

MACROECOLOGY OF NEOTROPICAL CLEARWING BUTTERFLIES
(NYMPHALIDAE: ITHOMIINI)

By

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Abstract of Thesis Presented to the Graduate School
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Macroecology is the study of large scale patterns in species abundance and distribution. While a positive relationship between abundance and distribution is widely documented, most studies to date have focused on vertebrate species in temperate regions, whereas the majority of Earth's biodiversity is concentrated in the tropics, particularly among invertebrates. To investigate several key macroecological phenomena for the first time in a diverse Neotropical insect group, the clearwing butterflies of the nymphalid tribe Ithomiini, I combined measures of mean local density gathered in the field (five sites in eastern Ecuador) with range size data compiled using ecological niche modeling, as well as measures of body size and dispersal ability measured from museum specimens, to investigate: 1) the relationship between mean local density and body size, 2) the relationship between mean local density and distribution, and 3) the relationship between dispersal ability and distribution. There was an overall negative relationship between density and body size, although inspection of arithmetic plots of density as a function of two estimates of body size, mean forewing length and mean thorax width, revealed rather triangular relationships, with species of intermediate body size displaying the highest densities in both cases. Two measures of

mean local density, density at field sites where species were found and density averaged over all visited sites, did not predict range size, and there was no relationship between density and range size within any field site. There was no relationship between mean local density and distribution within genera, and no relationship between density and distribution among closely related, sister species pairs. At a higher taxonomic level, no relationship was found between generic mean local density and generic range size. Finally, three indirect measures of dispersal ability, mean forewing length, mean forewing area, and mean wing load (ratio of thorax width to forewing length) failed to predict species range size. These results collectively suggest that macroecological patterns in the tropics, at least for ithomiine butterflies, might differ from those reported for temperate species. Future directions for research, in ithomiine butterflies and other Neotropical nymphalid groups, are discussed.

CHAPTER 1 GENERAL INTRODUCTION

Macroecology

Macroecology is the study of patterns in species abundance and distribution at large spatial and temporal scales (Gaston & Blackburn 1999). As opposed to the traditional ecologist's bottom-up approach to understanding biological systems, in which a system is reduced to components that are analyzed independently, macroecologists search for emergent properties of entire systems. For example, in a pioneering macroecological work, Brown (1984) showed that there was typically a positive relationship between abundance and geographic distribution among species comprising large, continental-scale biotas, such as North American birds, mammals, and plants. The number of studies aiming to document such large-scale patterns in species abundance and distribution has since proliferated (for a review see Blackburn *et al.* 2006).

While studies of the interactions between species and their local environments have certainly gone a long way in helping to uncover processes underlying the structuring of local communities, the search for broader trends has the unique potential to help reveal the processes that shape community composition and patterns in species richness at larger scales (Brown *et al.* 2002; Blackburn & Gaston 2002b; Brown & Maurer 1989). The implications for fields ranging from ecological and historical biogeography (e.g. Blackburn & Gaston 2002a) to evolutionary biology (e.g. Verbruggen *et al.* 2009) to conservation biology (e.g. Kerr *et al.* 2007) are diverse.

Study Group

There are several key considerations in choosing a model system for macroecological study. First, and perhaps most importantly, is the availability of the data required to evaluate the relationship between abundance, distribution, and ecological attributes of species in the system. Second, since species typically represent the units of analysis in macroecology, the system should be sufficiently speciose and widespread to investigate large-scale patterns. Finally, practical considerations dictate that the system be amenable to study using often limited resources. Currently, relatively few groups fulfill each of these criteria, and thus most macroecological work to date has focused on select vertebrates of temperate regions (e.g. birds, mammals), for which relatively large data sets are available. However, in light of the fact that most of Earth's species are not temperate vertebrates, but tropical invertebrates (Myers *et al.* 2000), macroecologists must seek groups for study that more accurately represent global biodiversity. Neotropical butterflies are emerging as an attractive model system for macroecological study, having been collected and studied extensively since the earliest European explorers visited the region. More distributional, taxonomic (e.g. Lamas 2004), and ecological (e.g. Beccaloni *et al.* 2008) information is currently available for many species of butterflies than for most other Neotropical groups. Furthermore, butterflies are extremely diverse and found commonly in most terrestrial ecosystems throughout the Neotropics, and can be easily sampled using simple techniques and inexpensive equipment.

The nymphalid butterfly tribe Ithomiini (ithomiines) is a diverse clade of diurnal Lepidoptera (Papilionoidea) found exclusively in the Neotropics, consisting of approximately 370 species (Lamas 2004) that inhabit moist forests from sea level to

approximately 3000 meters elevation. They range from Mexico through Central America, south to southern Brazil, northern Argentina and Paraguay, and across three Caribbean islands (Cuba, Hispaniola, Jamaica) (Willmott & Freitas 2006). The tribe is diagnosed by the presence in males of a patch of elongated, erectile androconial scales along the anterior edge of the dorsal hindwing (Brower *et al.* 2006). These scales, often called hair-pencils, are used by males to disseminate volatile pheromones used in courtship, the precursors of which are acquired in most species by feeding on flowers of Asteraceae and dried Boraginaceae plants (Schultz *et al.* 2004). These precursors, which comprise various dehydropyrrolizidine alkaloids, also make adults of all species unpalatable (Trigo & Brown 1990; Brown 1985). As a result of this unpalatability, ithomiine species form the basis of a diverse array of Batesian and Müllerian mimicry complexes (Beccaloni 1997) that have stimulated a wealth of study on natural selection, beginning notably with the theory of mimicry by Bates (1862) and Müller (1879).

Due in part to their peculiar biology and natural histories, and also to their overall abundance, charisma, and relative ease of sampling, distributional data in the form of georeferenced museum specimens is more readily available for ithomiines than for many other Neotropical insect groups. As such, they are an attractive choice for studies in biogeography and macroecology that employ recently developed tools that require extensive data sets, for example distribution or niche modeling applications. Furthermore, species-level phylogenetic hypotheses have been proposed for several genera and communities (de-Silva *et al.* 2010; Elias *et al.* 2009; Elias *et al.* 2008; Mallarino *et al.* 2005), allowing for the use of phylogenetic comparative methods, such as phylogenetically independent contrasts (Felsenstein 1985).

For all of these reasons, I have chosen the Ithomiini as a model group for investigating large-scale patterns in abundance and distribution, as well as for exploring some potential underlying factors such as dispersal and body size. The taxonomy that I follow is that of Lamas (2004), with the exception of the genus *Napeogenes*, for which I follow the revised nomenclature proposed by Elias *et al.* (2009).

Objectives

Throughout the following chapters, I explore several fundamental macroecological phenomena, using data on ithomiine butterfly density, distribution, and morphology gathered from various sources, including museum specimens, databases, and from the field. In Chapter 2, I describe a method for estimating geographic range sizes of ithomiine species found in the western Amazonian lowlands of eastern Ecuador, from where I also collected mean local density data. An analysis of these density data is presented in Chapter 3, where I also test for a relationship between density and body size. In Chapter 4, I explore whether the commonly observed relationship between density and range size applies to ithomiine butterflies. Finally, in Chapter 5, I investigate whether there exists a relationship between dispersal ability and range size. This is the first time such a macroecological study has investigated these phenomena in a Neotropical insect clade, and among the first for tropical invertebrates anywhere.

CHAPTER 2 MODELING ITHOMIINE BUTTERFLY RANGES

Introduction

The concept of species range size is central to a variety of fields in theoretical and applied ecology and their related disciplines. Although more attention has historically been paid to species traits such as abundance, a growing number of biogeographic studies have recently begun to investigate patterns in range size among species, driven in part by the increasing availability of distributional data sets and a growing recognition that an improved understanding of large scale patterns such as those among species' range sizes can lead to a better knowledge of the processes acting upon local assemblages (Gaston 1996a). Patterns in species richness are also increasingly being described in terms of range sizes (e.g. 'Rapoport's rule', Stevens 1989; the 'mid-domain' effect, Colwell & Lees 2000). With the popularization of the field of macroecology by studies such as Brown (1984) and Brown and Maurer (1989), a growing number of macroecological studies have attempted to compare such patterns in species distributions with other species attributes, including abundance and measures of resource usage or 'niche breadth' across a variety of spatial scales (Blackburn & Gaston 2002b; Brown 1984). In conservation, range size is often considered an important component of rarity, and is also often used as a criterion by which a species may be considered to be in danger of extinction. For example, according the International Union for the Conservation of Nature (IUCN) Red List Categories and Criteria (IUCN 2001), a widely recognized system for the establishment of species threat status, a species may be considered threatened if it is range-restricted (e.g. if its range size is $< 20,000 \text{ km}^2$).

Although a large number of studies have used measures of range size to answer often similar questions, there are major divisions between related studies in how it is actually measured. Measurements of range size typically fall into one of two categories: 1) geographic range size, often referred to as 'extent of occurrence', which is the area within the most widely spaced localities for a species, or 2) occupancy of grid cells drawn over a given area of interest (Gaston 1996b). Importantly, neither measurement scheme produces precise measures of range size, but estimations or predictions, and both methods have their limitations. For instance, the measures of range size derived from the extent of occurrence method are sensitive to bias in distributional or locality data from which they are derived, particularly at range edges. The method also likely overestimates range size in many cases, since no species occupies every single area within its range (e.g. species are not found in areas of suboptimal habitat). On the other hand, measures of occupancy are sensitive to the scale at which grid cells are considered. Large grid cells may overestimate range size if a species is counted in grid cells where its actual distribution is limited. Small grid cells may underestimate range size if species are not sampled but occur in cells. In macroecology, systematic sampling bias may lead to an artifactual relationship between abundance and distribution using the occupancy method, since rare species might not be sampled in all cells in which they occur (Gaston *et al.* 1997).

Additionally, it is important to draw a distinction between measures of global range size (i.e. the entire range area of a species, or its complete extent of occurrence) and partial range size (e.g. range size within a study area, usually a measure of occupancy). While studies that consider species range size at these differing resolutions might

attempt to explore similar fundamental questions, they may actually address different phenomena entirely and thus might not be comparable (Gaston 1996a).

The disparity between studies in their description of range size is almost certainly attributable, at least in part, to the quality of data available for different taxa and from different biogeographic regions. Rarely, distributional data representing species presence and absence are sufficient that species' entire ranges can be measured almost directly, such as in the case of North American and western European birds (e.g. Sauer *et al.* 2011; Hagemeyer & Blair 1997). Occasionally, species' partial distributions can also be measured almost directly, such as in studies where occupancy of grid cells is known over a given region (e.g. Cowley *et al.* 2001). In all other cases, however, species' ranges must be estimated or predicted, using distributional data compiled from various sources of variable accuracy and precision.

Recent technical and methodological advances in physiography (physical geography) have delivered large scale environmental data sets, such as global, high resolution digital elevation models and interpolated climatic parameters (e.g. high resolution interpolated global climate surface, Hijmans *et al.* [2005]). Such environmental data, coupled with powerful information systems, have opened the door to computer-based distribution modeling, and ecologists have responded with the development of a number of tools for predicting species distributions based upon comparatively limited distributional data sets. Key to this approach is the calculation of a species ecological niche, which is a mathematical representation of a species distribution in environmental space. For example, the bioclimatic predictive system BIOCLIM (conceptually developed by Nix [1986]) calculates a species' bioclimatic

'envelope', which is essentially a summary of a number of climatic variables from locations where the species is known to occur. BIOCLIM then employs an algorithm to predict the species' geographic distribution based upon its distribution in environmental space, or bioclimatic envelope, in a process known as environmental or ecological niche modeling. Similar approaches using different algorithms have also been developed, including the Genetic Algorithm for Rule Set Production (GARP; Stockwell & Peters 1999), and maximum entropy methods (e.g. MAXENT; Phillips *et al.* 2006, 2004), among others. Such ecological niche modeling techniques require that species are in equilibrium in their environments (i.e. distributions are stable), and that distributional data represent all relevant environmental gradients (i.e. no systematic bias in sampling, sufficient sampling of all habitats occupied by the species). In addition, and perhaps most importantly, these methods require that the climatic parameters used are, in fact, important components of species' ecological niches, and that they constitute determinants of species distribution (e.g. Peterson 2001; Mackey & Lindenmayer 2001). With these assumptions met, species' ranges may now be reliably estimated using relatively modest distributional data sources (Beaumont *et al.* 2005; Pearson & Dawson 2003). Precise range estimates are currently unavailable for most Neotropical butterfly taxa, and ecological niche modeling methods provide an objective, reliable, and efficient way of compiling such estimates. Here I outline a method for predicting and calculating butterfly range sizes using ecological niche modeling techniques, and present range size estimates for the ithomiine butterfly community of the Amazonian lowlands of eastern Ecuador. I end with a discussion of the range size frequency distribution for this ithomiine community.

Methods

Data

A total of 26,540 unique, georeferenced locality records were available from throughout the Neotropics for $n=73$ species of ithomiine butterfly species occurring in the Amazonian lowlands of eastern Ecuador. An average of 363.6 locality records were available per species ($s=378.1$), with a minimum of 21 records (*Hyaliris [n. sp.]*; recorded from 3 sites, with 19 records from a single site in Ecuador), and a maximum of 2,111 (*Mechanitis lysimnia*; recorded at a total 477 sites throughout the Neotropics). Data were compiled from various sources, including collections in Ecuador, the University of Florida (McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History), and databases compiled for the Butterflies of Ecuador Project (www.butterfliesofecuador.com) and the Tropical Andean Butterfly Diversity Project (Mallet *et al.* 2007; www.andeanbutterflies.org). Recently collected and databased specimens (i.e. those collected after the introduction of commercially available hand-held GPS units) were usually georeferenced rather accurately (e.g. coordinates measured at time of collection, with error usually <10 m). Older records were georeferenced by searching various sources for GPS coordinates, including published maps and online sources such as Google Earth (www.google.com/earth/index.html). The majority of these records were georeferenced at an accuracy of at least 2 to 3 decimal places (1.11 km and 111 meters at the equator, respectively), with a small number of records being georeferenced at an accuracy of 1 decimal degree (approximately 111 kilometers at the equator). Georeferencing errors were checked by inspecting maps of species locality records and investigating possible outliers or erroneous records.

Modeling Butterfly Ranges

Global range estimates for ithomiine butterflies were estimated using the ecological niche modeling tool BIOCLIM, implemented in the free GIS software DIVA-GIS (<http://www.diva-gis.org>). BIOCLIM was used to summarize 19 climatic parameters derived from global, interpolated precipitation and mean, minimum, and maximum temperature data (Hijmans *et al.* 2005) for each species. Histograms for each parameter were inspected, and those parameters for which histograms followed either a normal or highly skewed distribution were included in the model (mean=6.5 parameters per species, $s=2.56$), following Beaumont *et al.* (2005). Parameters with even distributions, or otherwise non-normal or non-skewed distributions, were deemed to have little influence in the determination of distribution, and were therefore excluded from models (see Introduction). BIOCLIM produces an initial predicted range divided into percentile-based categories, with the resulting range typically having core areas of high climatic suitability surrounded by areas of decreasing suitability. All areas deemed suitable (i.e. all areas that fell within the species' bioclimatic envelope) were reclassified as suitable, thus including all areas with climate similar to any location where a species was recorded in its predicted range. A distribution mask was then applied, to exclude areas deemed climatically suitable by BIOCLIM, but where a species was known not to occur due to biogeographic barriers, dispersal limitation, etc. Range estimates were then projected to a world cylindrical equal area projection in ArcGIS ([ESRI, Redlands, CA, USA](#)), since BIOCLIM calculates a predicted range without considering curvature of the Earth's surface (i.e. grid cells further towards either pole are smaller and thus should be weighted less in calculations of area). Range sizes were then calculated from these projected range estimates in ArcGIS. In addition, ranges were estimated using the

minimum convex polygon method in DIVA-GIS, and range sizes were subsequently calculated from projected minimum convex polygons in ArcGIS (excluding sea area where appropriate), for comparison with modeled ranges. All range sizes were calculated in km². Data were sufficient for calculating range sizes for 73 species using the minimum convex polygon method; since *H. [n. sp.]* (a very locally distributed species found only in eastern Ecuador) was recorded in so few grid cells of the digital elevation model used by BIOCLIM, data were insufficient for modeling the species' range using this program, and thus *H. [n. sp.]* was excluded from all analyses with range sizes derived with BIOCLIM (hence range sizes were calculated for 72 species using BIOCLIM).

Results

Range Size Frequency Distributions

Ecological niche modeling

Global range sizes for N=72 species of clearwing butterflies estimated using ecological niche modeling in BIOCLIM vary from approximately 4.3×10^4 km² (*Athesis acrisione*, found only in the eastern Andean foothills of Ecuador and extreme southern Colombia) to 1.5×10^7 km² (*M. lysimnia*, an extremely widespread species found throughout the entire Neotropical region), spanning 4 orders of magnitude. The frequency distribution for ranges modeled in BIOCLIM (Figure 3-1a) is strongly right-skewed, with a median value of 4.3×10^6 km². Most species have relatively small ranges (ca. 60% of species have a range size <5 million km²), whereas a smaller number have very large ranges (ca. 15% have range size >10 million km²). See Appendix A for a list of species and their range estimates with BIOCLIM.

Minimum convex polygon

Global range sizes for N=73 species estimated using the minimum convex polygon method spanned 7 orders of magnitude, ranging from approximately 2.7×10^2 km² (*H. [n. sp.]*, very narrowly distributed only in Eastern Ecuador) to 1.6×10^7 km² (*M. lysimnia*). With *H. [n. sp.]* removed from the analysis, range sizes for N=72 species ranged from 3.2×10^4 km² (*A. acrisione*) to 1.6×10^7 km² (*M. lysimnia*), spanning 4 orders of magnitude. The frequency distribution for these data (Figure 3.1b) are strongly right-skewed, with a median value of 3.6×10^6 km² (including *H. [n. sp.]*). Similar to ranges estimated using BIOCLIM, most species have range sizes that are comparatively small, with relatively few species very widely distributed throughout the Neotropics.

Comparing Methods for Estimating Butterfly Range Sizes

Global, untransformed range size estimates derived using both methods correlated very well (Figure 3-2; slope=0.96, $R^2=0.93$, $p<0.0001$), using range size estimated with the minimum convex polygon method as the predictor variable. *H. [n. sp.]* was excluded from the analysis due to lack of a modeled (BIOCLIM) range estimate. A power analysis was conducted to estimate type II error probability and to ensure that the analysis was conducted using a large enough sample size (power>0.999; N=72; null correlation=0.5). Nearly all of the most 'dramatic' deviations from the fitted model involve comparatively larger estimates of range size by the minimum convex polygon method compared to estimates using BIOCLIM; this is unsurprising, considering the biologically irrelevant restriction imposed upon the polygon method, that is, that the polygon must be convex. While serving as a way of introducing objectivity to the range estimation process, this is also likely to overestimate ranges in

cases where a 'concave' range might be expected, for instance along the arching Andean foothills. For this reason, and since range size estimates obtained using these two methods were otherwise generally very consistent, all subsequent analyses (see following chapters) were performed using range size estimates obtained using the BIOCLIM method.

Discussion

Ithomiine range sizes exhibited a right-skewed frequency distribution (Fig. 3-1), which is perhaps the most common distribution for range sizes among animals (Blackburn *et al.* 2004; Gaston 1998). Some authors have suggested evolutionary causes for such frequency distributions, for example in island regions where isolation and limited dispersal have promoted the evolution of geographically restricted species on islands (e.g. Beck *et al.* 2006). Historical biogeographic processes might also play a limited role. For example, small, secondary peaks in range sizes are apparent towards the right tails of ithomiine range size frequency distributions, which are comprised entirely of species that have distributions spanning both sides of the Andes, including into Central America and Mexico in all cases. These peaks might have arisen in one of two ways: 1) species comprising the peaks have breached a major biogeographical barrier (i.e. the Andes) after its formation, or 2) the formation of the barrier within multiple species' ranges (i.e. ithomiines) lead to speciation in some, but not all taxa, with newly formed sister species on either side of the barrier having smaller ranges than unspiciated taxa. The relative roles of these competing hypotheses remain to be explored. However, such skewed frequency distributions can also result from purely ecological processes (Gaston & He 2002), a hypothesis that I argue is the most well supported based upon my results for ithomiine butterflies. For example, processes

acting upon island faunas are not likely to have significant influence over a diverse, widespread, continental fauna. In addition, while a major geographic barrier seems to influence a small, secondary peak in species distributions, most species are distributed on only one side of the barrier (in South America) and thus other processes must be acting to determine their distributions. The next step is to search for underlying, ecological causes of such a distribution in ithomiine butterflies and to test them using carefully designed field and observational studies. To begin to explore this question, in subsequent chapters I examine further species attributes, such as local density and dispersal ability, in order to identify which attributes correlate with, and might help to explain, the distribution of range sizes that I observed.

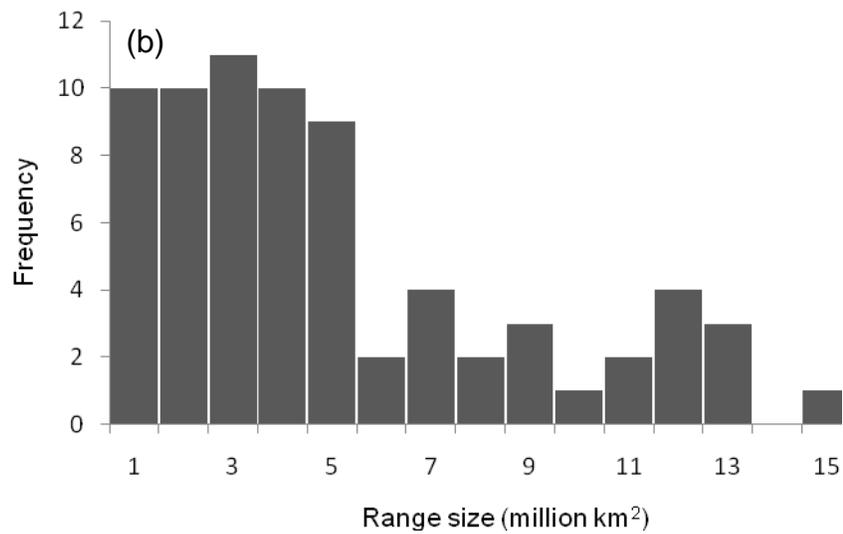
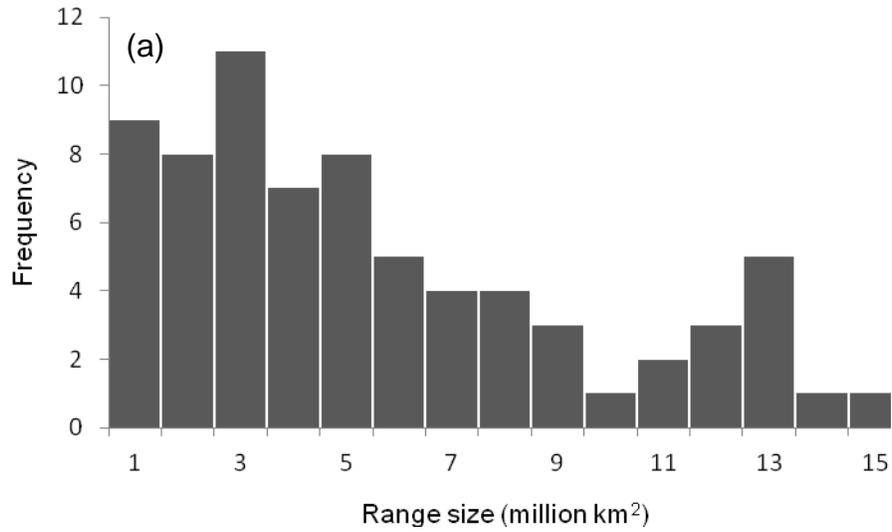


Figure 2-1. Frequency distributions of butterfly range sizes. Estimated using (a) ecological niche modeling (BIOCLIM) (N=72 spp.); (b) minimum convex polygon method (N=73 spp.).

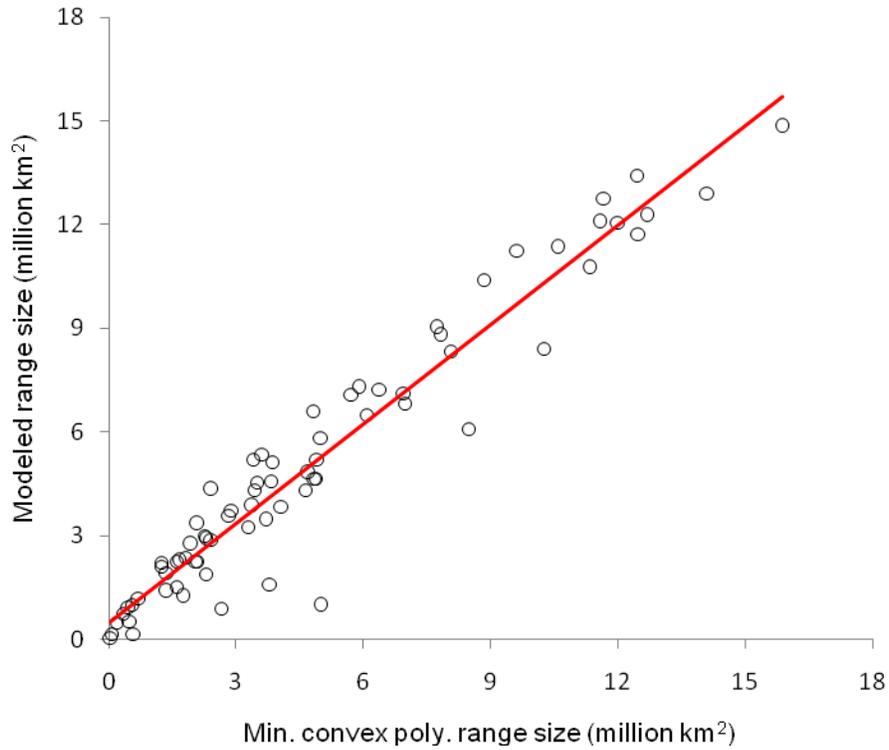


Figure 2-2. Arithmetic plot showing correlation between range size estimates obtained using two independent methods. X=minimum convex polygon method (MCP); Y=ecological niche modeling using BIOCLIM (MODEL). $MODEL=4.84 \times 10^5 + 0.96MCP$; $R^2=0.93$; $p<0.0001$; $N=72$.

CHAPTER 3 SPECIES RELATIVE DENSITY WITHIN BUTTERFLY COMMUNITIES

Introduction

Relative species density is a major topic of interest in ecology, and many ecologists work to understand its relationship with species distribution and the underlying causes. One universal feature of any biological community is that abundance is variable among the species comprising the community; some species are common, whereas others, and usually most others, are relatively rare (Magurran 2005). This common observation has led to the formation of a number of mathematical and ecological models of community structure (e.g. geometric series, Motomura 1932; log-series, Fisher 1943; log-normal, Preston 1948; unified neutral theory, Hubbel 2001). While the number of models for describing patterns in abundance within communities has grown, so too has the number of applications, in fields ranging from community ecology to macroecology to conservation biology.

Butterflies are an ideal system for investigating patterns in abundance for several reasons. First of all, they are extremely diverse and widespread, being found in most terrestrial ecosystems. Secondly, they are relatively easy to sample using simple, inexpensive techniques and equipment. Thirdly, due at least in part to their broad appeal among biologists and popularity with collectors throughout recent history, more distributional data is available for this group than for many other groups in the Neotropics, allowing the application of recently developed tools for modeling comprehensive ranges for many species. My main goal here is to compile data on species mean local density for ithomiine butterflies of the Amazonian lowlands of eastern Ecuador, an important first step towards a better understanding of key

macroecological phenomena, such as the relationship between species density and distribution.

Several authors have argued that body size in animals is negatively related to local density (Currie *et al.* 1993). For example, Damuth (1981) found a very tight, negative relationship between body size (mass) and local density for mammalian primary consumers found worldwide. In a subsequent test of Damuth's findings, Peters and Wassenberg (1983) found similar relationships in a number of widely distributed animal groups, including herbivorous and carnivorous mammals and birds, vertebrate poikilotherms, and aquatic and terrestrial invertebrates. Interestingly, however, studies that investigate the relationship between body size and local density within local or natural communities often fail to find this relationship, finding instead a relationship that is rather triangular, or no relationship at all. In a study of various guilds of birds and beetles in Borneo and North America, Blackburn *et al.* (1990) found no relationship between density and body size in any case. According to the authors, studies that find a tight negative relationship between density and body size might actually be showing the hypotenuse of a triangle since these studies use data collected in areas where species are most dense and thus worth studying. As a result, many species that are generally found at lower densities in natural communities are excluded from the plot of density versus body size, hiding a truly triangular relationship. In order to investigate this relationship in a diverse community of tropical insects, the clearwing butterflies of the nymphalid tribe Ithomiini, I used measures of body size compiled from morphological measurements and measures of mean local density gathered in the field.

Methods

Study Sites and Butterfly Sampling

Species density data for ithomiine butterflies were collected at 5 sites in the Amazonian lowlands of eastern Ecuador during August – December, 2010 (see Table 3-1, Figure 3-1 for a description of sites). Since population synchrony has been demonstrated at distances of up to approximately 1 km for butterflies in the study area (Engen *et al.* 2002), sites were located an average of 51 km apart, to avoid issues of spatial autocorrelation and to ensure that sites were independent samples of butterfly communities (i.e. not pseudoreplicates). All sites were within relatively close proximity of the Napo River (mean=7.4 km), a large Amazonian tributary, and the largest in eastern Ecuador. Habitat at each site comprised mostly ‘terra firme’ forest that is never flooded, with patches of ‘varzea’, or flooded forest, that is partially or fully inundated at least periodically. Ithomiine density data were collected along established trails, referred to here as transects. Under the reasonable assumption that trails are created rather haphazardly and therefore represent habitat types in roughly the proportion in which they occur at a site, measures of ithomiine density gathered from transects should be representative of overall local density patterns. Total trail length within sites varied from at least 5 km (Jatun Sacha) to >20 km (Yasuní Scientific Research Station). Transects were patrolled daily, weather permitting, and ithomiines found within 2.5 meters of either side of the transect were netted with a hand net following a modified form of the technique outlined by Pollard (1977, 1979). Each specimen was then given a unique voucher number and stored for later identification. No butterflies were collected during specimen processing in the field to avoid biasing collection towards preferred microhabitats, lekking sites (pockets), etc. Transect start and stop times were recorded.

Species mean local density was the number of individuals collected divided by the time spent collecting at sites where the species was found. I define density in the same manner throughout this chapter, and throughout the remainder of this thesis unless otherwise noted. The species rank density distribution was tested for goodness of fit to a standard distribution model, namely the lognormal distribution, using the non-parametric Kolmogorov-Smirnov test.

Completeness of Sampling and Species Richness at Sites

Species accumulation curves were used to determine the completeness of sampling of the ithomiine community at the study sites. These curves plot the total, accumulated number of species S by the total number of samples (hand-net days) n . Since the order with which samples are added can affect the form of the curve (Colwell & Coddington 1994), curves were produced using original sampling data and original data with 50 randomizations for comparison. In order to evaluate the total species richness of the ithomiine community at the study sites, total species richness was computed using the non-parametric estimator proposed by Chao (1984). This estimator takes the form:

$$\hat{S}_{max} = S_{obs} + (a^2/2b) \quad \text{(equation 3-1)}$$

where a is the number of species represented by 1 individual (singletons), b is the number of species represented by 2 individuals (doubletons), S_{obs} is the total number of species collected, and \hat{S}_{max} is the estimated total species richness.

The Relationship Between Mean Local Density and Body Size

In order to investigate a potential correlate of density, body size, regression analyses were performed using two estimates of body size: 1) forewing length, from wing base to apex and 2) thorax width at the base of the forewings (for a thorough description of these measurements see Chap. 5). These metrics of body size were the predictor variables in all analyses. All variables were \log_{10} transformed in both analyses to normalize residual distributions.

Results

Relative Species Density

A total of $N=55$ species were collected at the 5 field sites during the sampling period (Appendix A). The distribution of species' rank density fit the lognormal distribution well ($D=0.0998$, $p > 0.150$), when rank density data were included for all species sampled at the sites, including *H. sarepta* (an extremely abundant outlier, found very locally but abundantly at 1 site). When *H. sarepta* was excluded from the rank abundance calculations, the resulting rank abundance distribution still fit the lognormal distribution ($D=0.1094$, $p=0.104$). Species rank abundance curves are shown in Fig. 3-2.

Completeness of Sampling and Species Richness at Sites

Species accumulation curves (Fig. 3-3) stabilized after approximately 20 hand-net days, suggesting that the ithomiine community at the study sites was adequately sampled. While both curves begin to approach a similar asymptote after about 20 hand-net days, the curve constructed using actual, non-randomized data climbs more slowly and monotonically compared to the curve produced by a randomization process, which might be due to temporal turnover in species at least at the first site visited (Jatun

Sacha), a possibility that will be explored in a subsequent publication. Species accumulation curves constructed for each site individually (not shown) failed to reach asymptotes, due to the limited sampling period at each site. Using the so-called 'Chao I' estimator (Colwell & Coddington 1994) of species richness, total species richness at the sites was $\hat{S}_{\max}=61.25 \approx 62$ species (SD=34.6802), a value comparable to the apparent asymptotes of both species accumulation curves.

The Relationship Between Mean Local Density and Body Size

Forewing length, a surrogate for body size, predicted mean local density, when an extremely dense outlier (*H. sarepta*) was both included (abundance= $1.3187 + 1.1235$ forewing length; $R^2=0.1008$; $p=0.0193$) and excluded (abundance= $1.1138 + 1.0718$ forewing length; $R^2=0.1009$; $p=0.0205$) from the analysis. The remaining surrogate for body size, thorax width, also predicted mean local density, when an extremely dense outlier (again, *H. sarepta*) was included (abundance= $-1.7220 + 1.0200$ thorax width; $R^2=0.1077$; $p=0.0154$) and excluded (abundance= $-1.7931 + 0.9627$ thorax width; $R^2=0.1054$; $p=0.0177$) from the analysis. All variables were \log_{10} transformed to normalize residual distributions. See Figure 3-4 for double log and arithmetic plots of density as a function of body size.

Discussion

Data for species relative densities fit well with a lognormal distribution, a hollow-curve model that has been documented almost ubiquitously in biological communities (Magurran 2005; May 1975). This suggests that the community of ithomiine butterflies at the study sites contained a relatively small proportion of very abundant species, with the remainder and majority of the community comprising species that are relatively rare.

Two surrogates of body size were, overall, negatively correlated with mean local density for ithomiine butterflies found at the study sites, and double-log plots (Fig. 3-4) of each measure of body size with mean local density show a negative relationship, however with relatively little variation in density explained by body size in either case. Inspection of the arithmetic plots of mean local density as a function of mean forewing length and mean thorax width (Fig. 3-4) suggests that this negative relationship is heavily influenced by several comparatively large-bodied but rare species (e.g. forewing length: *Athesis acrisione*, *Methona curvifascia*, *M. grandior*; thorax width: *A. acrisione*, *M. confusa*, *M. curvifascia*, *M. grandior*). These arithmetic plots also suggest that the relationship between mean local density and body size may be somewhat triangular, with species of intermediate body size having the highest mean local densities. A similar, triangular relationship was reported for herbivorous beetles in Borneo by Blackburn *et al.* (1990), in which density increased with body size to some intermediate value and then subsequently decreased. For ithomiine butterflies, however, it is unclear the extent to which this relationship is truly triangular, with lower limits to body size (the smallest ithomiine species sampled at the Ecuadorian field sites was *Scada zibia*, with a mean forewing length of 17.61mm and a mean thorax width of 1.01mm) potentially obscuring the fully triangular form of plots of density as a function of body size.

Notably, studies of the relationship between body size and density at larger scales (e.g. global density measures compiled from the literature for a diversity of taxa) often find a much stronger negative relationship that is not triangular (e.g. mammals, Damuth 1981; birds, mammals, vertebrate poikilotherms, invertebrates, Peters & Wassenberg 1983). Blackburn *et al.* (1990) suggested this pattern results from, at least

in part, the exclusion of rare species in analyses, since data for these species is often difficult to gather. Second, they suggest such a relationship between density and body size might be an artifact of density data collected for species in areas of maximum density, since areas where species are common and thus easier to study are more likely to be visited. As a result, a tight, negative relationship might actually reflect the hypotenuse of a triangle, with species maximum density, but not necessarily overall density, being highly correlated with body size.

Interestingly, the relationship between body size and density in ithomiine butterflies in eastern Ecuador appears to be, at once, both triangular and yet generally negative. It remains to be seen what form this relationship will take with the inclusion of taxa in analyses that differ more widely in their ecology. For example, density and body size data are currently becoming available for other guilds of Neotropical butterflies, and in the future I plan to present results of tests of the relationship between density and body size among a wider variety of butterfly species, including bait-trapped butterflies of the nymphalid subfamilies Charaxinae, Biblidinae, and the genus *Adelpha*. In addition to allowing comparisons with ithomiine butterflies, data for these groups will permit analysis of the relationship between density and body size in a more diverse Neotropical butterfly community.

Table 3-1. Field sites in Ecuador, August-December 2010

Site name	Latitude	Longitude	Elevation (m)
Jatun Sacha Biological Reserve (JS)	S 01°04.2'	W 077°37.0'	450
Yarina Lodge (YL)	S 00°28.1'	W 076°50.6'	250
Sacha Lodge (SL)	S 00°28.0'	W 076°28.0'	235
Yasuni Scientific Research Station (YN)	S 00°40.6'	W 076°23.7'	230
Tiputini Biodiversity Station (TBS)	S 00°38.2'	W 076°09.0'	230

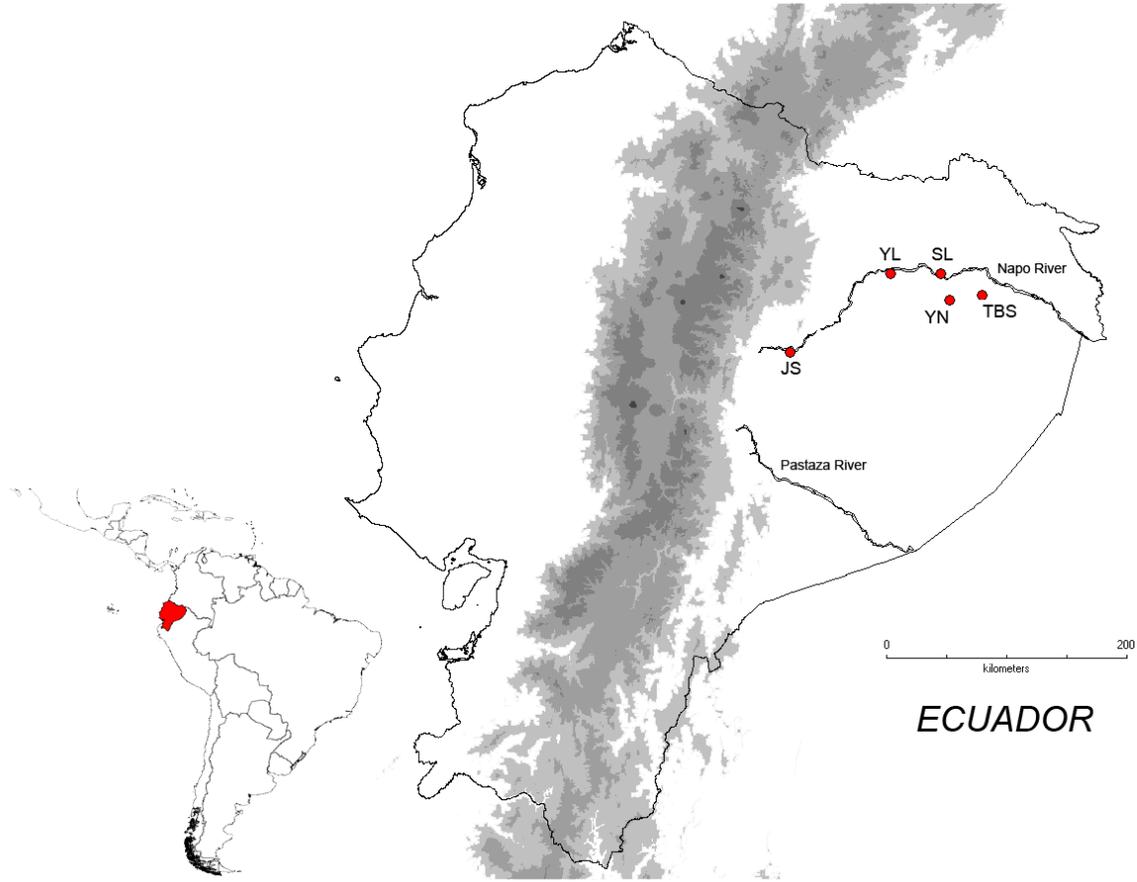


Figure 3-1. Field sites in eastern Ecuador. Sites were visited between Aug. and Dec., 2010 (JS=Jatun Sacha Biological Reserve; YL=Yarina Lodge; SL=Sacha Lodge; YN=Yasuní Scientific Research Station; TBS=Tiputini Biodiversity Station).

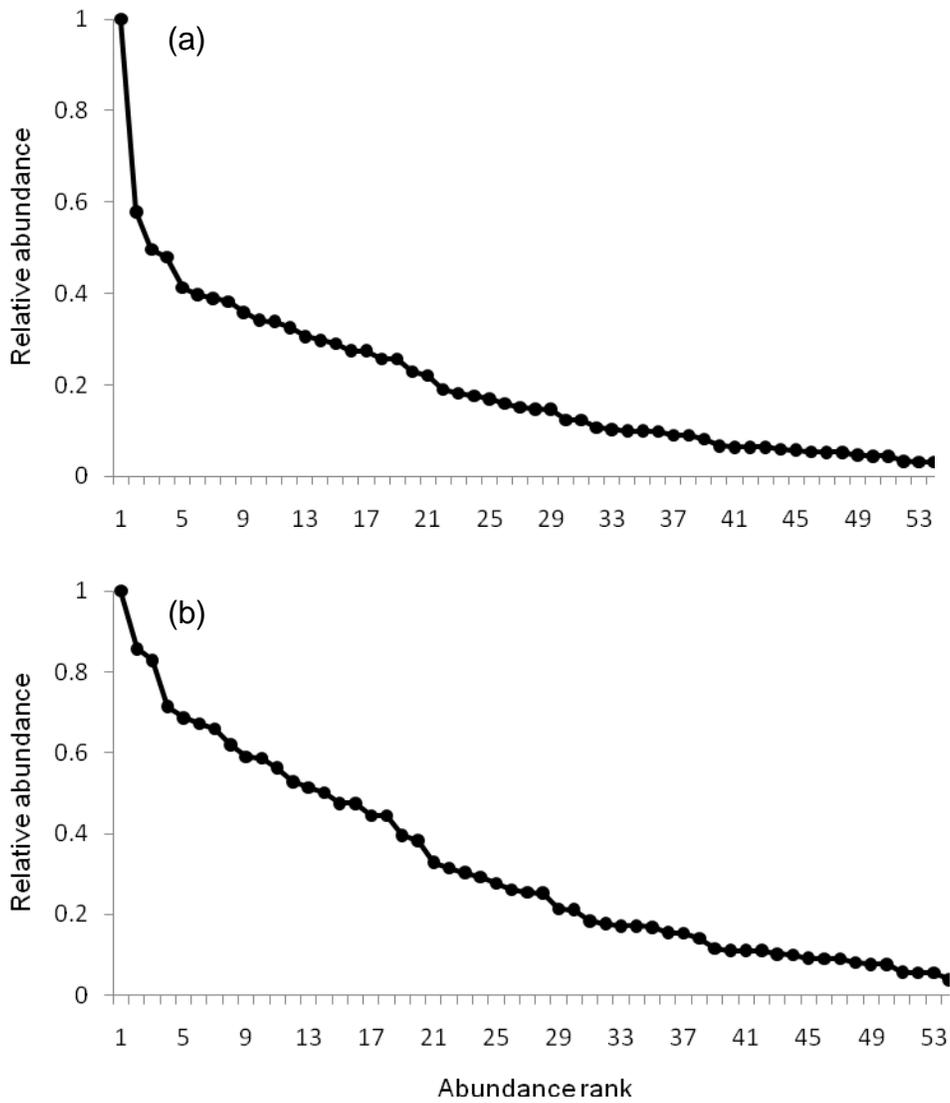


Figure 3-2. Species rank abundance curves (Whittaker plots) for ithomiines sampled at all study sites. (a) Including *H. sarepta* (an extreme outlier); (b) excluding *H. sarepta*. Species are ranked by abundance, i.e. the most abundant species have higher ranks (lower numbers). Note the strong right skew of both curves, indicating that ithomiine communities are comprised primarily of rare species.

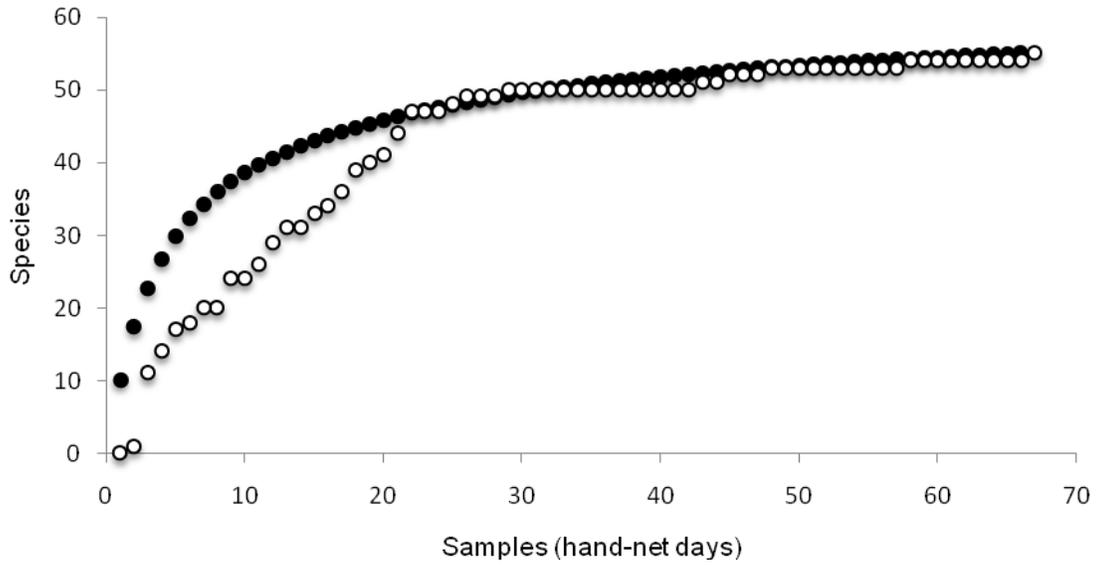


Figure 3-3. Species accumulation curves for Ithomiini at 5 eastern Ecuadorian field sites. Empty circles represent actual species accumulation curve; solid circles represent curve based on 50 randomizations calculated using EstiamteS v. 8.2 (Colwell 2009).

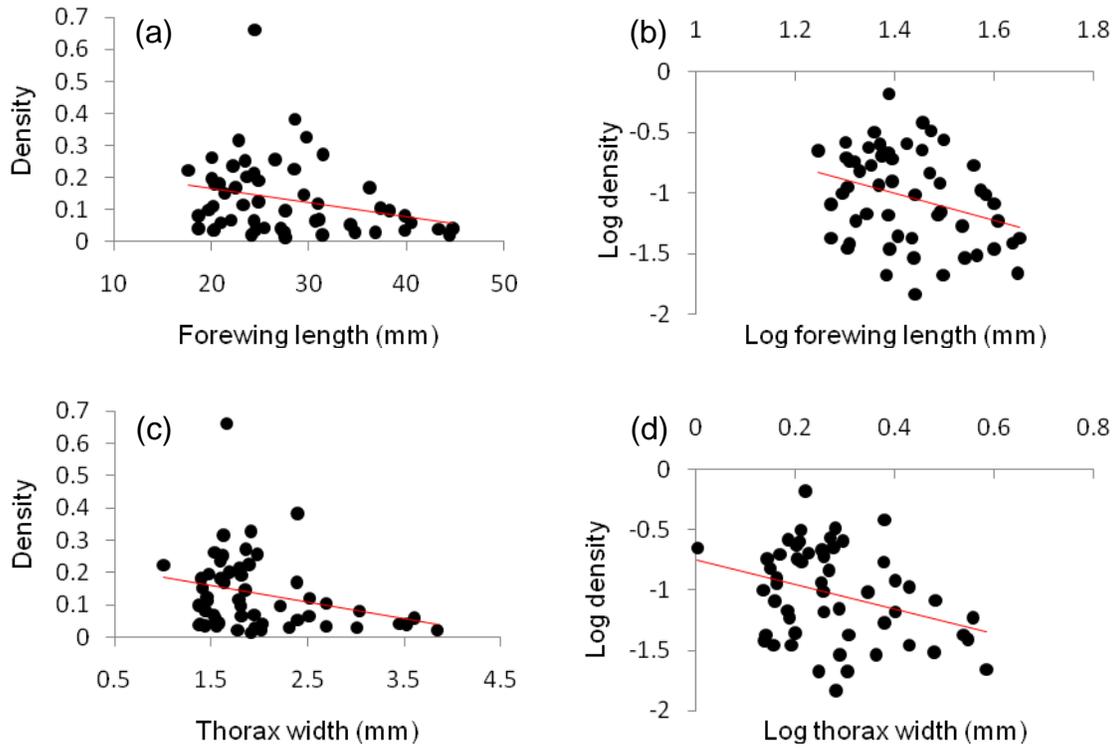


Figure 3-4. Species mean local density, where found, as a function of two measures of body size for ithomiine butterflies found at the field sites. (a) Arithmetic and (b) double-log plots of density as a function of forewing length; (c) arithmetic, and (d) double-log plots of density as a function of thorax width.

CHAPTER 4 THE RELATIONSHIP BETWEEN DENSITY AND DISTRIBUTION

“Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?”

C. Darwin (1859)

Introduction

A positive relationship between species abundance and distribution is very well documented, and it is often considered one of the few general rules in ecology (Bock & Ricklefs 1983; Brown 1984; Gaston & Lawton 1988). In a recent review and meta-analysis of 279 instances of a relationship between abundance and distribution, Blackburn *et al.* (2006) found a significant positive relationship in groups as varied as North American birds (Bock and Ricklefs 1983), British mammals (Blackburn *et al.* 1997), grassland, desert, and forest plants (Collins and Glenn 1990; Guo *et al.* 2000; Leite and Lopes 2001), British marine invertebrates (Foggo *et al.* 2003), and 444 species of moths, aphids, carabid beetles, and bracken-feeding insects in Europe (Gaston & Lawton 1988). However, while these studies span a variety of realms and taxonomic groups, their geographical scope is relatively limited, with most studies being conducted in temperate regions (Gaston & Blackburn 1999). Indeed, of the 253 studies included in the meta-analysis that could be assigned to broadly defined regions (i.e. Old/New World tropical/temperate areas), only 47 (ca. 19%) were from the tropics

(Neotropics, n=15; Afrotropics, n=28; Australasia, n=4), with the remaining 206 (ca. 81%) from temperate regions (Palearctic, n=174; Nearctic, n=32). In contrast, the overwhelming majority of Earth's species are invertebrates living in tropical regions (Myers *et al.* 2000; Reaka-Kudla *et al.* 1997; Erwin 1982). While disproportionately representing the world's less diverse biotas, such a focus on temperate species might have also largely failed to address potentially important issues associated with climatic differences between temperate versus tropical regions. For instance, temperate regions have experienced significant recent effects of glaciation (Hawkins & Porter 2003), and so patterns in species' abundance and distribution may reflect a lag in recolonization after the last glacial maximum. In addition, temporary colonization by cold-intolerant yet highly dispersive species during warm summer months may contribute further confounding effects in these regions (e.g. Hawkins & DeVries 2009). Clearly, more work is needed in order to justify the acceptance of an ecological 'rule' of a positive interspecific abundance-distribution relationship, with further studies needed especially for tropical invertebrates.

Here I investigate the relationship between mean local density (a measure related to, but not equal to abundance; see Chap. 3) and geographic range size, a measure of global distribution (Chap. 2), for the first time in a diverse Neotropical insect clade, the clearwing butterflies of the tribe Ithomiini.

Methods

Data

Measures of species mean local density were available for N=54 species of ithomiine butterflies occurring at 5 sites in the Amazonian lowlands of eastern Ecuador (see Chap. 3). Mean local density was the number of individuals collected, divided by

the time spent patrolling transects at all sites where the species was found. This measure of density, mean density at sites where a species is found, is often used in macroecological studies since it avoids the generation of an artifactual relationship between density and distribution via the inclusion of increasing numbers of zeroes in calculations of mean density for species that are found at fewer and fewer sites (Gaston 1996b). However, since species range maps predicted all species to occur at or near each of the 5 field sites, a second estimate of mean local density was calculated for comparison with density estimates at sites where species were found during the study period: mean density over all sites. The calculation of this measure of density addresses the possibility that all species found in the study region might occur at least rarely and/or occasionally at all sites even though they were not sampled during the study period, and might eventually be recorded with sufficient sampling. Global range size estimates were also available for the same N=54 species (see Chap. 2). For within-site analyses (see below), density was the number of individuals collected at that site alone divided by the total amount of time spent patrolling transects at that site. All range sizes were measured in km².

Statistical Analysis

The effects of mean local density (at sites where found) and mean local density (across all sites) on global range size were tested for all species (N=54) using simple linear regression. In addition, the effects of mean density (within sites) on global range size were tested for species occurring at individual sites (JS, N=20; YL, N=44; SL, N=37; YN, N=37; TBS, N=24) using Spearman's rank correlation tests, since tests conducted with linear regression produced non-normal residual distributions. To minimize the effects of sampling locally abundant but not generally abundant species

(e.g. *H. sarepta*, see results/discussion), linear regression analyses were performed using 2 subsets of the data: 1) excluding species found at only 1 site, and 2) excluding species found at only 2 sites. Potential effects related to phylogeny were controlled for using two additional analyses of the relationship between density and distribution: 1) Spearman's rank correlation tests for species within certain genera (e.g. *Hypothyris*, N=6; *Napeogenes*, N=6; *Oleria*, N=7) over all sites; 2) Wilcoxon signed-rank test to test for differences among species in sister-species pairs. In this analysis, N=13 sister-species pairs were identified based on a community phylogeny for Ithomiini species found at the study sites from Elias *et al.* (2008), and species in each pair were ordered so that the first species in each pair had higher mean density than the second. A Wilcoxon signed-rank test was then performed for the resulting paired values of range size for each sister-species pair. This test examined whether range sizes for the sister species in the first group (i.e. sister species with larger mean densities) were larger than those for the second group (i.e. sister species with smaller mean densities). This procedure was repeated, removing the 6 species pairs with an interspecific difference in mean density < 0.1 (leaving N=7 pairs), since species with only marginally different densities might not be expected to also differ substantially in range size (assuming a positive relationship between density and distribution). These tests were performed to investigate the relationship between density and distribution at comparatively fine scales (i.e. within genera and among sister-species pairs), since the existence of a relationship at this scale might be obscured by the inclusion of multiple, ecologically divergent genera in analyses. Typically, however, so-called phylogenetic comparative methods, such as phylogenetic independent contrasts (Felsenstein 1985), are used to account for

niche conservatism in macroecological studies; since some species traits, such as range size, tend to show a phylogenetic signal (e.g. Beck 2007), species may not always constitute independent data points, possibly leading to an artifactual relationship between density and distribution.

In order to homogenize the scales of the variables in regression analyses, global range sizes were divided by 10^7 . Where necessary, measures of mean local density or range size were transformed (\log_{10} or square root) to produce normal residual distributions for parametric (i.e. ordinary least squares regression) tests. In all analyses, species mean local density was used as the predictor variable.

Since different relationships between density and range size have been reported at different taxonomic levels (e.g. Harcourt *et al.* 2005), the effects of taxonomic level were investigated by simple linear regression of measures of generic range and density for N=23 genera. Generic range size was the outline of all overlapping congeneric species ranges found at the field sites. No range data were available for *H. mamercus*, so that species was excluded from generic range estimation for the genus *Hypothyris*. Values for generic range size were divided by 10^7 to homogenize the scales of the two variables for analysis. Generic density was mean local density, where found, averaged over all congeneric species. Variables were otherwise untransformed, and generic density was the predictor variable.

Results

Species mean local density (at sites where found; log-transformed) did not predict range size (square root-transformed) (range size = $0.6548 + 0.1291$ density; $R^2=0.0029$; $p=0.7$) when all species (N=54) were included in a linear regression analysis (Fig. 4-1). Species mean density (averaged over all sites) did not predict range size in a linear

regression analysis ($R^2=0.0370$; $p=0.1632$; in all subsequent analyses, mean local density is density where found) (Fig. 4-1). Spearman's rank correlation tests similarly did not show a relationship between mean local density and range size for species found within sites in any case (JS, $\rho=0.0570$, d.f.=18, $p=0.8112$; YL, $\rho=0.2282$, d.f.=46, $p=0.1187$; SL, $\rho=-0.0612$, d.f.=35, $p=0.7190$; YSRS, $\rho=-0.2179$, d.f.=34, $p=0.2016$; TBS, $\rho=0.0734$, d.f.=22, $p=0.7331$). Linear regression, using (log-transformed) density as a predictor of range size (log-transformed), produced no significant results using the data set with species occurring at only 1 site removed (range size = $-1.0017 + -0.0702$ density; $R^2=0.0039$; $p=0.6920$). Similarly, no significant relationship was found using the data set (double log-transformed) with species found at only 2 sites removed (range size = $-1.1856 + -0.2191$ density; $R^2=0.0458$; $p=0.2240$). Spearman's rank correlation tests conducted for species within genera showed no relationship between mean local density and range size in any case (*Hypothyris*, $\rho=-0.0286$, d.f.=4, $p=0.9572$; *Napeogenes*, $\rho=0.4857$, d.f.=4, $p=0.3287$; *Oleria*, $\rho=0.1429$, d.f.=5, $p=0.7599$). Results from a Wilcoxon signed-rank test for N=13 sister-species pairs (all available pairs) showed that species in pairs that had higher mean densities did not tend to have larger range sizes ($p=0.7354$). Results were similar when pairs whose constituent species differed in density by < 0.1 were removed from the analysis, with species in pairs that had higher mean density not tending towards larger range size ($p=0.8125$).

At the generic level, congeneric mean density did not predict generic range size (range size = $0.74886 + -0.39182$ density; $R^2=0.0096$; $p=0.6558$) (Fig. 4-4).

Discussion

Several analyses clearly show no relationship between two measures of mean local density and range size for ithomiine butterflies, both across the 5 study sites and

within each site (Figs. 4-1 & 4-2, respectively). Furthermore, no relationship was apparent when species occurring at only 1 and 2 sites were removed from the analyses to minimize the influence of very locally abundant but not generally abundant species. The relationship between mean local density and range size was investigated among closely related, congeneric species, in order to minimize the potential confounding effects of including more distantly related taxa in analyses. No relationship was found. Finally, two analyses conducted for sister species pairs in the ithomiine community of the study area similarly showed no relationship. Taken together, these results provide very strong evidence against a relationship between mean local density and range size for ithomiine butterflies at the field sites in eastern Ecuador.

While I argue that my results rather strongly suggest that there is no relationship between density and distribution for ithomiine butterflies, I acknowledge two potential confounding factors in my analyses. First is the issue of scale, and whether density data collected on a local scale (5 sites in eastern Ecuador) is comparable to distributional data at a much larger scale (global, spanning species' entire Neotropical distributions). Indeed, in a meta-analysis of 71 instances of a relationship between abundance and distribution, Blackburn *et al.* (2006) were unable to reject their hypothesis that studies which employed different measurement scales for density and distribution had an overall lower effect size (i.e. weaker positive relationship) than those for which the scales were roughly equivalent. However, the mean effect size of 0.13 for $n=17$ studies employing different scales was still significantly different from 0, suggesting that studies that employ differing scales should produce similar results to those employing equal scales, even if they are less strong. The second potential argument for error in the

analyses is related to local measures of species density at the field sites, and whether these estimates represent overall patterns in species density. Local density estimates might be argued to differ from overall densities in two ways: spatially or temporally. Spatial disagreement between local versus broader density patterns might arise from so-called 'range position' effects (Gaston *et al.* 1997a). For example, since many species included in the analyses were found near the edge of their geographic or elevational ranges at the base of the Andes in Ecuador (i.e. most were lowland Amazonian species near the western edge of their ranges in the Amazon basin), spurious patterns in density might lead to an erroneous relationship between density and distribution if species abundance tends to decline towards the edge of the range (Grinnel 1922). However, I argue that this is unlikely a source of error for two reasons. First, the 'range position' hypothesis is usually offered to explain an artifactual positive relationship (Gaston *et al.* 1997a), not a lack of relationship. Furthermore, the Andes are a rather abrupt, geographic boundary, and there is little reason to believe that species density should systematically decrease as one approaches the boundary, before its effects (i.e. changes in temperature, precipitation) are felt by actually increasing in elevation. The field sites, with the exception of perhaps Jatun Sacha, were all firmly within the Amazonian lowlands of eastern Ecuador (Jatun Sacha, 450 m; all others, ca. 230 m elevation), despite relative proximity to the Andes (as opposed to, say, a site in central Brazil), and climatic factors such as temperature at these sites were essentially unaffected by proximity to the Andes (i.e. climate at the field sites is strictly lowland Amazonian). On the other hand, disagreement between my local density estimates versus overall estimates might also arise due to temporal effects (i.e. limited sampling

period). For example, several studies of other nymphalid butterflies in the study area have demonstrated strong temporal or seasonal turnover in community composition and abundance patterns (e.g. Checa *et al.* 2009; DeVries *et al.* 1997), and it is unclear whether sampling during only part of a single year may reliably represent general patterns in density over time. However, the abundance-ranking of ithomiine species found at the field sites is similar to that based on an 'expert opinion' ranking, based on 211 days spent in the field collecting butterflies, spanning 14 years and 87 sites in the study region (K. Willmott, pers. comm.). Furthermore, my sampling scheme thoroughly measured density of an actual community (Fig. 3-3), and if ecological 'rules' such as the often-cited positive relationship between density and distribution are robust and broadly applicable, then they should apply to communities as they exist at any randomly selected point in space or time.

While my results are in contrast to many studies of the relationship between density and distribution, particularly in temperate regions, they agree with a small but growing body of evidence that suggests the relationship may be weaker or even non-existent among tropical taxa. For example, in Blackburn *et al.*'s (2006) meta-analysis, the mean effect size for $n=15$ studies from the Neotropics was not statistically significant from zero, indicating that there was no overall relationship between density and distribution for Neotropical taxa. However, these studies were conducted exclusively on mammals, and in particular, primates. More work is needed, especially for other taxa such as butterflies and other invertebrates that are more representative of tropical biodiversity, in order to explore the relationship between density and distribution in diverse tropical regions, and to confirm whether the form of this relationship is generally

different for tropical versus temperate faunas. If a different relationship truly exists among tropical taxa, then this will provide a unique opportunity to test mechanisms and search for species attributes that drive a relationship in temperate regions but not in the tropics.

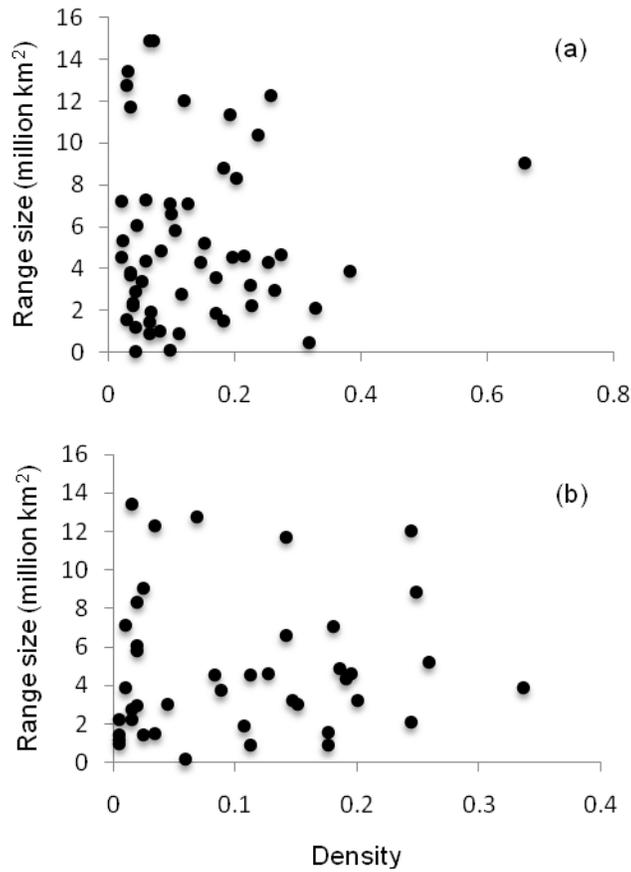


Figure 4-1. Arithmetic plots of global range size as a function of mean local density for ithomiine butterflies. (a) Where found; (b) across all sites, for ithomiines at 5 sites in eastern Ecuador (N=54). Outlier in (a) is *H. sarepta*. Data shown are untransformed.

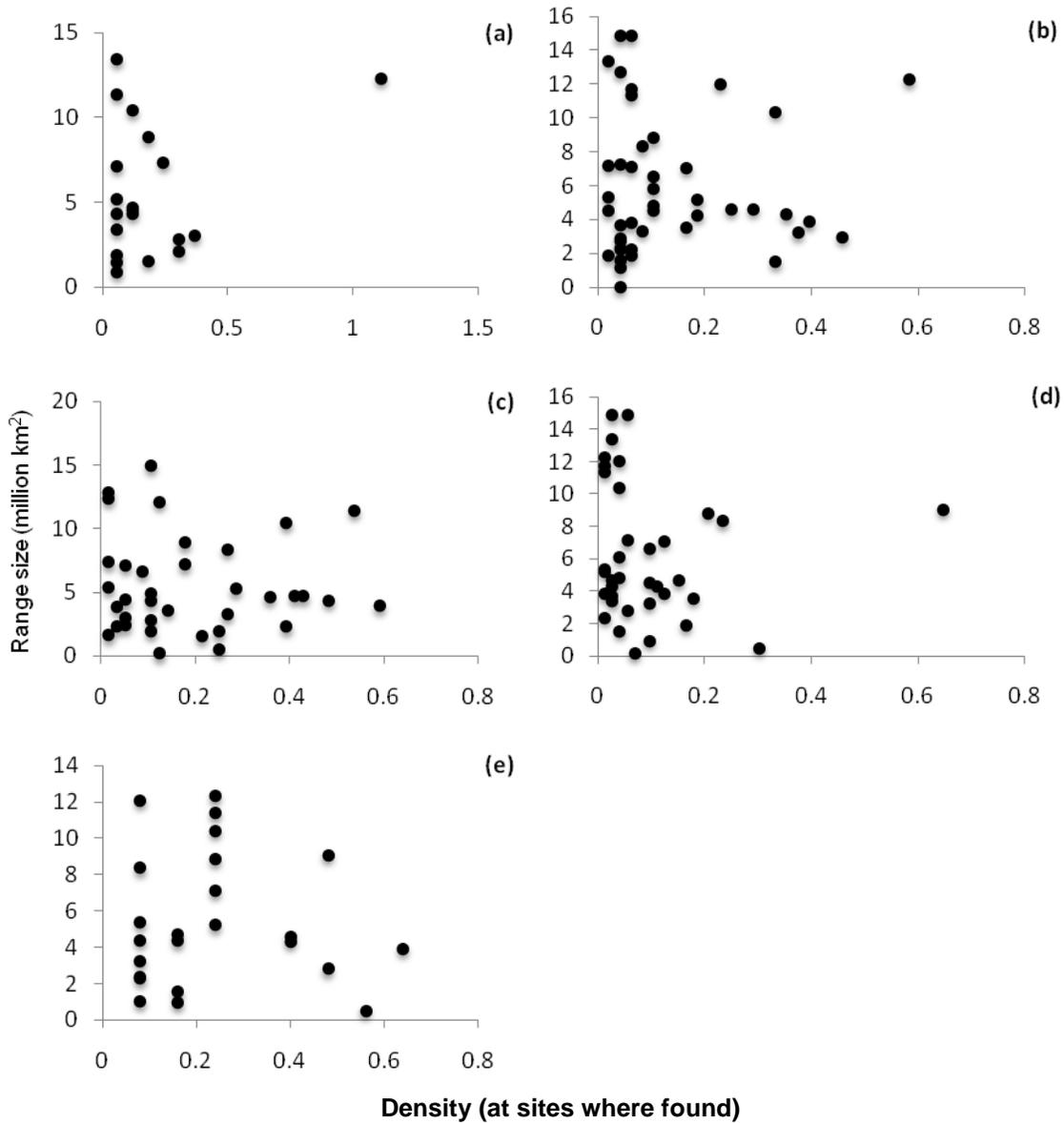


Figure 4-2. Arithmetic plots of global range size as a function of mean local density within field sites. (a) JS (Jatun Sacha), outlier is *H. euclea* (N=20); (b) YL (Yarina Lodge), outlier is *H. euclea* (N=44); (c) SL (Sacha Lodge) (N=37); (d) YN (Yasuní Scientific Research Station), outlier is *H. sarepta* (N=37); (e) TBS (Tiputini Biodiversity Station) (N=24). All data shown are untransformed.

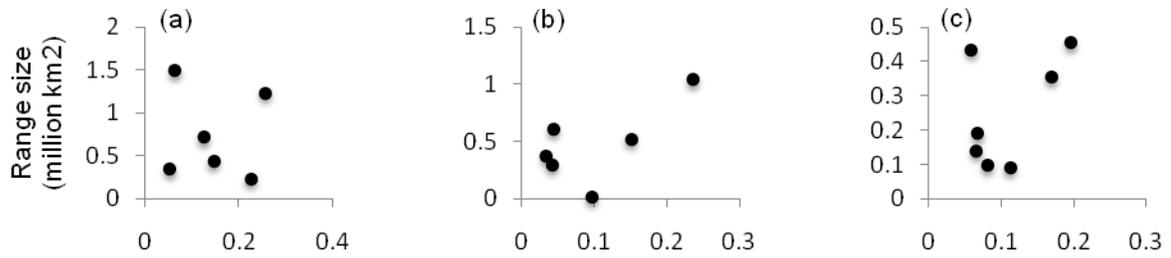


Figure 4-3. Arithmetic plots of global range size as a function of mean local density within genera. (a) *Hypothyris* (N=6); (b) *Napeogenes* (N=6); (c) *Oleria* (N=7). Data shown are untransformed.

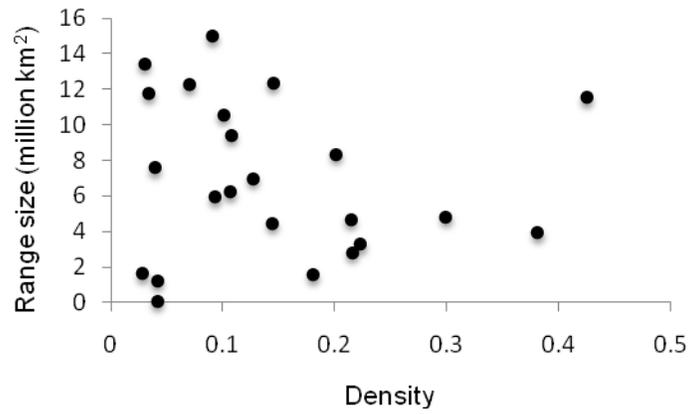


Figure 4-4. Arithmetic plot of generic global range size as a function of generic mean local density (N=23). Data shown are untransformed.

CHAPTER 5 DISPERSAL ABILITY AND DISTRIBUTION

Introduction

Overview

A species' ability to disperse is inextricably linked to its ability to maintain, expand, or shift its range (Rundle *et al.* 2002), and also to its ability to sustain a meta-population structure in fragmented landscape (Baguette 2003; Conradt *et al.* 2000; Hill *et al.* 1996). In the context of increasing global anthropogenic disturbance, including habitat fragmentation and climate change, understanding dispersal and its role in shaping patterns in species abundance and distribution will be important if we are to successfully manage natural populations and mitigate biodiversity loss (Stevens *et al.* 2010).

There is some evidence that rarity is linked to poor dispersal ability (Gaston 1994; Kunin & Gaston 1993), and that species that are better dispersers are also able to attain wider distributions, for example in Iberian carabid beetles (Gutiérrez & Menéndez 1997), Swedish mayflies (Malmqvist 1999), and British butterflies (Cowley *et al.* 2001; Dennis *et al.* 2000). To date, however, very few studies have investigated the influence of dispersal on range size in tropical taxa. Importantly, present and historical climatic conditions in the tropics have exerted different influences on populations there as opposed to temperate areas (Hawkins & Porter 2003; Stenseth *et al.* 2002), and it remains to be seen how the dynamics of dispersal and distribution differ in these areas as a result of different climatic effects.

Defining Dispersal

Many definitions of dispersal exist, with the definition chosen in a particular study being dependent upon its context, and the motivation underlying the dispersal behavior

(Bowler & Benton 2005; Clobert *et al.* 2001). For example, in macroecology, which is concerned with large-scale patterns in species' abundance and distribution, dispersal might be the process by which one or more individuals reach a new site and establish a population there (e.g. Beck 2007). In evolutionary biology, where interest is focused on the evolution of life history traits and speciation, dispersal might be any movement that drives gene flow (Ronce 2002). Alternatively, dispersal might describe any movement of an individual, regardless of purpose, whether it be movement by one individual away from another, for example during territorial disputes, or movement of an individual away from its natal site (Johnson & Gaines 1990). However, all of these definitions of dispersal entail movement of individuals, and both the propensity for and capacity for such movement can be quantified. An individual or species' dispersal ability can thus be estimated, allowing for investigation of its influence on other species attributes. Regardless of the purpose of a dispersal event, it is a species' dispersal capacity, or mobility, that makes it, in part, a successful or unsuccessful disperser. Thus, throughout this chapter, when I mention dispersal, I mean mobility, or a species' dispersal ability.

Objectives

Here I investigate the relationship between dispersal and distribution for the first time in a diverse, Neotropical insect group, the clearwing butterflies of the tribe Ithomiini. Information regarding butterfly dispersal was gathered from museum specimens and from specimens collected in the field. Estimates of distribution were compiled for butterfly species in the form of geographic range sizes, estimated using ecological niche modeling techniques.

Methods

Dispersal Ability

Instead of direct measures of dispersal ability such as those obtained using mark-release-recapture techniques (e.g. Hill *et al.* 1996), species dispersal ability was estimated indirectly using morphological data (e.g. Beck 2007; Hill *et al.* 1999). Species included in the analyses were those predicted to occur in the western Amazonian lowlands of eastern Ecuador based on range maps created using niche modeling techniques (see Chap. 2), and for which both range sizes and pinned specimens or photographs were available (for a list of species included in analyses see Appendix A). Three morphological characters related to flight morphology were measured for N=570 pinned individuals (≥ 5 specimens per species, mean=8.03, s=3.51) representing 69 species. Specimens were fairly evenly distributed by sex, with N=236 females, N=329 males, and N=5 undetermined. Measurements were: 1) forewing length (measured from the base of the forewing to its apex), 2) area of the forewing (measured from the dorsal surface of the wing), and 3) width of the thorax (at the base of the forewing). These metrics were then used to calculate 3 surrogates for mobility/dispersal ability in each species: 1) mean forewing length, a common estimator of body size in Lepidoptera (Loder *et al.* 1998) and a correlate of flight ability in butterflies (e.g. Chai & Srygley 1990); 2) mean forewing area, a second measure of body size/flight ability; and 3) mean wing load (ratio of thorax width: forewing length), a measure of flight strength (Beck, 2007; Dudley & Srygley 1994; Chai & Srygley 1990) in which larger values denote greater flight strength. All measurements were taken from photographs of pinned specimens using the digital imaging software Photoshop CS4 (Adobe Systems, Incorporated, San Jose, CA, USA).

Range Size

Range size estimates (in km²) for N=72 species were available, including 69 for which dispersal estimators were tabulated, based on range estimates calculated using ecological niche modeling implemented in DIVA-GIS using the BIOCLIM modeling software (for details see Chap. 2; Appendix A).

Statistical Analysis

The independent effects of each dispersal estimator on range size were tested using ordinary least squares regression models for N=69 ithomiine species, with range size as the dependent variable in all cases. Where necessary, variables were transformed (square root, log₁₀) to normalize residual distributions.

Results

No measure of dispersal ability was useful in describing variation in range size for ithomiine butterflies: untransformed mean forewing length did not predict untransformed range size (range size = $3.0 \times 10^6 + 7.2 \times 10^4$ forewing length; $R^2=0.0183$; $p=0.2679$); untransformed mean forewing area did not predict untransformed range size (range size = $4.0 \times 10^6 + 3.7 \times 10^3$ forewing area; $R^2=0.0148$; $p=0.3201$); square root-transformed mean wing load did not predict square root-transformed range size (range size = $3.5 \times 10^3 + -5.6 \times 10^3$ wing load; $R^2=0.0063$; $p=0.5162$) (Fig. 5-1).

Discussion

None of the estimators of dispersal ability (forewing length, forewing area, wing load) predicted range size for ithomiine butterflies. If the metrics that I chose to represent dispersal ability do, in fact, serve as valid surrogates, then my study provides strong evidence against a general relationship between dispersal ability and distribution in this group. While support for the notion that dispersal ability can be reliably estimated

using morphological characters is mixed, there is some direct evidence for butterflies that suggests that it can be (e.g. Berwaerts *et al.* 2002; Chai & Srygley 1990). In the only related study of a tropical lepidopteran taxon that I am aware of, Beck (2007) found little evidence of a relationship between dispersal ability and range size in southeast Asian moths of the family Sphingidae, using similar measures of dispersal ability. In contrast, some evidence supports a positive relationship between dispersal ability and distribution in temperate butterflies (e.g. Cowley *et al.* 2001; Dennis *et al.* 2000). While this topic has, by no means, been exhaustively examined, if these studies do represent trends in temperate and tropical Lepidoptera, then it begs the immediate question of why this pattern is observed in temperate but not tropical taxa. With a lack of relationship in ithomiine butterflies further supported (see below), I would proceed to test hypotheses related to differences in current and historical climate between temperate versus tropical regions (e.g. Hawkins & Porter 2003) that might help to explain differences between patterns of dispersal and distribution observed in taxa from these two regions.

On the other hand, it is of course possible that dispersal ability cannot be reliably estimated using morphological characters. In gathering estimates of butterfly mobility or dispersal ability, several authors have employed rather different methods than those I used here, including the circulation of questionnaires among experienced lepidopterists (e.g. Komonen *et al.* 2004; Cowley *et al.* 2001), and the more direct measurement of dispersal through mark-release-recapture methods (e.g. Pollard & Yates 1993) and the analysis of vagrancy in grids (e.g. Cook *et al.* 2001). Without direct tests of the usefulness of morphological characters as surrogates for dispersal ability in ithomiine

butterflies, it is difficult to conclude irrefutably that dispersal ability does not influence range size. Data for actual dispersal ability in this group, as measured using mark-release-recapture techniques, or with more direct surrogates such as experimental estimates of flight speed measured in the field/laboratory or perhaps even using radio telemetry techniques (e.g. Wikelski *et al.* 2010) would go a long way in corroborating or refuting my findings and confirming the validity of indirect estimators of dispersal ability in Neotropical butterflies. If it turns out that, after thorough examination of dispersal ability, dispersal ability really does not account for distribution in ithomiine butterflies, other explanations will have to be explored to account for the incredible variation in range size observed in this group (see Chap. 2).

The role of species' dispersal ability in determining their distributions remains unclear. Nevertheless, other factors almost certainly exert additional influence, and it is likely that multiple factors ultimately combine to determine species' distributions. For example, in addition to competitive interactions, abiotic factors such as climate are key components of species' ecological niches, which have been shown to be important determinants of distribution in animals (Peterson 2001; Mackey & Lindenmayer 2001). Cowley *et al.* (2001) found that habitat breadth, a measure of the size of a species' ecological niche, correlated significantly with distribution in British butterflies. Similarly, Beck (2007) found that larval diet breadth, another measure of ecological niche breadth, was significantly correlated with range size in southeast Asian sphingid moths. I recently visited Ecuador (Aug. – Dec. 2010) to collect diverse behavioral and ecological data for ithomiine butterflies data that I intend to use to estimate ecological niche breadth and to examine how this is related to distribution; I also plan future field work to collect host

plant utilization data for larval ithomiine butterflies, in order to explore the relationship between larval host plant breadth and distribution.

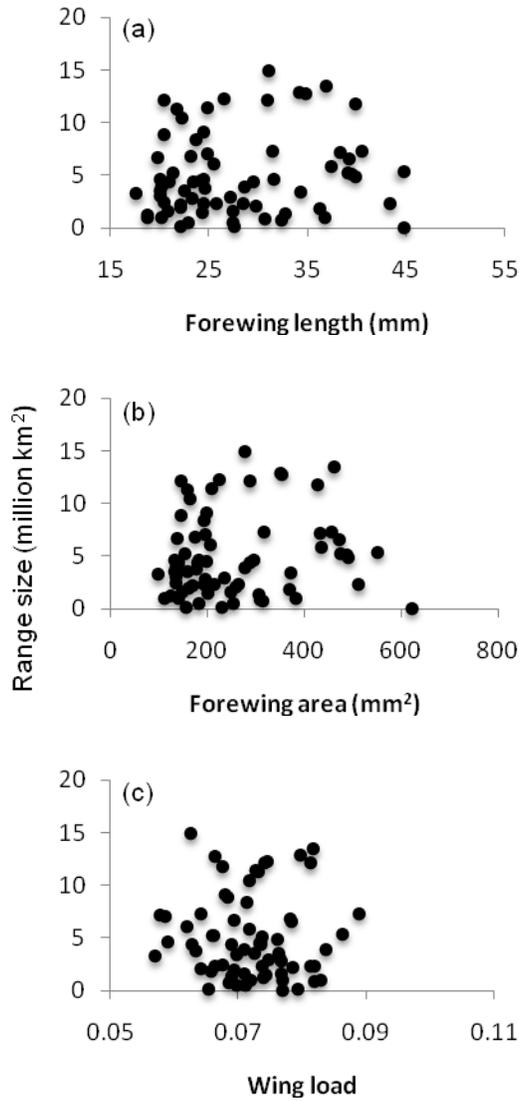


Figure 5-1. Arithmetic plots of range size as a function of 3 estimators of dispersal ability for ithomiine butterflies. (a) Forewing length (N=69); (b) forewing area (N=69); (c) wing load (ratio of thorax width to forewing length) (N=69). All data shown are untransformed.

CHAPTER 6 GENERAL CONCLUSIONS

Macroecology and Study Group

In Chapter 1, I introduced the field of macroecology, which is the study of large-scale patterns in abundance and distribution. Throughout the remainder of the thesis, I attempted to tackle some fundamental macroecological questions. Are species that are locally abundant also more widespread? Do species with greater dispersal ability occupy larger geographic ranges? To answer these questions, I chose the Neotropical butterfly tribe Ithomiini. Ithomiines have fascinated biologists since the time of the earliest South American explorers. Indeed, their ubiquity, ease of collection, and fascinating biology make them an ideal model system for study in a diversity of fields, including macroecology.

Species Range Sizes

In Chapter 2, I presented geographic range sizes for ithomiines occurring in the western Amazonian lowlands of eastern Ecuador. Since distributional data are limited for this group, as with most other groups in the Neotropics, I elected to estimate species' ranges using niche modeling techniques. As was expected, few species had large ranges throughout the Neotropics, with the majority being more narrowly distributed. Such information is a prerequisite for almost any macroecological analysis, several of which I pursued in subsequent chapters.

Relative Density Within Butterfly Communities

In Chapter 3, I outlined recent field work to collect local density data for ithomiines in Ecuador (Aug. – Dec. 2010). I described the species rank abundance distribution from the 5 field sites and compared that to a standard distribution model, the lognormal

model, to which my data fit. Few species were locally very abundant, but the remainder, and majority, were much more rare. I also evaluated completeness of sampling at the field sites using species accumulation curves, and showed that I had a thorough sample of the species occurring at the sites. Finally, I investigated the relationship between local density and body size, finding that two separate measures of body size, forewing length and thorax width, both predicted local density; larger-bodied species tended to have lower densities.

The Relationship Between Density and Distribution

In Chapter 4, using measures of range size and density compiled in previous chapters, I investigated the relationship between density and distribution (range size) in ithomiines. Using several different methods, including two in which potential phylogenetic non-independence was accounted for, I found no relationship.

The Relationship Between Dispersal Ability and Distribution

Finally, in Chapter 5, I explored the relationship between dispersal ability and distribution (range size) for ithomiines. I measured dispersal ability indirectly using morphological measures associated with flight ability in butterflies. I found no relationship between dispersal and distribution, and discussed future prospects for further study on this topic.

Outlook

Most of my analyses challenge well-documented patterns within the animal kingdom, with the unsurprising exceptions of ithomiine rank density curves and range size frequency distributions. Most unexpectedly, I found strong evidence against a relationship between density and distribution for ithomiine butterflies. There are several potential methodological difficulties worth mentioning, namely my use of measures of

density and distribution compiled at different scales, and of potential sampling bias due to the relatively small temporal and spatial scale of my density sampling effort. In the future, I plan to address these concerns, by adding density and distributional data for additional species, from other locations and times from throughout the Neotropics. Nevertheless, I strongly advocate the publishing of these, as well as all other, 'negative' results. It is probable that there is at least some (and perhaps much) underreporting of such results, as they are often more difficult to publish (Gaston & Blackburn 1999). If we fail to generate a balanced body of literature, it will be difficult to investigate macroecological patterns as they truly exist in nature (if they exist at all). Indeed, a more well-supported lack of relationship between density and distribution in the mega-diverse Neotropical ithomiine butterflies might be more interesting, and perhaps more informative, than a confirmation of patterns observed in other groups and regions.

APPENDIX A
BUTTERFLIES COLLECTED IN THE FIELD WITH RANGE SIZES

(Above) Total numbers of each species collected by hand net, per field site (JS=Jatun Sacha; YL=Yarina Lodge; SL=Sacha Lodge; YN=Yasuní Scientific Research Station; TBS=Tiputini Biodiversity Station), during field work (August-December 2010), with species' range sizes. (Below) Additional species for which ranges were estimated with BIOCLIM. Range sizes are in km². Numbered superscripts (1-13) indicate species pairs (each pair with unique number) included in Wilcoxon signed-rank test (Chap. 4). (*) indicates no range size data available from range modeling. Superscript (^d) indicates taxa included in dispersal ability analysis (Chap. 5).

Species	JS	YN	SL	YL	TBS	Range size
<i>Aeria eurimedia</i> Cramer 1777 ^{11,d}	0	17	15	4	1	8,328,526
<i>Athesis acrisione</i> Hewitson 1869 ^d	0	0	0	2	0	43,000
<i>Brevioleria arzalia</i> Hewitson 1876 ^d	3	3	12	16	2	1,518,976
<i>Callithomia alexirrhoe</i> Bates 1862 ^{5,d}	0	0	0	1	0	7,233,941
<i>Callithomia lenea</i> Cramer 1779 ^{5,d}	0	3	7	11	1	12,058,406
<i>Ceratinia tutia</i> Hewitson 1852 ^{3,d}	2	2	24	12	0	4,639,863
<i>Episcada sulphurea</i> Haensch 1905 ^{3,d}	0	0	0	2	0	1,189,846
<i>Forbestra olivencia</i> Bates 1862 ^{12,d}	0	11	23	14	2	4,648,919
<i>Forbestra proceris</i> Weymer 1883 ^{12,d}	5	0	0	0	0	2,093,783
<i>Godyrus zavaleta</i> Hewitson 1855 ^d	0	9	34	19	8	3,886,202
<i>Heterosais giulia nephele</i> Hewitson 1855 ^d	0	0	1	2	0	1,585,144
<i>Hyaliris [n. sp.]</i> Willmott & Lamas*	0	1	0	0	0	no data
<i>Hyaliris coeno</i> Doubleday 1847 ^d	1	0	0	0	0	880,582
<i>Hypoleria lavinia</i> Hewitson 1855 ^d	1	1	30	3	3	11,363,417
<i>Hypoleria sarepta</i> Hewitson 1852 ^d	0	47	0	0	6	9,051,825
<i>Hyposcada anchiala</i> Hewitson 1868 ^{2,d}	1	8	6	9	5	4,301,553
<i>Hyposcada illinissa</i> Hewitson 1852 ^d	2	2	27	17	2	4,319,711
<i>Hyposcada kena</i> Hewitson 1872 ^{2,d}	0	1	3	2	1	2,365,818
<i>Hypothyris anastasia</i> Bates 1862 ^d	1	2	0	4	0	3,373,879

<i>Hypothyris euclea</i> Godart 1819 ^{7,d}	18	1	1	28	3	12,294,947
<i>Hypothyris fluonia</i> Godman 1900 ^d	0	9	3	8	3	7,087,153
<i>Hypothyris mamercus</i> Hewitson 1869* ⁷	0	2	6	3	0	no data
<i>Hypothyris semifulva</i> Salvin 1869 ^d	0	0	22	3	1	2,244,316
<i>Ithomia amarilla</i> Haensch 1903 ^d	0	22	14	0	7	482,717
<i>Ithomia salapia</i> Hewitson 1853 ^d	5	4	6	2	6	2,775,514
<i>Mechanitis lysimnia</i> Fabricius 1793 ^d	0	4	6	2	0	14,879,369
<i>Mechanitis mazaesus</i> Hewitson 1860 ^d	1	4	10	3	0	7,121,808
<i>Mechanitis messenoides</i> Felder & Felder 1865 ^d	0	12	14	3	0	1,871,241
<i>Mechanitis polymnia</i> Linnaeus 1758 ^d	0	0	1	2	0	12,754,819
<i>Melinea menophilus</i> Hewitson 1856 ^{13,d}	0	3	6	5	0	4,853,140
<i>Melinea satevis</i> Doubleday 1847 ^{13,d}	0	0	0	5	0	5,826,009
<i>Methona confusa</i> Butler 1873 ^d	4	0	1	2	0	7,314,041
<i>Methona curvifascia</i> Weymer 1883 ^d	0	0	2	2	0	2,256,255
<i>Methona grandior</i> Forbes 1944 ^d	0	1	1	1	1	5,350,135
<i>Napeogenes aethra</i> Hewitson 1868 ^{8,d}	0	5	7	0	0	139,498
<i>Napeogenes inachia</i> Hewitson 1855 ^{10,d}	2	3	22	17	3	10,400,295
<i>Napeogenes larina quadrilis</i> Hewitson 1856 ^{8,d}	0	0	0	2	0	2,936,230
<i>Napeogenes pharo</i> Felder & Felder 1862 ^{9,d}	0	2	0	2	0	3,717,056
<i>Napeogenes rhezia</i> Geyer 1834 ^{9,d}	0	3	0	0	0	6,083,537
<i>Napeogenes sylphis</i> Guérin-Ménéville 1844 ^{10,d}	1	1	16	9	3	5,196,811
<i>Oleria agarista</i> Felder & Felder 1862 ^d	0	0	0	0	1	994,144
<i>Oleria assimilis</i> Haensch 1903 ^d	1	0	6	1	0	1,907,958
<i>Oleria gunilla</i> Hewitson 1858 ^d	2	7	20	5	5	4,562,477
<i>Oleria ilerdina</i> Hewitson 1858 ^{1,d}	0	0	3	0	1	4,363,231
<i>Oleria onega</i> Hewitson 1852 ^{1,d}	0	13	8	8	0	3,565,964
<i>Oleria sexmaculata</i> Haensch 1903 ^d	0	7	0	0	2	929,668
<i>Oleria tigilla</i> Weymer 1899 ^d	1	0	0	0	0	1,418,977
<i>Pseudoscada florula</i> Hewitson 1855 ^{6,d}	3	15	10	5	3	8,830,916
<i>Pseudoscada timna</i> Hewitson 1855 ^{6,d}	0	1	2	3	0	3,825,920
<i>Pteronymia primula</i> Bates 1862 ^{4,d}	0	7	5	5	0	6,602,995
<i>Pteronymia sao</i> Hübner 1813 ^d	0	0	0	1	0	4,540,145
<i>Pteronymia vestilla</i> Hewitson 1853 ^{4,d}	6	0	3	22	0	2,995,068
<i>Scada zibia</i> Hewitson 1856 ^d	0	7	15	18	1	3,237,947

<i>Thyridia psidii</i> Linnaeus 1758 ^d	0	1	0	3	0	11,729,265
<i>Tithorea harmonia</i> Cramer 1777 ^{11,d}	1	2	0	1	0	13,407,300
<i>Brevioleria seba</i> Hewitson 1872 ^d	n/a	n/a	n/a	n/a	n/a	3,489,241
<i>Ceratinia neso</i> Hübner 1806 ^d	n/a	n/a	n/a	n/a	n/a	6,816,812
<i>Dircenna dero</i> Hübner 1823 ^d	n/a	n/a	n/a	n/a	n/a	12,889,417
<i>Dircenna loreta</i> Haensch 1903 ^d	n/a	n/a	n/a	n/a	n/a	1,019,544
<i>Episcada mira</i> Hewitson 1877 ^d	n/a	n/a	n/a	n/a	n/a	156,984
<i>Forbestra equicola</i> Cramer 1780 ^d	n/a	n/a	n/a	n/a	n/a	5,196,547
<i>Godyris dircenna</i> Felder & Felder 1865 ^d	n/a	n/a	n/a	n/a	n/a	1,276,646
<i>Hypoleria aureliana</i> Bates 1862 ^d	n/a	n/a	n/a	n/a	n/a	521,443
<i>Hypothyris moebiusi</i> Haensch 1903 ^d	n/a	n/a	n/a	n/a	n/a	734,176
<i>Hypothyris ninonia</i> Hübner 1806	n/a	n/a	n/a	n/a	n/a	10,773,151
<i>Ithomia agnosia</i> Hewitson 1855 ^d	n/a	n/a	n/a	n/a	n/a	12,100,866
<i>Ithomia arduinna</i> d'Almeida 1952 ^d	n/a	n/a	n/a	n/a	n/a	2,212,192
<i>Mcclungia cymo</i> Hübner 1806 ^d	n/a	n/a	n/a	n/a	n/a	11,232,270
<i>Melinea marsaeus</i> Hewitson 1860 ^d	n/a	n/a	n/a	n/a	n/a	5,132,662
<i>Melinea mnasias</i> Hewitson 1856 ^d	n/a	n/a	n/a	n/a	n/a	6,491,833
<i>Napeogenes duessa</i> Hewitson 1859 ^d	n/a	n/a	n/a	n/a	n/a	2,302,551
<i>Pteronymia tucuna</i> Bates 1862 ^d	n/a	n/a	n/a	n/a	n/a	2,254,233
<i>Scada reckia</i> Hübner 1808	n/a	n/a	n/a	n/a	n/a	8,398,236

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BIOGRAPHICAL SKETCH

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