and Beck 1962; Spoecker 1967) and time (Loomis and Stephens 1973) have been documented for lizards. However, there have been few studies documenting the effects of ectoparasites on the physiology of lizards. Dunlap and Mathies (1993) found that tick larvae significantly reduced the hematocrit and body condition of lizards that were also infected with malaria. Effects of mites on performance have been addressed previously (Chapter 3); but there is another aspect of performance that is frequently overlooked: metabolic recovery from exercise.

The significance of anaerobic metabolism to the natural histories of amphibians and reptiles has been well documented. It is a major source of energy for intense burst activities such as predator escape, intraspecific combat, and subduing large prey items (Pough and Andrews 1985a; Gatten 1985). As glycogen is depleted in muscles, lactate accumulates, resulting in reduced strength and endurance. In order to regain their full capabilities, the animals replenish levels of muscle glycogen via gluco- or glyco-neogenesis (Gleeson 1991; Gatten and Clark 1989). Gleeson (1982) found that replenishment of muscle glycogen through these mechanisms can take up to
2.5 h at 35 °C in *Sceloporus occidentalis* following exhaustion. This recovery period is a cost of anaerobiosis that must be repaid following any intensive activity, and is a function of many factors [e.g., body size, temperature (Gleeson, 1980; Wagner and Gleeson, 1997), epinephrine and glucagon, which stimulate lactate removal (Gleeson et al. 1993; Scholnick et al. 1997), and seasonality (Gleeson, 1985)].

Any factor that increases this recovery time could be of ecological importance. The adult female pterygosomid mite *Geckobiella texana*, sucks blood from its *Sceloporus* hosts (Goodwin 1954). The potential for anemia, reduced blood volume, and dehydration due to parasitism by mites requiring blood-meals, provided an excellent opportunity to examine physiological and ecological effects on the recovery time of the host following intense exercise. In this study I tested whether *Geckobiella texana* mites reduce endurance and increase recovery time of the Florida scrub lizard *Sceloporus woodi*.

**Methods**

Lizards were captured in Ocala National Forest, Marion County, Florida and maintained in a colony at the University of Florida, Gainesville, Florida. Animals were kept in terraria illuminated with full-spectrum fluorescent lighting, and provided with mealworms every day and water *ad libitum*. These trials were run in the Fall of 1997, when animals were post-reproductive. A total of 12 females and 8 males were used over the course of the study. At 25 °C, lizards were chased on a circular indoor track, 4 m in circumference with a natural sand substrate, until they lost their righting response [for further discussion of this technique, see Huey et al. (1984)]. This duration, measured in seconds, was defined as "endurance." The exhausted lizards were then placed on their backs in terraria and timed until they
righted themselves and began moving and behaving normally. This duration was defined as "recovery time." The number of adult *Geckobiella texana* mites on each lizard was counted and defined as "mite intensity." The maximum duration and minimum recovery time for each level of intensity was to used to better delineate the limits of lizard performance. Lizards were later sprayed with ivermecten [a 1% sterile solution of Ivomec®, Merck & Co., Inc., Rahway, NJ diluted with water (0.5 ml Ivomec®/ liter H2O), after Abrahams (1992)] to remove the mites and then one week later were again subjected to the endurance and recovery trials.

To analyze the data, I used linear regression with mite intensity as the independent variable and the maximum endurance, and minimum recovery time for each level of intensity as the dependent variables. Data were checked visually for normality and analyzed using JMP In software (SAS Institute 1996). I performed a Wilcoxon signed-rank test (the non-parametric equivalent of the paired-t test) with the pre- or post- treatment recovery times.

**Results**

Endurance declined from about 2 min with no mites to 0.5 min with an intensity of 35 adult mites (Figure 4.1). Maximum endurance was negatively correlated with mite intensity. Minimum recovery time increased from 2.5 min to 12.5 min, (Figure 4.2) and was positively correlated with mite intensity.

In trials conducted after mites were removed from the lizards, the average recovery time decreased 40%, from 10.3 min to 6.5 min (Table 4.1). A Wilcoxon signed-rank test indicated that the 3.8 min in recovery time difference between the two treatments was highly significant ($Z = 22.5, P =$
0.02, df = 9). None of the other performance variables were significantly different between treatments.

Discussion

Florida scrub lizards (*Sceloporus woodi*) infested with adult mites (*Geckobiella texana*) showed decreased running endurance and increased recovery times. The decline in endurance is concordant with the results presented in Chapter 3. The increase in time to recover from exhaustion is strong, though the mechanism behind it is not clear. Perhaps the muscle inflammation shown in histological sections (Chapter 3) interferes with glyconeogenesis that occurs in skeletal muscle (Gleeson et al. 1993). An increase in hematocrit is correlated with mite parasitism, and the associated increased viscosity of blood could reduce the rate of lactate clearance from muscle tissue.

Recovery is a frequently underappreciated aspect of ectotherm whole-organism performance. For sit-and-wait predators such as phrynosomatid lizards, short, rapid, anaerobic sprints for food capture and territorial displays are the most common type of activity (Pough and Andrews 1985a). The advantages of anaerobic sprint capability is its relative insensitivity to temperature and dehydration (Crowley 1985). The disadvantages include accumulation of lactate and hydrogen ions in muscle tissue that must be cleared and "processed" before anaerobic capacity can be regained. Animals that are paying off an oxygen debt do not engage in foraging or social activities. They also could be vulnerable to predation. The inescapable cost of this debt may be factored into the behavioral decisions animals make (e.g., the turnaround distance measured in the previous chapter). Animals in excellent condition may be able to recover from a sprint in a fraction of the time it takes
animals in poor condition to do so. A lizard faced with sprinting away from a predator at full speed or making short, evasive maneuvers to escape, may choose the latter if the cost of recovery time from an extended sprint is high and either tactic is equally successful in avoiding predation. The cost of increased recovery time caused by parasites could shift the point at which that behavioral switch from "flee" to "evade" is made.

The fivefold increase in metabolic recovery time from exhaustion in heavily parasitized individuals compared to unparasitized individuals, and the 40% decrease in average recovery time following mite removal suggest that parasitism may significantly reduce the time available for other activities in lizard time budgets. The effects of parasitism by mites may be more substantial for their lizard hosts than previously appreciated.

Table 4.1. Effect of treatment with ivermecten on lizard performance measures.

<table>
<thead>
<tr>
<th>Performance Variable</th>
<th>Difference from Zero</th>
<th>Signed-Rank Statistic</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>endurance</td>
<td>-2.8</td>
<td>2.5</td>
<td>0.82</td>
</tr>
<tr>
<td>recovery time</td>
<td>3.78</td>
<td>22.5</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Figure 4.1. Maximum endurance as a function of mite intensity. As mite intensity increases, endurance declines ($y = 108.78 - 2.60 \times \text{Mite Intensity}$, $n = 14$, Adjusted $R^2 = 0.39$, $F = 9.44$, $P = 0.0097$).

Figure 4.2. Minimum recovery time as a function of mite intensity. As number of mites per lizard increases, the time required for full recovery from exhaustion increases ($y = 3.18 + 0.22 \times \text{Mite Intensity}$, $n=14$, Adjusted $R^2 = 0.60$, $F = 20.84$, $P = 0.006$).
CHAPTER 5
SPATIAL AND TEMPORAL ASPECTS OF CHIGGER AND MITE ABUNDANCE WITH SPECIAL REFERENCE TO LANDSCAPE BURNING AND DISTURBANCE

Introduction

The Florida scrub was unique. . . . There was perhaps no similar region anywhere. . . . The soil was a tawny sand, from whose parched fertility there reared, indifferent to water, so dense a growth of scrub pine...that the effect of the massed thin trunks was of a limitless, canopied stockade. . . . It seemed inpenetrable. . . .Wide areas, admitted of no human passage. . . . In places the pines grew more openly, the sunlight filtered through and patches of ground showed bald and lichened. . . . A random patch of moisture produced, alien in the dryness, a fine stand of slash pine or long-leaf yellow. These were known as pine islands. To any one standing on a rise, they were visible from a great distance.

-Marjorie Kinnan Rawlings, South Moon Under

As described by Rawlings (1933), the Ocala region is primarily a matrix of two upland ecosystems: scrub and high pine. The Florida scrub ecosystem is perhaps best summarized by (Myers 1990, p. 151) as “mature forests of tall, twisted leaning sand pine (Pinus clausa) rising above an impenetrable mass of evergreen scrub oaks; rusty lyonia, rosemary; unusual varieties of holly, bay; and hickory, and an array of inconspicuous species, many with restricted distribution.” An estimated 40-60% of its species are endemic, making scrub Florida's most distinctive ecosystem (Myers 1990). Scrub is pyrogenic and maintained by fires that occur every 15-100 years. The “varieties” of scrub patches seen today reflect their different fire histories (Myers 1990).
Embedded in these extensive areas of scrub are islands of high pine consisting of open woodlands of longleaf pine (*Pinus palustris*) over a cover of wiregrass (*Aristida stricta*), and occasional clumps of turkey oaks (*Quercus laevis*). High pine is maintained by fires recurring every 1-15 years. In the absence of fire, turkey oak begins to dominate in sandhills. Despite their difference in appearance, scrub and high pine are strongly associated with one another as they both occur on dry, infertile uplands whose soils are derived from the same parent material, both are maintained by fire, and the ignition of scrub depends on flammable high pine (Myers 1990).

In Ocala National Forest, long leaf pine islands are burned on a regular basis to mimic what is thought to have been the natural burn cycle. This burn cycle is used to prevent the pine islands from being overgrown by hardwoods and sand pine. However, to create "edge" for deer, land managers have allowed some clumps and stands of oak to persist in the pine islands. Kerr Island, for example, has alternating patches long leaf pine and turkey oak in some areas.

In much of Ocala National Forest, sand pine (*Pinus clausa*) is managed for pulpwood production. To protect this asset, U.S. Forest Service personnel normally quickly extinguish fires in sand pine scrub. Accidental burns are salvage logged. Clear cuts of unburned sand pine (typically 8-25 ha) leave tree slash and crushed shrubs throughout the site. Site preparations for new sand pine plantings include roller-chopping, which disturbs 100% of the soil surface to 15 cm depth or "bracke" seeding which disturbs about 30% of the soil surface by drilling and depositing seeds at fixed intervals (Greenberg 1993).

Campbell and Christman (1982) argued that clear cutting mimics wildfire by creating a similar habitat structure. Similarities between clear-cuts
and wildfire include above-ground tissue death, biomass removal, and bare-ground exposure. These effects are why many scrub plants (Greenberg et al. 1995b), birds (like the Florida scrub jay, *Aphelocoma coerulescens*, a disturbance specialist; Greenberg et al. 1995a), and reptiles (Greenberg et al. 1994) respond similarly to fire and clear-cuts. There are however differences in nutrient cycling, coarse woody debris and standing dead biomass (Greenberg 1993).

This study was undertaken to 1) assess whether fire frequency affects chigger densities in long leaf pine/turkey oak habitats and chigger intensities on Florida scrub lizard (*Sceloporus woodi*) populations associated with these patches having different fire histories, 2) identify microhabitat preferences of chiggers, 3) identify daily and seasonal patterns of chigger activity, and 4) identify if there are any patterns of ectoparasite distribution associated with United States Forest Service (USFS) silvicultural practices.

To better understand how landscape level modifications could affect ectoparasite populations I reviewed the life cycles of the ectoparasites and their interactions with hosts and habitat. *Eutrombicula alfreddugesi* is a trombiculid mite. Only the larval, "chigger" stage in this mite family is parasitic on vertebrates; however they are not host specific. *E. alfreddugesi* has been found on 126 species (Benton 1987). The juveniles and adults are free-living in the soil and eat small arthropods and their eggs in the leaf litter. Because of the juveniles' and adults' dependence on leaf litter arthropods, I hypothesized that any landscape modification that affected leaf litter would have an impact on chigger intensity. In contrast, the pterygosomid mite *Geckobiella texana* lives its entire life cycle on its lizard host and has been found only on lizards of the genus *Sceloporus* (Lane 1954; Jack 1959). I have observed larvae, juveniles and adults moving from one individual lizard
host to another in captivity. Because they are so tightly bound to their lizard host for their entire life cycle, I predicted that any landscape modifications that affected lizard densities or frequency of interactions would also affect *Geckobiella* prevalence on the lizards.

**Methods**

**Microhabitat: Longleaf vs. Turkey Oak**

To determine densities of chiggers in habitats with different burning frequencies, I surveyed plots in Kerr Island, Ocala National Forest, Marion County, Florida. Kerr Island is an island of high pine (*Pinus palustris*) embedded in an alternating matrix of turkey oak (*Quercus laevis*). High pine habitat is shown in Figure 5.1. Turkey oak habitat is shown in Figure 5.2. In May of 1997, I randomly placed two sets of fifteen, 10 cm square black ceramic tiles in each the two different habitat types and examined them for chiggers after 10 min (Williams 1946).

**Lizards**

To determine the intensity of chigger infestations on *Sceloporus woodi*, I captured animals by noose, noted the habitat type (long leaf pine or turkey oak) at the site of capture and did total body counts with the aid of a hand lens. Comparisons among sites were made with the Wilcoxon rank sum test.

**Diel Cycles**

To determine daily patterns of chigger activity, I placed fifteen 10 cm black square tiles out in the field (Williams 1946) and examined them for
chiggers every hour from 0800-2000 h on 29 June 1997 at a site 2 km E. of Mill Dam Lake, on the south side of State Road 40 (SR40). The tiles were divided into 3 groups of 5 tiles each. Each of the groups was placed within 5 m of the other. One group was placed along an edge between an old (> 10 yrs) sand pine stand and the U.S. Forest Service road ringing a young (6-9 yrs) sand pine stand. A second group was placed in open, sandy areas between the road and the young scrub. The third group was placed at the edge of the young scrub and the open sandy areas. A typical edge between a young scrub and mature sand pine is shown in Figure 5.3.

**Annual Cycles**

To determine seasonal patterns of chigger activity, I made monthly surveys of chigger intensity by noosing lizards at a site 2 km E. Mill Dam Lake, on the south side of SR40 (same site as above) and counting all chiggers on them. This site was clear cut and reseeded in 1988. I did not sample the habitat for chiggers on a monthly basis.

**Silvicultural Practices**

To assess the potential effects of silvicultural practices on *Geckobiella texana* populations, I determined the prevalence of *Geckobiella* mites on *Sceloporus woodi* at 8 sites that had well documented histories and were either roller-chopped (n = 4) or not roller-chopped (n = 4). Histories and localities of these sites are given in Table 5.1.
Results

**Microhabitat**

In 1997, examining two 15 tile plots of each habitat type (n = 60 tiles), I found no chiggers in the longleaf pine habitat using the tile method. Chiggers averaged 0.4/tile (40 chiggers/m²) in the turkey oak habitat. There was a highly significant difference in chigger density between the habitat types (Kruskal-Wallace rank sum, S = 1020, Z = 2.77, P > |Z| = 0.0055).

**Lizards**

The intensities of chiggers on *Sceloporus woodi* was related to habitat type in which they were found. In May of 1994, in longleaf pine habitat, the average intensity was 13.4 chiggers per lizard (n = 13). In turkey oak, the average intensity was 68.8 chiggers per lizard (n = 12), (Figure 5.4a). The intensities were significantly different, (Kruskal-Wallace rank sum, S = 225, Z = 3.73, P > |Z| = 0.0002). In May of 1997 in different plots of longleaf pine habitat, the average intensity was 26 (n = 7). In turkey oak habitat, the average intensity was 53 (n = 8), (Figure 5.4b ). The intensities were significantly different, (Kruskal-Wallace rank sum, S = 35, Z = -2.38, P > |Z| = 0.017).

**Diel Cycles**

There was a pronounced diel cycle of activity for the chiggers. They were active just after dawn and very active especially around dusk (Figure 5.5). There was also a spatial component to their activity. No chiggers were ever found on the road. There were more chiggers active along the mature sand pine outer edge than the young scrub inner edge.
**Annual Cycles**

There was a definite seasonality of chigger intensities with peaks in the summer (Figures 5.6 and 5.7). Male lizard chigger intensity peaked in May, whereas on females, August was the peak month of chigger infestation. Intensities were essentially zero from December to February. Males had higher intensities than females for every month except for August.

**Silvicultural Practices**

There is some indication of a relationship between silvicultural practices and prevalence of *Geckobiella texana*. Roller-chopped sites had uniformly high prevalences (> 60% of lizards sampled were infested), whereas unchopped sites had a bimodal distribution of mites, with both high and low prevalences (Figure 5.8).

**Discussion**

**Fire and Microhabitat**

The long leaf pine at Kerr Island and other pine islands in Ocala Forest is burned on a regular schedule of 2-3 years (Laura Lowery, USFS, pers. comm.). The turkey oak habitats within Kerr Island exist because these areas are not burned. Because of differences in fire regime, conditions on the ground in the two habitat types are quite different. In the long leaf pine areas there is less shade and a thin (2-3 cm), homogeneous ground cover of pine needles that is depauperate of arthropods (pers. obs.). The ground cover of pine needles is reduced following a fire, and with frequent fires, never accumulates to be more than a centimeter or two. Chiggers in long leaf pine
are probably limited by a lack of food for juveniles and adults. In contrast, the turkey oak areas have more shade and a thicker (5-6 cm), heterogeneous layer of leaf litter that hosts a diverse assemblage and high density of arthropods upon which the juvenile and adult *Eutrombicula alfredugesi* can feed.

**Fire and Pest Control**

Fire has long been used to control arthropod pests in agricultural, range and pasture lands (Komarek 1970). In the first half of this century, north Floridians used to burn areas around their homes on a regular basis in part to reduce chigger and tick populations (R. Franz, pers. comm.).

Wilson (1986) found reduced abundance of *Ixodes dammini* adult ticks by up to 88% for as long as 6 months after a burn. Mather (1993) found that the abundance of *Ixodes dammini* nymphs was reduced by 49% in burned wood lots as compared to unburned ones. However, the risk of encountering nymphs infected with the spirochete, *Borrelia burgdorferi*, which causes Lyme Disease, was the same because different subpopulations of nymphs (feeding on rodents or deer) were disproportionately affected by the fire.

Reed et al. (1977) reported a 91% reduction in chigger populations 2 days after a burn. The populations recovered to reflect just a 22% reduction within a month. Rapid increases in the populations following the burn led them to conclude that gravid female mites and/or eggs in the soil were not as heavily affected by fire. Stressing the dynamics of the situation, they also pointed out that if hosts were attracted to the burn, replete chiggers detaching from them could actually increase the chigger population in subsequent years.
Effects of Fire on Arthropods

In general, fire causes declines in arthropod abundance and diversity. In the New Jersey pine barrens, post-fire decreases in soil fauna of 50% and arthropod taxa of 80% were attributed to decreases in organic material, drier conditions, and greater temperature extremes (Buffington 1967). In loblolly pine (Pinus taeda) habitat in North Carolina, the soil fauna was reduced by one third with proportions remaining roughly the same except for a greater decrease in earthworms and an increase in ants (Pearse 1943). In loblolly pine (Pinus taeda) in South Carolina, micorarthropod abundance is reduced by periodic and annual burns (Metz and Farrier 1973; Dindal and Metz 1977). Populations of springtails decreased dramatically and ant populations increased in response to frequent fires (Metz and Dindal 1975; Dindal 1979). In longleaf pine, there were 11 times more organisms in the upper 5 cm of unburned soil than in burned soil (Heyward and Tisson 1936).

Post-Fire Recovery of Arthropods

Metz and Farrier (1971) found mesofaunal recovery was less than 43 months in South Carolina. Neumann (1991) found that nearly all arthropod diversity rebounded within 5 years after a burn in Australian mountain ash forest. It is likely that burning every 2-4 years will keep many arthropod species' densities low.

Effects on Hosts

Following fires, endo- and ectoparasites may be reduced to benefit birds and mammals. There is some evidence to support this assertion in the game management literature (e.g., Brynard 1971; Grange 1949). Prescribed burns
reduced tick infestation in young wild turkeys under experimental conditions (Jacobson & Hurst 1979). Fire has also been used in anthrax control programs for Canadian bison (Novakowski et al. 1963) and African wildlife (Pienaar 1967). Bendell (1974) examined blue grouse after a fire and found low levels of internal, external and blood-borne parasites that increased steadily with time. Bendell (1955) found that *Dispharynx* and *Plagiorhynchus* worms (which cause damage to blue grouse chicks) appeared 12 years following a burn where they had not been found 5 years following the burn. Both worms are transmitted by a sowbug (*Porcellio* sp.) intermediate host, which does not tolerate xeric postfire conditions. Worm intensity of birds in an older burn was twice that of birds in a 14 year younger burn. Interestingly, pathology was only in young birds. The clutch size of adults was not affected by worm infections.

**Effects on Reptiles**

The effects of fires on amphibians and reptiles are not well studied. Prescribed burning in fire-adapted communities, by limiting succession to other forest types, may well be beneficial to them (Means and Campbell 1982). However the interactions between fire, reptiles, and their parasites may have other effects. Cogger (1969) documented a higher density of *Amphibolororous fordi* lizards in 10-year post-fire regrowth than in unburnt control areas. Barbault (1983), Caughley (1985), Fyfe (1980) and Lillywhite (1977) all found changes in post-fire community composition and relative abundance. Braithwaite (1987) found responses of different lizard species ranging from intolerance to preference of burned patches.

Anderson and Tiebout (1993), studying lizard communities in Ocala National Forest, found it difficult to distinguish between effects of burns and
salvaging operations in sand pine scrub because nearly all burns are salvaged for timber. They recommended that salvaging operations be suspended in some burned stands to allow the study of just the effects of fire.

There is probably no universal effect of fire on reptiles. Some species will thrive, some decline, and others show no effects. Management decisions that affect fire frequency may unintentionally benefit some species at the expense of others.

Lizards and Microhabitat

The pattern of chigger infestation at Kerr Island was closely related to the microhabitat type in which the lizards were found. S. woodi have relatively small home ranges (350-700 m², in Avon Park, Florida, Grant Hokit, pers. comm.). Sampling of the lizards was not intensive enough to determine if lizards that lived near edges had intermediate intensities of chiggers. Microhabitats at Kerr Island are closely tied to their particular fire histories (see above).

Diel Cycles

Peaks of chigger activity around dawn and dusk found in this study are consistent with Clopton and Gold (1993) who found that summer activity of E. alfreddugesi chiggers in Oklahoma was greatest in the late afternoon and early evening, with another small peak of activity occurring around sunrise. Crepuscular hours represent "temporal ecotones" when both diurnal and nocturnal hosts are likely to be encountered. The activity peaks at dawn and dusk may indicate physiological (e.g., thermal or water balance) constraints on the chiggers as well. Activity times that extend into the early morning and evening (i.e., dawn and dusk) may incur costs of parasitism to reptiles.
Perhaps this cost needs to be considered in optimal foraging/activity models of reptiles.

My results from the edges of the Forest Service road (Figure 5.5) agree with Clopton and Gold (1993) who found high densities at the edges of habitat types and in areas with dense ground vegetation. They found chigger densities were highest in forest edge areas of high relative humidity, moderate temperature, low incident sunlight, and increasing substrate vegetation. Chiggers were rarely found in undergrowth beneath the tree canopy. This spatial distribution makes sense for a generalist ectoparasite (E. alfreddugesi has been found on 126 species of vertebrate hosts, Benton 1987) that is likely to find many different host species and individuals at ecotones.

Annual Cycles

There was a definite peak in summer activity of chiggers compared to other seasons of the year. Intensity of infestation on males peaked in May when they are actively defending home ranges. Female infestation levels peaked in August when they are searching for appropriate nesting sites, and foraging actively to yolk up their last clutch, rather than simply mobilizing fat reserves, as they do earlier in the season (Hahn and Tinkle 1965; Derickson 1976). Adult males were scarce in August (pers. obs.). Maybe this placed the chigger burden on females that month. Seasonality of chigger infestations has been noted in other lizard-host systems (Loomis and Stephens 1973; Spoecker 1967; Bennett 1977) and mammals as well (Elton and Keay 1936; Jameson and Brennan 1957; Jenkins 1948).

The sexual dimorphism in infestation levels has been observed in other reptile systems. Smith (1996) found that male Sceloporus virgatus tended to have more mites than females, though the difference was
marginally significant \((p = 0.061)\). Bauwens et al. (1983) found that males tended to have higher tick loads than females, but only in areas that he designated as high tick load areas. Males had similar tick loads to females in low tick load areas. Male *Sceloporus woodi* home ranges in south Florida are about twice that of females (Grant Hokit, pers. comm.); thus they would have twice the opportunity to pick up waiting chiggers as they moved through the habitat. My impression is that males also have larger home ranges in the ONF.

Because of the immunosuppressive effects of testosterone \((T)\), males may be less able to resist parasite infestations. Salvador et al. (1996) found that males realized higher levels of infestation when implanted with \(T\). This result could be due them having larger home ranges and/or being immunocompromised.

**Silvicultural Practices**

Roller-chopped sites had uniformly high prevalences (>65%), while sites that had not been roller-chopped had both high and low prevalences clustered around 75% and 25%. Roller-chopping may homogenize the environment, hence the low variance in the chopping treatment. Mite prevalence in the no-chopping treatment is bimodally distributed. The sites represented by the two low-prevalence populations are near one another so spatial autocorrelation may be involved. One of the sites (YB) burned in 1989. Lizard population density may be important in regulating mite prevalence; however, YB showed a maximum lizard density of 180 animals/hectare (Anderson and Tiebout 1993). One working hypothesis is that roller-chopping reduces the amount of vegetative cover on a plot and therefore may increase the encounter frequency of lizards (see Figure 5.9). This would
increase transmission rates of mites among hosts and thereby increase their prevalence in the population. More work is needed to better understand how habitat disturbance affects mites and their host species.
Figure 5.1. Longleaf pine at Kerr Island, ONF in May 1994.
Figure 5.2. Turkey oak at Kerr Island, ONF in May 1994.
Figure 5.3. A typical edge between a young scrub and mature sand pine. The young scrub on the left hand side of the photo is compartment 213, stand 8, which was logged and roller-chopped in October, 1993.
Table 5.1. Histories of sites in Ocala National Forest used to assess mite prevalence.

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Stand</th>
<th>Location&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Date</th>
<th>Treatment</th>
<th># of lizards with mites/ # sampled</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>211</td>
<td>17&amp;18</td>
<td>BC1</td>
<td>1989</td>
<td>burned</td>
<td>2/20</td>
<td>south end</td>
</tr>
<tr>
<td>211</td>
<td>9</td>
<td>BC1</td>
<td>1993</td>
<td>chopped</td>
<td>8/11</td>
<td>north end</td>
</tr>
<tr>
<td>276</td>
<td>9</td>
<td>BC2</td>
<td>1988</td>
<td>chopped</td>
<td>6/11</td>
<td>east end</td>
</tr>
<tr>
<td>276</td>
<td>7</td>
<td>BC2</td>
<td>1988</td>
<td>logged, not chopped</td>
<td>17/21</td>
<td>west end</td>
</tr>
<tr>
<td>276</td>
<td>7</td>
<td>BC2</td>
<td>1993</td>
<td>chopped</td>
<td>17/21</td>
<td>not seeded</td>
</tr>
<tr>
<td>245</td>
<td>13</td>
<td>BC3</td>
<td>1988</td>
<td>not chopped</td>
<td>1/6</td>
<td></td>
</tr>
<tr>
<td>247</td>
<td>6</td>
<td>BC3</td>
<td>1994</td>
<td>not chopped</td>
<td>1/6</td>
<td></td>
</tr>
<tr>
<td>211</td>
<td>19</td>
<td>IS1</td>
<td>1993</td>
<td>not chopped</td>
<td>1/6</td>
<td></td>
</tr>
<tr>
<td>277</td>
<td>22</td>
<td>IS2</td>
<td>1993</td>
<td>chopped</td>
<td>31/38</td>
<td></td>
</tr>
<tr>
<td>213</td>
<td>8</td>
<td>IS3</td>
<td>1993</td>
<td>chopped</td>
<td>31/38</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> BC = broad contact between adjacent stands  
IS = isolated stands (i.e., not adjacent to similar-aged stands)
Figure 5.4. Chigger intensity (number of chiggers per lizard) of *Sceloporus woodi* by habitat at Kerr Island in a) May, 1994; b) May, 1997. Center lines of the means diamonds are group means. Tops and bottoms of the diamonds are the 95% confidence intervals. Since the confidence intervals do not overlap, the means are significantly different between habitat types but not between years within habitat type.
Figure 5.5. Diel patterns of chigger activity, June 1997. Densities are estimates of number of chiggers per square meter of habitat. Activity was greater along the edge of an unpaved road facing rosemary and mature sand pine (closed circles) than the edge facing young scrub (open circles).
Figure 5.6. Monthly intensity of chiggers on male lizards, 1996.
Figure 5.7. Monthly intensity of chiggers on female lizards, 1996.
Quantiles: 90%, 75%, 50%, 25%, 10%

Figure 5.8. Comparison of *Geckobiella* prevalence in roller-chopped (n = 4) and unchopped (n = 4) sites.
Figure 5.9. Possible effects of roller-chopping on vegetation spacing. Shaded circles represent vegetation before roller-chopping (above) and after (below). Reduced cover available for lizards after roller-chopping would increase their likelihood of interaction under the remaining vegetation, which could increase the transmission frequency of mites.
CHAPTER 6
CONCLUSIONS

Introduction

Ocala National Forest is a rich system of which many interesting questions can be asked. Its recent management history has yielded many "replicate" stands of sandpine-scrub of different ages and treatments with which to examine the effects of burning, clearcutting, and roller-chopping on its species and communities. This study has shown that the interactions among Florida scrub lizards, their mites, and their habitat are complex yet fathomable (summarized in Figure 6.1). It has explored the implications of parasite-caused pathology to the physiology and ecology of the host. The integrity of the lizard host's integument is compromised by the presence of chiggers, with an associated increase in evaporative water loss. Running speed and stamina are decreased, and time for metabolic recovery from exhaustion is increased by the presence of adult Geckobiella texana mites.

Prevalence and intensity of chiggers and mites are related to landscape modifications. There are strong negative correlations between burn frequencies and chigger populations in long leaf pine/turkey oak associations (Chapter 5). The relationship between clear-cutting and mite populations is less clear. Whether these problems affect individual fitness and, ultimately, population viability has yet to be determined (Figure 6.1). More data are needed before any major changes to land management practices, (e.g., a halt to the practice of roller chopping) can be recommended.
It is not difficult to generate scenarios that involve interactions between physiological effects of mites on lizards and landscape modifications. If mites decrease sprint endurance and roller-chopping increases the spacing of cover vegetation, then these two factors together could result in increased lizard mortality greater than mites or habitat changes alone might predict. Changes in land use can result in the emergence of new diseases. The regeneration of northeastern U.S. forests coupled with suburban residential development has led to the recent infection of humans by Lyme disease, which was previously confined to deer and field mice (Stolley and Lasky 1995). Penetration of human activities into once isolated areas of Africa has apparently given us Marburg virus, Ebola virus, and HIV (Garrett 1994). There is no reason to think that similar human-induced plagues could not affect other species. My hope is that this study will prompt some serious thinking about how the remaining scrub in Florida will be managed for future generations.

The addition of yet another factor to include in land management plans could be daunting, however, there are compelling reasons to include parasites and disease. The field of conservation biology has shown repeated cycles of growth following enrichment from other disciplines. The application of island biogeographic theory (MacArthur and Wilson 1967) to conservation questions gave rise to a body of work concerned with biological reserve design and effects of habitat fragmentation (Soule and Simberloff 1986). The application of theoretical population genetics led to studies of effective population size, drift, and bottlenecks as they related to conservation genetics (Lande 1988). The role of disease has been highlighted by distemper in the black-footed ferret (Williams et al. 1988). These examples focused on sampling error and its effects on probability of random extinction or
susceptibility to disease. However, most species declines and extinctions are due to habitat loss, fragmentation or modification (Diamond 1989).

Comparatively little work has been done to explore links between habitat modification, disease and conservation. Loye and Carroll (1995) reviewed effects of fragmentation on parasites and concluded that managing for edge can alter relationships between parasites and hosts. Fragmentation, by increasing habitat edges, increases the probability that interior populations can be parasitized because they are now accessible by edge specialists [e.g., Brown-headed Cowbirds (Brittingham and Temple 1983; Rothstein and Robinson 1994)]. Increased contact between different populations and species can introduce new pathogens (see “corridors”, below).

Habitat loss may confine animals to areas that have built up high parasite populations (Loye and Carroll 1995). Yellow baboons (Papio cynocephalus) in Amboseli Park, Kenya move among patches of acacia groves to reduce contact with larval nematodes in their feces. The average time before returning to a grove is greater than the typical duration of the infective part of the nematode’s life cycle (Haufstater and Meade 1982). If acacia groves were lost to landscape modifications (i.e. development), then the average return time of the troops would have to decrease thus exposing them to greater risk of nematode infection.

Stress from reduced habitat quality can increase pathogenicity (Loye and Carroll 1995). Nelson (1962) found that injecting lambs with adrenocorticotropic hormone (ACTH) reduced resistance to keds (hippoboscid flies). This physiological effect can cascade upwards to impact populations. Esch et al. (1975) reviewed stress and parasitism and effects on host population sizes.

Habitat destruction can lead to unusually high populations of refugee species in nearby undisturbed areas (Leck 1989; Lovejoy et al. 1986; Noss 1981).
Long term implications of this crowding effect are not yet known, however higher host densities can increase disease transmission rates, and ultimately select for increased virulence of pathogens (Ewald 1994).

Do human modifications of populations and landscapes have the potential to increase the virulence of pathogens? To explore this question, this review will briefly summarize hypotheses about the evolution of virulence then synthesize ideas about the evolution of infectious disease as they relate to issues in landscape ecology and conservation biology.

The Evolution of Virulence

Parasitology and epidemiology have enjoyed a renaissance in the ecological and evolutionary sciences over the last 15 years (Lehmann 1993). Part of the reason for this revival has been the recognition that in many situations the virulence of pathogens can increase rather than inexorably decrease to benignness as assumed by many earlier workers (Ewald 1994). There are several ways for pathogens to become virulent. The evolutionary logic behind all of them is that natural selection will favor features that increase the passage of genes to the next generation. If virulence is correlated with the rate of pathogen reproduction in the host, then in some situations rapidly reproducing pathogens will be favored and in others, slower reproducing pathogens will be favored. When a pathogen is likely to get transmitted to a new host, rapid reproducers will be favored, because even if they cause the death of their host, their genes will still be transmitted to the next generation. If transmission is unlikely, then a rapid reproducer will not be favored, because it may debilitate or kill its host before transmission is achieved. In this situation, slow reproducers will be favored. Pathogenicity
therefore should be correlated with modes and rates of transmission (Ewald 1994).

Vectors

Vector-borne pathogens can be extremely virulent because they can depend on the vector to insure their transmission. Directly transmitted pathogens (like the common cold virus), rely on their host being mobile enough to encounter other potential hosts. Thus, malaria can totally immobilize its host, yet still be transmitted by a mosquito. The virulence of HIV strains transmitted among IV-drug users is also high as syringes are effective vectors for disease.

Transmission rates can be even higher in hosts that are too ill to keep mosquitoes away. What would the fate be of a cold virus that so debilitated its host, that he or she could not get out of bed? By the same logic, the effects of pathogens on the vectors should be low. A debilitated mosquito is more likely to get swatted, which would mean the end of the pathogen as well.

Transmission Rates

High transmission rates can favor virulence for the reasons outlined above. Ewald (1994) argues that high rates of partner change may have fostered the evolution of increased virulence of HIV in certain communities (e.g., gays in North America and prostitutes in Central Africa). A sexually transmitted disease in a population of mostly monogamous individuals has a difficult job of getting transmitted. It must prolong its period of infectiousness in order to survive in the host long enough to be transmitted in a rare extra-pair copulation.
Selection for virulence can also occur within a host. HIV infections provide a good example. Because it is a retro-virus, HIV has a relatively high mutation rate. If a mutant virus were to either to reduce its latent period or increase replication rate when actively reproducing, then it would have an advantage over its less active kin. Within an individual host, variants that increase viral replication will be favored. Intra-host evolutionary increases in virulence have been documented. Why don’t rapidly replicating strains of HIV dominate in the entire population of HIV positive individuals? Because a host will at some point become so ill that sexual transmission effectively ends (and with it, the lineage of that viral strain). Intra-host selection towards virulence is balanced by inter-host selection towards benignness. As rates of sexual transmission (a function of number and type of unprotected sexual contacts) between hosts increase, the virus can, in effect, afford to replicate more quickly. Like the case of the mosquito-borne pathogen above, a virus assured of transmission can cause greater pathology. Inter-host selection can be seen in the different strains of HIV that have been identified. In West Africa, where social conditions support monogamy, less virulent HIV-2 is prevalent. In East Africa, where economic and social changes have resulted in high rates of prostitution, the more virulent HIV-1 predominates.

Sit-and-Wait Pathogens

Ewald (1994) also argues that “sit-and-wait” pathogens can be extremely virulent because debilitating the host and thereby limiting transmission isn’t important if the host happens upon a very long-lived pathogen. He cites some examples. The prion-based diseases kuru, scrapie, and bovine spongiform encephalopathy (BSE or “mad cow disease”) persist for years in soil and animal remains. Diphtheria and tuberculosis last for months in the
environment. Small pox can live outside a host for 10 years. An island off the coast of Scotland deliberately infected with anthrax during a war-time test in 1942 is still uninhabitable and may remain so for a century or more (Ewald 1994).

**Cultural Vectors**

Ewald (1994) discusses cultural vectors of disease. Attendant-borne transmission and water-borne transmission are linked to high virulence. They should already be in conservation workers’ consciousness because good sanitation and hygiene are important from a patient-oriented clinical perspective. Still, Ewald adds an important evolutionary outlook. Hospital attendants are cultural vectors that move among frequently immobilized patients. As predicted, virulence increased over the durations of diarrhea outbreaks in maternity wards.

Water-borne transmission is another predictor of high virulence for a pathogen. Water can be seen as another cultural vector because of the way humans use it. It pays off handsomely for a pathogen to use its host as a reproductive factory if water will ensure the pathogen’s transmission. An individual debilitated by diarrhea will soil clothing, bedding and the water used to wash them. If waste water mixes with unprotected drinking water, then that host has the ability to infect perhaps hundreds of other people who drink that water. Natural “experiments” have been conducted as water quality has been upgraded and less virulent strains of water-borne pathogens evolve and replace pathogenic ones.

The key to minimizing the virulence of these cultural vectors is cleanliness. This is no surprise, however it is critical to realize that there is an ultimate, evolutionary basis to understanding the effects of these cultural
vectors, in addition to a proximate, physiological one. An evolutionary perspective in this case gives added weight to conventional arguments. Cleaning up a water supply will not only reduce the population size of pathogens, but also their virulence. The flip-side is also true: Degradation of water supplies for humans and wildlife will not only allow pathogens to flourish, but select for especially virulent ones.

**Conservation Implications of the Evolution of Virulence**

**Vectors**

As Ewald has shown, vector-transmitted diseases can be especially nasty. Any landscape level treatments that improve conditions for vectors are likely to downgrade those of their hosts. For example, in the Ivory Coast, the conversion of forest into agricultural lands has increased the population of *Simulium* sp. blackfly vectors of onchocerciasis, the nematode infection that causes river blindness (Traore et al. 1977). Human activities, such as forest clearing and agriculture, have also increased populations of *Lutzomyia intermedia* sandflies, which are the intermediate hosts for cutaneous leishmaniasis in Brazil (Tolezano 1994).

**Transmission Rates**

Transmission rates can be increased when intermediate hosts increase in numbers because of anthropogenic habitat alterations. *Eustrongylides ignotus* perforates the stomach of heron and egret nestlings with up to 80% mortality. Infected mosquitofish (*Gambusia holbrooki*, the 2nd intermediate host) were only found in physically altered areas that had anthropogenic sources of nutrient pollution. Densities of an oligochaete worm, the 1st
intermediate host, were higher in areas with nutrient pollution (Frederick et al. 1996; Spalding et al. 1993).

Transmission rates of aquatic parasites can be affected by the rate of water flow, e.g., *Schistosoma mansoni* (Upatham, 1973; Jewsbury, 1985). Could changing the hydrology of the Everglades have also increased transmission rates of parasites to bird and snail hosts? Perhaps parasites could account for some of the 90% decline in Everglades wading birds in this century.

If we define habitat structure in the broadest sense to include other species, then we can see that the results of habitat modification can include species removals. In some systems, unsusceptible animals interfere with the transmission of parasites by acting as sinks for them (i.e., non-host species reduce the rate at which target species become infected). If unsusceptible species are lost from the community, then this could increase rate of infection of susceptible species.

Corridors have also been implicated as potential pathways for "contagious catastrophes" such as disease and fire (Simberloff and Cox 1987). In a simulation model, Hess (1994) found that corridors could increase probability of metapopulation extinctions when mortality from a pathogen is low enough to allow infected individuals to spread disease yet high enough to reduce populations to the point where random extinction events became common. In a later study, Hess (1996), using four spatial arrangements of populations: island, necklace, loop, and spider, and then establishing quarantine populations, he found central quarantine zones in spider and necklace arrangements were most effective in lowering extinction probabilities. What is interesting about Hess’ models is that intermediate virulence has the potential to cause the most harm to wildlife populations. A
pathogen that is extremely virulent will in effect burn itself out by killing its host before it has a chance to infect others. Low virulence pathogens will not have much of an effect on host population dynamics or persistence. However, if a pathogen were selected to be more virulent, it could, under the conditions of Hess’ models, spread contagiously and increase local extinctions. Ewald’s arguments can be added to the balance. Corridors can increase transmission rates of pathogens between individuals and populations and enable them to, in effect, get away with being more virulent than they could be in isolated populations.

Even human corridors can influence disease transmission in unexpected ways. White et al. (1993) found that badgers (Meles meles) urinate on pastures every time they cross a road or other linear, anthropogenic landscape feature. White hypothesized that these urination sites became infection foci of bovine tuberculosis whose prevalence was correlated with the density of linear features on the landscape. This example illustrates how species-specific behaviors can interact with landscapes to influence disease transmission.

**Sit-and-wait pathogens**

Ewald states that sit-and-wait pathogens should be especially effective when host living sites are limited and protected (a common leitmotif in conservation biology!). Are bird boxes used in some species conservation programs (e.g., Eastern Blue Birds, Red Cockaded Woodpeckers, and Wood Ducks) potential havens for sit-and-wait pathogens? What about the silvicultural practice of leaving single snags in clear-cut stands? Though these habitat elements may be crucial for some species’ survival, they could also increase the effectiveness of some pathogens by exposing more individuals to
infection at the site of that limited resource. Habitat corridors have been
criticized for exposing animals to humans, domestic animals and predators
(Simberloff and Cox 1987). They may also channel animals through areas
where they are more likely to acquire sit-and-wait pathogens.

**Cultural vectors**

Could the same virulence increases observed in maternity wards be
selected for in sea turtle head-start programs, captive breeding colonies of
endangered species, or industrial agricultural systems where humans are
intimately involved with animal care? Most animal caretakers are acutely
aware of the problem of periodic infectious disease outbreaks in colonies
under their care, however until Ewald’s synthesis “why” periodic outbreaks
occurred was not appreciated.

Water-borne transmission and virulence could affect wildlife
populations as well. Perhaps it is no accident that world-wide amphibian
debates have been linked to a water-borne Chytridiomycete fungus (Berger et
al. 1998). A directly transmitted pathogen would likely not be as lethal.

**Virulence Summary**

Vector-transmitted pathogens, increased transmission rates of directly
transmitted pathogens, sit and wait pathogens, and cultural vectors are all
virulence selecting factors (see Table 6.1). They all depend on variables that
affect the rate of pathogen transmission. The rest of this review will focus on
understanding wildlife disease in light of these factors and on landscape
modifications and how they alter rates of transmission and hence the
evolution of virulence.
Habitat Structure, Parasites and Scale

Links between disease and habitat structure have been established with regard to human illness (Audy 1958). Landscape epidemiology has existed in Russia for the last half-century (Pavlovsky 1966). Swynnerton (1936) showed relationships among habitat types and tsetse fly abundance. Audy (1947) documented relationships among small mammals, their Trombiculid mites, ecotones, and outbreaks of scrub typhus (tsutsugamushi disease) in South Asia.

Landscape structure is expressed in a series of hierarchical scales (O’Neill et al. 1986). The effects of habitat structure on parasite transmission depend on the stage and type of parasite and the scale of observation (Sousa and Grosholz 1991). Ticks provide good examples of the cross-scale effects of habitat structure on population regulation. From the tick’s perspective, microhabitat environmental parameters are extremely important. Soil moisture and temperature determine how long an individual can survive before finding a host. These microclimatic variables are primarily a function of vegetation cover. Hoch et al. (1971a) found mechanical clearing of undergrowth combined with herbicide application reduced tick populations, especially larvae. Hoch et al. (1971b) found that herbicide applied to mechanically cleared woodlots increased soil surface temperature 6.6 °C, decreased relative humidity 6.2%, and reduced soil moisture by 22%. After 3 years, tick populations were reduced 90%.

Despite these susceptibilities to environmental alteration, ticks can ameliorate some problems behaviorally. Semtner et al. (1971a) found caged adult ticks survive longer in more heavily vegetated habitats. In response to rising temperatures in July, ticks migrated down vegetation to the soil and
duff. Semtner et al. (1971b) found nymphs and adults at highest densities near ecotones. Nymphs were the most common in treed areas and least common in open prairie. Nymphs were also common where brush was thin or absent, while adults were common where brush coverage was high. Both life stages were common in brush and low trees, and the height of vegetation may determine a tick’s success at finding hosts.

**Edges, Ecotones, Patch Size and Shape**

Patch size and shape are important determinants of the amount of edge relative to the amount of core habitat. A large patch will have more core habitat relative to edge habitat than a smaller patch. Semtner et al. (1971b) found nymphs and adults highest densities near ecotones. Lane et al. (1985) found higher densities of adult ticks at ecotones between grassland and chaparral, which declined rapidly within 3-5 m of either side of the ecotone. This may in part be due to choices made by the ticks, however at a larger scale it is more related to host behavior. There is a higher density of black-tailed deer at edges for adult ticks to feed on and increased numbers of small mammals for larval and nymphal stages to feed on. Scrub lizards (*Sceloporus woodi*) are also edge specialists, though they are likely to perceive edges at a smaller scale than deer.

We need to develop a behavioral ecology of ecological landscapes (Lima and Zollner 1996). How do animals perceive landscapes and how does this affect decisions they make about dispersal? Perhaps we can apply principles of scaling and allometry to perception. *Geckobiella* mites can detect heat and CO$_2$ from mammalian hosts from at least 1 m away (pers. obs.). *S. woodi* can detect 1 m tall vegetation from about 12-15 m (pers. obs.).
Links Among Sublethal Effects

In the last decade, the importance of sublethal effects in ecology has been recognized. Rather than seeing individuals or species as either being present or absent from a system, we have begun to realize that there is a continuous distribution of effects between 0 and 1 that is important.

Though I identified the factors that select for the virulence of pathogens above, the effect that pathogens have on their hosts is dependent on the interaction between the pathogen and the host. For example, there are links between virulence and the reduced genetic variation frequently observed in small host populations. New World peoples and Polynesians have reduced heterogeneity in the highly polymorphic class I and II major histocompatibility (MHC) genes. Measles may have increased in virulence with person to person transmission in inbred populations (Black 1993), thereby contributing to the decline of native peoples after the introduction of diseases by Europeans. Thus there is a “cost of consanguinity” (Kilbourne 1996). Past bottlenecks could have contributed to genetic homogeneity in cheetah populations, making them especially susceptible to disease (O'Brien et al. 1983).

Immunity can also be reduced within individuals. Ross et al. (1995) linked immune suppression in harbor seals to dietary exposure to PCB’s and other environmental contaminants in herring they ate. Contaminant-based immune suppression could be related to outbreaks of distemper and morbillivirus in marine mammals. Contaminants, like immune-suppressing diseases, may make it easier for pathogens to gain a foothold in previously resistant populations. Tuberculosis has reemerged as a major health problem as its spread has been helped by the spread of HIV (Ewald 1994). Stress, as
mentioned above, can also reduce immunity. Whether in the past, like bottlenecks, or present, like environmental contaminants, or stress, sublethal effects may be additive or even multiplicative in their effects.

**Prognosis**

Kitron (1998) argues that geographic information systems (GIS), global positioning systems (GPS), satellite imagery and spatial statistics give us powerful tools to better record, analyze, and understand epidemiology at the landscape level. Metapopulation models of disease (Hess 1994, 1996) add another predictive tool, as does modeling of connectivity and successional processes (Tiebout and Anderson 1997). We will likely need these advances to deal with the consequences of emerging diseases and global change.

Ewald (1994) ends his book on a hopeful note. He argues that rather than engage in an escalating arms race with evolving pathogens, we can, in effect, domesticate them by deliberately selecting for less virulent forms. Similarly, we may be able to lessen the effect of pathogens on wildlife by carefully evaluating the full effects of landscape modification on the evolution of pathogen virulence.

Just as ecology and evolutionary biology have begun to fully integrate parasitism and disease, epidemiology has become more evolutionary and ecological. All three disciplines are in the process of explicitly incorporating elements that operate across spatial scales. Only by understanding the complex interactions among organisms and the environment that cross these disciplines, will we begin to be able to anticipate and perhaps even ameliorate our impact on the biosphere.
Landscape-level effects such as burning, clear-cutting and roller-chopping affect prevalence and intensity of both *Eutrombicula* chiggers and *Geckobiella* mites. The mites in turn have various effects on the physiology of the *Sceloporus* host, which impacts its maximum speed, endurance, behavior and recovery. These traits in turn may affect the fitness and perhaps even the viability of populations of this species.
Table 6.1 Variables that affect virulence (after Ewald 1993).

<table>
<thead>
<tr>
<th>Transmission Mode</th>
<th>High Virulence</th>
<th>Low Virulence</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vector</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>arthropod</td>
<td>direct</td>
<td></td>
<td>malaria vs. free-living flagellates</td>
</tr>
<tr>
<td>attendant</td>
<td>direct</td>
<td></td>
<td>amplification of diarrhea outbreaks in maternity wards</td>
</tr>
<tr>
<td>syringe</td>
<td>direct</td>
<td></td>
<td>HIV in intravenous drug users vs. general population</td>
</tr>
<tr>
<td>untreated water</td>
<td>treated water</td>
<td></td>
<td><em>Shigella dysenteriae</em> vs. <em>S. flexneri</em></td>
</tr>
<tr>
<td>Direct</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sit-and-wait</td>
<td>short-lived pathogens</td>
<td></td>
<td>Anthrax, prion-based diseases vs. rhino virus</td>
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<tr>
<td>Transmission Stage</td>
<td></td>
<td></td>
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<tr>
<td>definitive host</td>
<td>intermediate host</td>
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<td>malarial pathology in humans (high) vs. mosquitos (low)</td>
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<tr>
<td>Transmission Rate</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>high</td>
<td>low</td>
<td></td>
<td>E. African HIV-1 vs. W. African HIV-2</td>
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<td>Selection Mode</td>
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<td></td>
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<tr>
<td>within host</td>
<td>between host</td>
<td></td>
<td>multiple vs. single infections</td>
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</table>
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[URL: http://water.dnr.state.sc.us.climate/sercc/].


BIOGRAPHICAL SKETCH

Kevin Baldwin was born in 1963 just outside of Ann Arbor, Michigan. After a peripatetic childhood, in which his family travelled all over the U.S., he went to UC Berkeley and graduated with a double BA in biological sciences and history in 1986. After spending some time at UC Santa Barbara working on an MA in biological sciences and doing some ecological consulting, he came to the University of Florida in 1990.
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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