

COMPARATIVE THERMAL BIOLOGY AND ASSOCIATED
NICHE DIFFERENTIATION AMONG
THE FIVE-LINED SKINKS

by

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ABSTRACT

COMPARATIVE THERMAL BIOLOGY AND ASSOCIATED
NICHE DIFFERENTIATION AMONG
THE FIVE-LINED SKINKS

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Three species of five-lined skinks (*Plestiodon fasciatus*, *P. laticeps*, and *P. inexpectatus*) occur in regional sympatry across much of the Southeastern United States. These closely-related species, at one or more levels of development, all exhibit a similar phenotype and a high amount of prey resource overlap as documented by published data. Under the competitive exclusion hypotheses, these species should therefore not locally co-occur. This study confirms, through analysis of habitat type and canopy cover at the point of capture, that *P. inexpectatus* and *P. fasciatus* do not typically inhabit the same forest habitat. In fact, where their ranges overlap, *P. fasciatus* inhabits closed-canopy hardwood forests, while *P. inexpectatus* inhabits open forested habitats such as longleaf pine savannah and coastal scrub forests. *P. laticeps* is routinely found in sympatry with either species. Due to their large adult size, *P. laticeps* may be able to utilize

larger prey, thereby partitioning available resources. Physiological data, such as oxygen consumption (VO_2) and its temperature response (Q_{10}), support the hypothesis that these species differ with respect to their metabolic response to temperature. *P. fasciatus* exhibits a high Q_{10} at the interval that exceeds the mean daily summer temperature of sampled closed canopy forests ($\sim 25^\circ\text{C}$). *P. inexpectatus* exhibits a dramatic decrease in metabolic rate on the interval that falls below the mean daily summer temperatures of sampled Longleaf Pine Savannah habitat. The VO_2 of *P. laticeps* is the least temperature sensitive. The specific dynamic action (SDA), a measure of the amount of energy required to digest a food item, and SDA coefficient, the relative efficiency of food digestion, were also measured and support the hypothesis that *P. fasciatus* is physiologically better suited for cooler, closed-canopy habitats while *P. inexpectatus* is physiologically suited for warmer, open-canopy habitats. Collectively, these findings indicate that an evolutionarily conserved physiological niche among species may play an important role in spatial resource partitioning and maintenance of biodiversity among closely-related species.

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CHAPTER 1

INTRODUCTION

1.1 The Niche

1.1.1 A Brief History of Niche Theory

The ecological niche has been an integral part of evolutionary ecology since the coining of the term in 1917. Historically, naturalists before Darwin recognized that different species performed specific functions within an ecosystem, and Darwin himself noted that there was speciation via specialization in regard to the beaks of finches on the islands of the Galapagos Archipelago (Darwin, 1859). In addition, there are biblical references to animals' filling of specific roles (Chase and Liebold 2003). Therefore, the basic idea of niches and how they affect species composition and evolution has been around longer than the concept of evolution itself.

With the exception of the concept of the species, perhaps no other concept in biology is so fundamentally arguable, yet intrinsically important, as the niche. The concept of the niche was first introduced by Grinnell (1917) and refined early on in classic works by Elton (1927) and Gause (1936). Grinnell described the niche of the California Thrasher, *Toxostoma redivivum*, in the general terms of habitat association and the species' range. Elton added to the concept by describing the function of the species within its niche, and Gause first experimentally investigated the implications of species interactions when he authored the competitive exclusion hypothesis (Elton 1927, Gause 1936, Chase and Leibold 2003).

In the early 20th century, ecology began to incorporate more quantitative methods in theoretical explanations of biological phenomena. In 1926 Vito Volterra first applied mathematical concepts to competitive interactions, contributing to what would later be combined with the

independently-formulated 1925 work of Alfred J. Lotka and ultimately termed the Lotka-Volterra equations. This provided a mathematical competition model that could be tested in laboratory trials. Gause (1936) did just that using *Paramecium aurelia* and *Paramecium caudatum*, finding that, over time, one species drove the other to extinction in controlled experiments. This work contributed to the competitive exclusion hypothesis, and competitive interactions were then described as the Volterra-Gause Principle (Hutchinson 1959).

Drawing heavily from this principle, the niche concept was revolutionized by Evelyn Hutchinson who, in two seminal works, expanded the niche concept in its current form (Hutchinson 1957, 1959). The niche, as defined first by Hutchinson (1944), is the n -dimensional hyper-space that a species inhabits. This term was later redefined as the n -dimensional hypervolume and is the space defined along a number of axes that define a niche (Hutchinson 1957). This concept provided a structural framework for quantification of axes that describe and limit a species' niche.

Hutchinson also made an important distinction between the niche space that a species can inhabit in the absence of other species and the niche space that it inhabits in the presence of species interactions and competition. He termed the hypervolume required for a species to exist its "fundamental niche," while the constrained niche was termed "incomplete" (Hutchinson 1957). This "incomplete" niche was later termed the "realized niche" and is the state in which most species typically exist in nature. The fundamental niche is, by definition, larger in hypervolume. Species interactions and resource availability/limitations can only shift the realized niche within the bounds of this fundamental niche. Therefore, the realized niche is simply a subset of the species' fundamental niche and is constrained by the amount of partitioning with other species or the limitations of the local habitat and climate.

In another landmark work, Hutchinson described mechanisms that can allow animals to differentiate their niche and co-exist (Hutchinson 1959). He introduced a ratio of 1.3:1 as the minimum size ratio, for either actual body size or food procuring body parts (i.e. the mouth or head), that two similar species must maintain in order to co-exist in close association. This has

become known as the “Hutchinsonian Ratio” and has received much attention and scrutiny over the years (e.g., Simberloff and Boecklen 1981, Losos 1989). In fact, the actual ratio has been shown to be accurate in less than half of the cases examined by Simberloff and Boecklen (1981). Nevertheless, the exact ratio is relatively unimportant when there is an obvious size difference between species as it is clear that larger species can utilize larger prey resources, thereby not exhibiting complete niche overlap with the smaller species. The exact ratio may be more important for more similarly sized species.

The two decades following Hutchinson’s innovation of the niche concept were marked by a number of major theoretical advancements in ecology that use the niche concept as their basis. Incidentally, many of these advances were made by members of Hutchinson’s academic progeny. Most notably, Robert H. MacArthur applied the niche concept together with predator-prey interactions and optimal foraging theory to further the field of biogeography in his book-length work, Geographical Ecology (1972). MacArthur teamed with a Hutchinson lab mate, Peter Klopfer to publish a pair of papers dealing directly with niche size, species diversity, and niche overlap (Klopfer and MacArthur 1960, 1961). MacArthur’s close academic associates and graduate students included E.O. Wilson, Daniel Simberloff, and Eric Pianka, each of whom co-authored seminal works that advanced ecological theory using niche concepts. With the niche as a recurring theme, investigators with academic ties to Hutchinson and MacArthur contributed works toward such monumental theories and applications as island biogeography (MacArthur and Wilson 1967, Simberloff and Wilson 1969), character displacement (Brown and Wilson 1956), optimal foraging (MacArthur and Pianka 1966), population biology (MacArthur and Levins 1967) and ecological modeling (Odum 1960).

1.1.2 Problems with the Niche

In recent years, the concept of the niche has met some opposition. Niche-based experiments do not easily lend themselves to modern scientific methodology of hypothesis testing with null hypotheses as made popular by Popper (1963). This flaw, considered fatal by many, has drawn considerable scrutiny for classic studies that founded niche theory and has led to a

reduction (or re-naming) of the term “niche” in modern scientific literature (Chase and Leibold 2003). An alternative theory has further added to the skepticism of the niche. Hubbell’s self-termed “Universal Neutral Theory of Biodiversity and Biogeography” downplays the roles of competition and other species interactions in observed ecological patterns (Hubbell 2003). This theory endeavors to describe patterns in biodiversity and biogeography as a function of chance and relative abundance. While this theory has had some support in some systems, however, its “universality” has been empirically disproved in the scientific literature (e.g., Fargione *et. al.* 2003, McGill 2003).

1.1.3 *The Niche in Application*

Even with these assaults on its application, modern niche theory still basically includes axes as described by Hutchinson as “ecological variables” that include both variables influenced by competition and climatic variables that are typically considered free of competition, such as temperature. This is clearly evidenced by his inclusion of both variable types in Figure 1 of *Concluding Remarks* (Hutchinson 1957). Since then, the scientific community has shown relative bias to those axes which describe the hypervolume of a species’ niche in terms of resource availability and competition (Chase and Leibold 2003). In fact, the restriction of the niche to only those variables that are subject to competition was suggested to Hutchinson prior to *Concluding Remarks* by his then graduate student, Robert MacArthur (Hutchinson 1957). These limiting variables that are subject to competition are typically referred to as resources and are the predominant axes by which an animal’s niche is often conceptualized.

Chase and Leibold (2003) simply described the niche as the relationship between a species and its environment. They include a more quantitative definition that specifically includes the relationship of a species’ zero net growth isocline and the impact vector in multivariate space. This multivariate space is basically the same as the n -dimensional hypervolume originally described by Hutchinson. If the niche is of n - dimensions, then it stands to reason that the traits that an animal expresses to suit its niche are also multi-dimensional. The niche is thereby a suite of heritable traits that set the limits of phenotypic plasticity and are influenced by natural selection.

Therefore, having a genetic basis, a species' niche can evolve by the same means of any other trait and be influenced by such phenomena as geographic isolation, genetic drift, and founder effects.

1.1.4 The Niche Through Evolutionary Time: Speciation and Niche Conservatism

Speciation can occur in either allopatry or sympatry (Campbell and Reese, 2002, Pianka 2000). Allopatric speciation, often referred to as geographic speciation, involves complete geographic isolation between species, resulting in no gene flow and accumulations of changes in allele frequencies through selective pressures unique to each population. Sympatric speciation is the evolution of a new species from an ancestor that it maintains contact with throughout the process. Some mechanisms that could promote sympatric speciation are reproductive isolation such as polyploidy (Segraves and Thompson 1999), differentiation of food utilization (Bush 1969), and, rarely for animals, hybridization (Mavarez *et al* 2006). Following a speciation event, there would typically be some persistence of differences in resource utilization in order to maintain the presence of both species. This persistence was formally termed "niche conservatism" by Peterson *et. al.* (1999). This is relatively easy to understand and apply in the case of allopatric speciation. Simply, populations that are held disjunct would evolve traits most suitable to the environment to which they were isolated. Upon secondary contact, these populations, depending on the type and degree of change, would maintain these traits and thereby no longer occupy the same niche as the sister/parent population. These changes can be morphological, physiological, or behavioral. In the arguably rare cases of sympatric speciation, there has to be fundamental niche differentiation within a continuous population. In this case, one population may be separated by a dimension of the niche that is relatively independent of space. In either case, niche differences must be maintained or else one species will theoretically drive the other to extinction in a stable, resource-limited ecosystem.

Niche conservatism is most evident and applicable in the context of biogeography (Wiens and Donoghue 2004). Wiens and Graham (2005) contend that climatic niche specialization may be of great importance in determining the geographic range of a species. Different physiological

limitations and tolerances can evolve in allopatry and persist to reinforce species at the geographic scale. It stands to reason that if these climatic differences can affect the distribution of a species, then the related micro-climatic niche can also be conserved and would affect species composition and distribution at the local level. In this case, differences in one or more axes of these two species' climatic niche could also allow them to persist in close association through microhabitat segregation associated with conserved microclimatic adaptations.

1.1.5 Niche Axes: Resources and Non-Resources

Resources, as defined by Grover (1997) are "entities which contribute positively to population growth, and are consumed in the process." In this case, the use of resources as primary axes would be just as MacArthur suggested and exclude non-competitive axes such as climate variables. This, as discussed by Hutchinson, does not "abolish the difficulty" of defining the niche among multiple non-consumptive and abiotic factors. He stated that this difficulty can be negated by simply defining the hypervolume by less than n dimensions for the purposes of defining specific niche models (Hutchinson 1957).

Grover acknowledges climatic variables such as temperature as influential to the species' niche due to the effects that these variables have on the organism. However, there is no feedback resulting from their consumption. He argues that when organisms compete for these climatic variables, they are actually competing for the space in which these variables exist (Grover pers. comm.). Magnuson *et al.* (1979) contend that some climatic variables, particularly temperature, act as a resource and should be treated as such. They state that fundamental thermal niche overlap is homologous to competition for resources in ecological systems: species compete for and partition preferred temperatures just as they would food resources. Roughgarden *et al.* (1981) further contend that, while temperature acts as a resource, it cannot be considered a resource independent of time and space.

This point of contention, for the purpose of this study, is best dealt with by simply allowing for the inclusion of non-resources as niche axes. All resources and non-resources are spatially limited, ultimately making space the most important resource in any system (Cunha and Vieira

2004). Whether a species is directly competing for a specific set of climatic conditions or indirect for the space or time in which these conditions are limited, two specimens cannot physically inhabit the same space at the same time (Cunha and Vieira 2004). Species interactions may further limit the availability of preferred climatic conditions and lead to partitioning of climate space. Limitations of this space, by competition or otherwise, will constrain the fundamental niche and define the limitations of the realized niche.

Temperature, in itself, violates the definition of a resource set forth by Grover (1997) because it is not fundamentally consumed or limited by utilization. However, temperature can influence an organism's niche in many ways and, for the purposes of this study and in accordance with Hutchinson (1957), will be considered an axis for describing and limiting a species' niche. Temperature can alter physiological and behavioral processes of individuals and have a dramatic effect on such factors as oxygen availability, humidity, and evaporative water loss. Predator and prey species are also affected by temperature in many of the same ways as the target species, thereby interrelating variables at multiple trophic levels in a community that is influenced by temperature (Begon et. al.1996).

1.1.6 Fitness and the Niche

The relationship of the niche to fitness is intuitive, but not very well represented in the literature. Levins (1963) recognized an association between fitness and the availability of resources, which can be different between niches. He states that each phenotype present in a population theoretically selects the niche space where it can maximize fitness. This niche space can be modified by such factors as competition, resource availability, and species density. Therefore, the individuals whose phenotype is most fit under the available niche constraints will have a greater chance of persistence. Grover (1997) contends that competition for resources can change the phenotypic expression of physiology, morphology, and behavior through natural selection. This further indicates that differences in aspects of an organism's realized niche can result in differences in fitness, and natural selection will favor the most fit phenotype. This has

been empirically proven with *Escherichia coli*, which exhibits differential fitness trade-offs at different temperatures within its thermal niche (Mongold *et al* 1996).

1.1.7 Ectothermic organisms

Temperature is basically energy and is harnessed by ectothermic organisms to achieve proper body temperatures so that daily life processes can be performed. Some ectothermic organisms can harness this energy by behaviorally thermoregulating (i.e. basking). Others, assume the temperature of the habitat, thereby limiting activity to those times that the ambient temperature is favorable. Thermal conformers, or those species that are generally active at ambient temperatures, are at the base of the thermoregulation gradient and are limited by the temporal availability of thermal energy at the levels needed to physiologically maintain activity (Huey and Slatkin 1976). Species at the other end of this gradient must actively thermoregulate, relying on such behaviors as basking, substrate selection, and body posturing/surface area manipulation to maintain the core body temperature within the thermal parameters of normal physiological processes (Heath 1970, Huey 1982). Physiological factors that influence ectothermic animals fitness related to temperature that are typically measured are standard metabolic rate (SMR), specific dynamic action (SDA), and sprint speed.

1.1.8 Measures of Direct Effects of Temperature on the Organism

Standard metabolic rate (SMR) is a measure of the energy used during periods of inactivity at different temperatures. This is often referred to as the resting metabolic rate (RMR). The factor by which an animal's metabolic processes change over a 10°C interval is known as the animal's Q_{10} (Prosser 1991). A higher Q_{10} indicates greater temperature sensitivity of metabolic processes over that interval. A lower Q_{10} would thereby indicate metabolic stability and would be considered favorable. The "low SMR, low energy hypothesis" as formulated by Mautz and Nagy (1988) predict that species will adopt a lower standard metabolic rate to correspond to lower food availability and thermal energy input. Therefore, species that inhabit shady habitats with decreased amount of solar energy hitting the ground level should maintain a low metabolism to compensate. Conversely, species in an energy-rich environment should maintain a relatively

higher metabolism. In many cases, though, the shaded habitat may have greater resource availability in the form of leaf-litter detritivores and would thereby predict a higher metabolism of the ectothermic predator.

An animal's specific dynamic action (SDA) is the amount of energy required for digestion and assimilation of food (Iglesias *et al* 2003). Rubner (1885) first reported this phenomenon, which has since been shown to occur in all vertebrates (Randall *et al* 2002). SDA has two main applications of ecological importance. The first is in terms of cost and efficiency. Temperature affects the amount of energy used to digest a prey item. Therefore, one set of temperatures would allow a species to maximize the amount of energy derived from each unit of food. Differential optima for digestive efficiency could, along with spatial limitations on these optimal temperatures, lead to spatial segregation of species. Secondly, when an animal is using energy to digest food, that energy is unavailable for other processes, such as locomotion or reproduction (Owen 2001). This disruption in an animal's energy budget can result in required periods of inactivity or reduced reproductive output (reduced fitness). Therefore, it would be advantageous for an organism to digest the prey item as quickly and efficiently as possible. Increased temperature typically decreases the duration and increases the efficiency of digestive processes in ectotherms (Wang *et al* 2002).

Sprint speed is a particularly good measure of fitness because it represents two aspects of the animal's ecology. As with digestion and assimilation, there is an inherent cost to locomotion that varies among temperatures. It also relates to the functional ability of an animal to escape from predators and chase down prey. Sprint speed has been used to describe differential performance across temperatures for many lizards, fish, and invertebrates (e.g., Hertz *et al* 1983, Amaya *et al* 2001).

1.1.9 Geographic Distribution and Thermal Heterogeneity of Habitats

Temperature, along with rainfall, is often considered among the most influential factors that determine a species' geographic distribution (MacArthur 1972, Hengeveld 1992, Brown and Lomolino 1998). Based on latitudinal stratification of many species' ranges, including the species

covered in the current study, temperature may be the most important abiotic factor in determining geographical distribution in ectothermic animals. A species' distribution is determined by the continuous area that can support the requirements of the species. Therefore, it can be constrained by climatic variables that fall outside of the physiological tolerances of that species, limitations of resources, and competition.

Patterns of distribution and biodiversity indicate that those areas on the globe with the highest energy input are also the most biodiverse. This phenomenon has been termed the energy theory in relation to species richness (Turner *et al* 1988, Elkins 1989). Thermal boundaries for each species can be indirectly determined by randomly sampling points both within and outside of the species range and plotting the position of each point based upon the highest and lowest annual temperature experienced at that point. If the species' range is highly influenced by temperature, a line can be fitted that optimally discriminates the points within a species' range from points outside of that species' range. This line represents the limiting thermal values for that species and can be compared to established geographic isotherms (Hengveld 1992).

Temperature may also be important at the local level due to stark differences within and between habitat types. Prairies are exposed to more sunlight at the ground level than forests, and ponds vary in temperature based upon variables such as shade, depth, and conductivity. Even within forested systems, open areas in the canopy allow sunlight to reach the forest floor at higher intensity than areas where the canopy is closed. This thermal heterogeneity can allow for close spatial association of completely different thermal conditions and, potentially, different thermal niches (Begon *et. al.* 1996, Present Study: Chapter 3). Therefore, species that are considered regionally sympatric may, in fact, be allopatric at the local scale. This can be described by direct field observations regarding presence/absence of species in different habitat types, characterization of the thermal differences between these habitats, and correlation of thermally significant habitat variables at point of species observation with different species.

In order to investigate how temperature can effect species distribution and biodiversity at both the local and geographic scale, a system of ectothermic congeners occurring in regional sympatry and exhibiting a high degree of phenotypic and ecological similarity were identified. These three lizard species within the family Scincidae and the genus *Plestiodon* (formerly *Eumeces*) were chosen due to the aforementioned traits. Lizards have historically served as model organisms for ecological studies and, because they are ectotherms, are particularly well suited for investigations in thermal ecology (Huey *et al* 1983).

1.2 The Study Organisms

1.2.1 Lizards as Subjects of Study for Ecological Hypotheses

Lizards, having been said to rival birds as the “paradigmatic organism of ecology” (Huey *et al* 1983) are at the forefront of ecological study. Prominent ecologists who work primarily with lizards include Joan Roughgarden, Jonathan Losos, Eric Pianka, Thomas Schoener, and Ray Huey. Historically, the lizard species used as models to test or develop ecological hypotheses have been largely Anoline lizards of the Caribbean Islands (e.g., Losos 1990, 1992, Roughgarden 1995, Huey 1982). This is due in part to the interest of the investigators, but also because they occur in various levels of sympatry within well-defined geographic boundaries. Studies that dealt with foraging theory and the ecological significance of sexual dimorphism (Schoener 1967), optimal temperatures (Huey 1982), character displacement (Losos 1990), and island biogeography (Williams 1969) all have included Anoline lizards as subjects for study. Eric Pianka spent much of his career investigating desert-dwelling lizards in North America and Australia, publishing papers regarding lizard communities’ spatial relationships (1966), niche dynamics (1975), and resource partitioning (1969). He published a book titled *The Ecology and Natural History of Desert Lizards* (1986) that synthesized his work with lizards in this biome. Three volumes have been published dealing directly with lizard ecology (Milstead 1965, Huey *et al* 1983, Vitt and Pianka 1994), and the ecological literature continues to include investigations in ecology using lizards as model organisms.

1.2.2 Lizards and Thermal Ecology

Lizards are widespread throughout tropical and temperate regions and, as ectotherms, are particularly sensitive to changes in temperature. Therefore, they make a good model organism for the study of thermal ecology. Lizards have served as popular model organisms for the study of thermal ecology since the 1940's, when Cowles and Bogert (1944) first reported on lizard thermoregulation. Paul Hertz and Ray Huey have since popularized questions and techniques regarding the effects of temperature on such aspects of lizards' behavior and physiology as sprint speed and behavioral thermoregulation (e.g. Hertz *et al* 1983, Huey 1983). These two investigators integrated physiological techniques with ecology in order to better understand how a species' thermal environment affects ecologically relevant processes. Owing to the straight-forward experimental techniques, many other investigators followed suit with empirical studies, and now the lizard thermal physiology/ecology literature is well populated. By the late 1970's the rate of publication of papers dealing with the thermal physiology of lizards was nearly 15 per year (Huey *et al* 1983), and there is no reason to believe that the rate has since declined.

1.2.3 Lizards of the Family Scincidae

Members of the family Scincidae, the skinks, receive less attention from ecologists than *Anolis*, but many skink communities possess attributes that are equally interesting and of general utility to application of ecological hypotheses. World-wide, species within this family often occur in sympatry and therefore partition resources such as space. One community in southern Luzon, the Philippines includes 11 sympatric skink species in dense forest habitat (Auffenberg and Auffenberg 1988). Furthermore, skinks are part of a group that is thought to be sister to snakes and relatives. Therefore, physiological and behavioral experiments using this family may serve as more general models for lizard and snake communities.

General attributes of skinks make them well-suited for scientific study. They typically are abundant where found, relatively short-lived, with relatively small home ranges, and they are not difficult to maintain in the laboratory. The lineage that was selected for this study includes

members of the genus *Plestiodon*. They occur throughout the Southeastern United States and have been suggested to be sympatric throughout much of their range (Conant and Collin 1998, Fitch 1954). The way that these species respond to their thermal environment offers insight into maintenance of biodiversity, competitive exclusion hypothesis, and physiological constraints in relation to biogeography.

1.2.4 The Genus *Plestiodon*

Until recently, the genus *Eumeces* included the current old-world *Eumeces* as well as all species within the currently recognized Asian and North American genus of *Plestiodon*. In light of recent molecular studies, the genus *Plestiodon*, originally assigned by Dumeril and Bibron (1839), was revived to denote this group's East Asian and North American clade (Brandley *et al* 2005, Schmitz *et al* 2004). Within this genus, there are 15 currently recognized species, with members occupying habitats ranging from xeric desert-scrub to temperate hardwood forest. These skinks generally follow a retained juvenile phenotype that includes some level of longitudinal striping against a dark brown to black background and a blue-colored tail, presumably used to divert the attack of would-be predators away from vital areas of the body (Poulton 1890, Cott 1966, Cooper and Vitt 1985b). Exceptions to this phenotype include the non-striped juveniles of *Plestiodon obsoletus*, red tail coloration of members of the *P. skiltonianus* and *P. egregious* complexes, and the generally colorless fossorial *P. reynoldsi* (Conant and Collins 1998, Stebbins 2003).

Within *Plestiodon*, there are two generally accepted complexes that exhibit similar relationships and natural histories: the *Plestiodon skiltonianus* group of western North America and the *Plestiodon fasciatus* group of Eastern North America (Richmond 2006). The *P. skiltonianus* group is found on the west coast of North America and includes *Plestiodon skiltonianus* and *P. gilberti*, both of which exist in no less than three forms that are often referred to as sub-species. Each of these complexes includes at least one large species and more than one smaller species or sub-species. All members of both complexes exhibit some level of retained phenotype in at least one stage of development (Richmond 2006).

1.2.5 The *Plestiodon fasciatus* species complex

Once thought to be a monophyletic group consisting of the forest-dwelling *Plestiodon fasciatus*, *P. laticeps*, and *P. inexpectatus* (Murphy *et al* 1983), the *Plestiodon fasciatus* species complex has been recently expanded to include the more xeric *P. multivirgatus*, *P. obsoletus*, *P. septentrionalis*, and *P. tetragrammus* (Richmond 2006, Brandley *et al* 2005, Richmond and Reeder 2002). These new inclusions, based upon maximum likelihood methods and DNA sequencing, did not just represent an addition of another monophyletic group. Instead, the relationships of these species to the three established species indicate that the forest-dwelling species are not only paraphyletic, but they are not even one another's closest relatives (Figure 1.1). *Plestiodon laticeps* is the most basal species with *P. fasciatus* more closely allying with *P. septentrionalis*, and *P. inexpectatus* exhibiting a closer relationship to *P. tetragrammus* and the common ancestor of *P. fasciatus* and *P. septentrionalis* (Figure 1.1). These updated relationships resolve the issue highlighted by Fitch (1954) that these species are in violation of Jordan's Rule, which states that a species' nearest relative should not be found in general sympatry or distant allopatry, but rather in adjacent allopatry, separated by a geographic barrier.

Until 1932, these three five-lined species from the southeastern United States were all considered to be one species, *Eumeces fasciatus* (Cope 1898, Ditmars 1936). The type-specimen was actually a drawing sent to Linnaeus by Mark Catesby from Charleston, South Carolina. Taylor revived the specific epithet of "*laticeps*" to denote the large, more arboreal species and formally described *P. inexpectatus* from museum specimens in the same year (Taylor 1932a, 1932b). In 1935, Taylor published the first, and only, comprehensive text regarding all species within the genus then known as "*Eumeces*" (Taylor, 1936). The ecology of certain populations of *P. fasciatus* is well known and *P. laticeps* has received limited attention (Fitch 1954); however, the range-wide ecology of *P. inexpectatus* has received limited attention and remains generally unknown. Accounts of these species vary greatly in respect to habitat descriptions. *P. laticeps* has been reported to exclusively inhabit dry upland forest (Netting, 1939, Conant 1951) while also being described as a bottomland swamp and woodland species (Fitch

1954, Conant and Collins 1998). There may be some variation in habitat choice over the geographic range of this species, but these disparities probably are a product of the anecdotal nature of the accounts and the ability of this species to inhabit a wide variety of habitats.

Plestiodon fasciatus is reported to be a forest species in the more southern parts of its range, while inhabiting open lots and meadows in the northern extent of its range (Harding and Holman 1997, Mount 1975). *Plestiodon inexpectatus* is often described as inhabiting drier open habitats (Conant and Collins 1998, Fitch 1954). Mushinsky (1992) further connected *P. inexpectatus* to open, fire-maintained habitats in Southern Florida in the only comprehensive account of a population of *P. inexpectatus*. Despite these differences, Fitch (1954) notes that those ecological and morphological differences found between *P. fasciatus* and *P. inexpectatus* are, at most, of the degree most often found between sub-species.

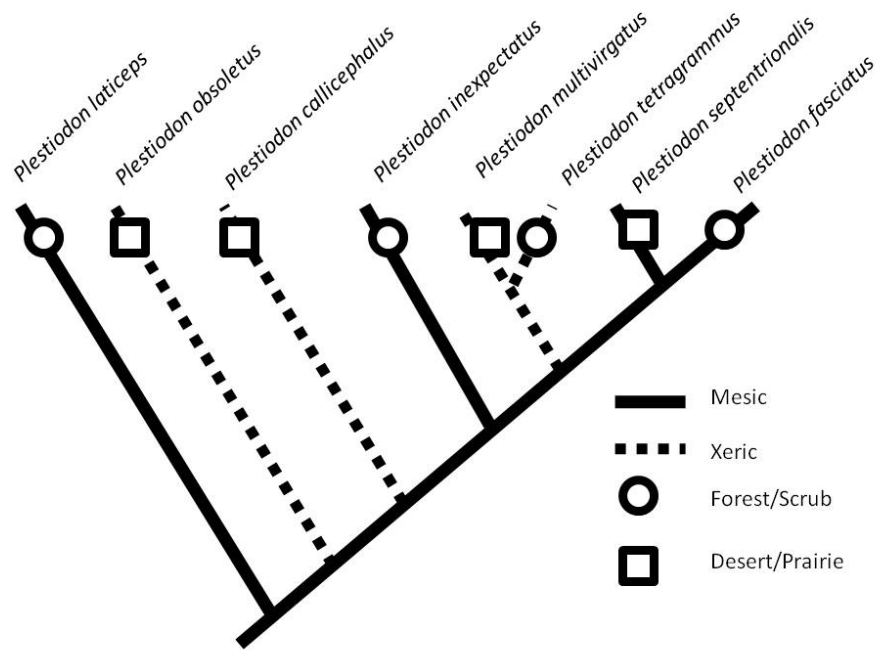


Figure 1.1 Phylogeny of the *Plestiodon fasciatus* species complex with general descriptions of hydrology and habitat. Relationships derived from Richmond (2006) and hydrology/habitat data from Conant and Collins (1998).

1.2.5.1 Identification

Field identification of these three species can prove difficult, even to those experienced with them. Davis (1969) noted increased variation in the morphological traits used by Taylor to originally describe these species among some populations. In some populations encountered over the course of this study, such as those sampled in Smith County, Texas and Talladega National Forest in Alabama, these anomalies were more common (5 animals at each site) whereas the majority of the sampled sites produced none to one animal with mixed characters. Individuals with mixed characters are periodically encountered and, for the purposes of this study, such specimens are excluded from all analysis. A simple key to the five-lined skinks encountered in this study is provided in Table 1.1. *Plestiodon inexpectatus* is the most readily identifiable of the three species. The subcaudals do not exhibit widened scales, a trait shared by both *P. laticeps* and *P. fasciatus* (Figure 1.2). *P. fasciatus* typically exhibits four superlabials while *P. laticeps* exhibits five (Figure 1.3). Juvenile specimens of *P. laticeps* are often indistinguishable from *P. fasciatus*, so only sexually mature adults were used in laboratory experiments and questionable identifications were excluded from analysis of field data. Adult *P. laticeps* are significantly larger than either of the other two species. In fact, based on maximum lengths as reported by Conant and Collins (1998), *P. laticeps* meets the size requirement for co-existence of 1:1.3 as suggested by Hutchinson (1959) when compared to both *P. fasciatus* and *P. inexpectatus*. However, *P. fasciatus* and *P. inexpectatus* do not when compared to one another.

Table 1.1. Field identification key to the five-lined skinks of the Southeastern United States (derived from Conant and Collins 1998)

1.	Subcaudals widened or generally same-sized (Figure 1.2)
a.	Widened: Question 2
b.	Same-sized: <i>Plestiodon inexpectatus</i>
2.	Number of Superlabials (Figure 1.3)
a.	Four: <i>Plestiodon fasciatus</i>
b.	Five: <i>Plestiodon laticeps</i>

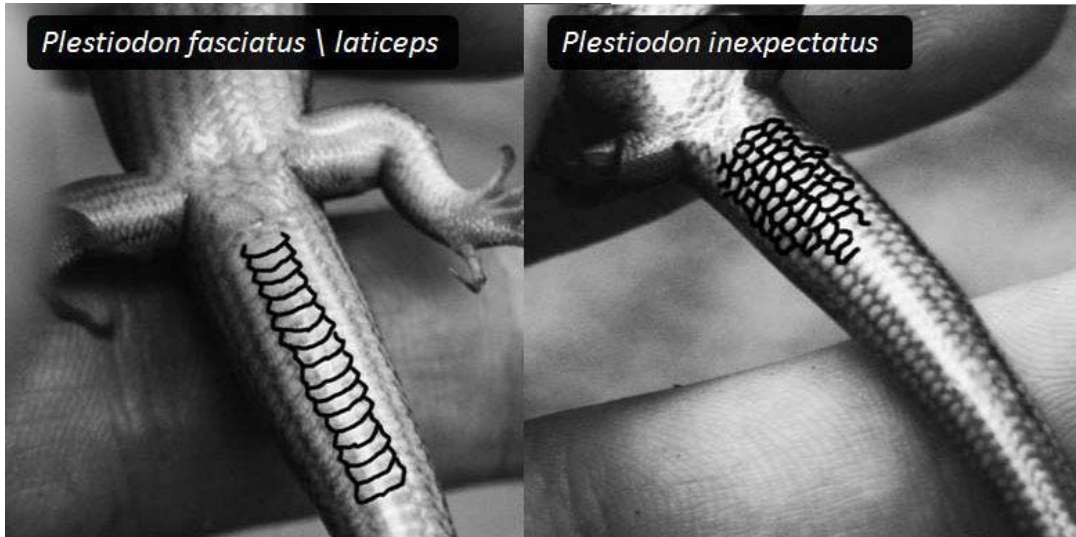


Figure 1.2. Wide center row of subcaudals of *Plestiodon fasciatus* and *P. laticeps* and the same-sized subcaudals of *P. inexpectatus* outlined in black.

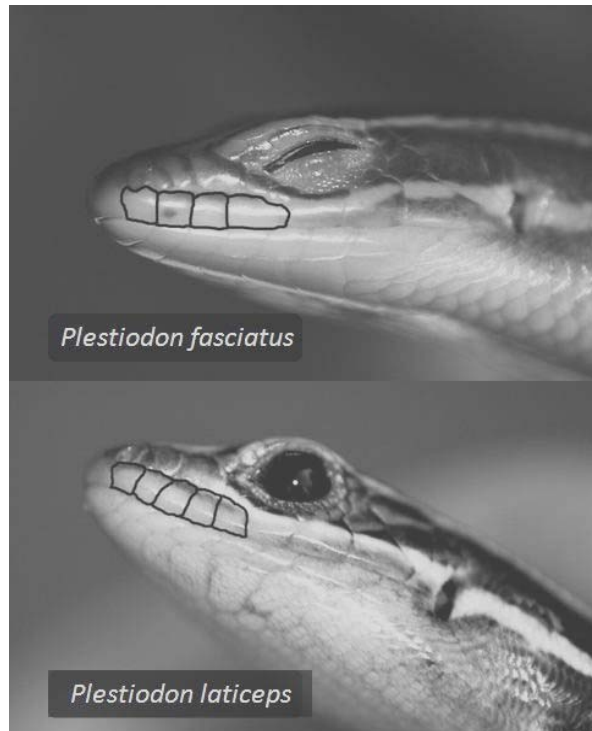


Figure 1.3. Superlabials of *Plestiodon fasciatus* and *P. laticeps* outlined in black.

1.2.5.2 Biogeography

Plestiodon multivirgatus, *P. obsoletus*, *P. septentrionalis*, and *P. tetragrammus* exhibit varying levels of range overlap along a longitudinal hydrocline while *P. fasciatus*, *P. laticeps*, and *P. inexpectatus* exhibit a defined nesting of ranges that overlap along a latitudinal thermocline (Figure 1.4). *P. fasciatus* exhibits the widest range of any North American lizard, extending from Canada to Florida, east to the Atlantic Coast, and west to the eastern extent of the Central Plains. *P. laticeps* exhibits roughly the same longitudinal boundaries, but reaches northward only to the glacial line extending across the midsections of Ohio and Indiana, and does not extend farther south than central Florida. *P. inexpectatus*' inland range is limited northward to Southern Kentucky but this species extends further north along the coastline to Maryland and is the only species present in the Florida Keys. This species is limited westward by the Mississippi River basin. In the southeastern United States, all three species are widely synoptic (Conant and Collins 1998, Richmond 2007).

The recognized fossil voucher specimen for *Plestiodon inexpectatus* is from Levy County, Florida, indicating that this species may have originated in or around Florida (Holman 1959). Given the location, this species may have experienced a vicariance event due to the formation of islands during Holocene glacial retreat. The fact that these animals colonize and dominate coastal islands lends further evidence to this hypothesis. The recognized fossil of *P. laticeps* was found in Pendleton County, West Virginia. A number of *Plestiodon fasciatus* fossils have been found throughout the southeast (Parmley 1988). While many barriers were in place during the evolution of these three species, it is possible that *P. laticeps*, due to its enormous relative size, could have been the result of sympatric speciation via character displacement.

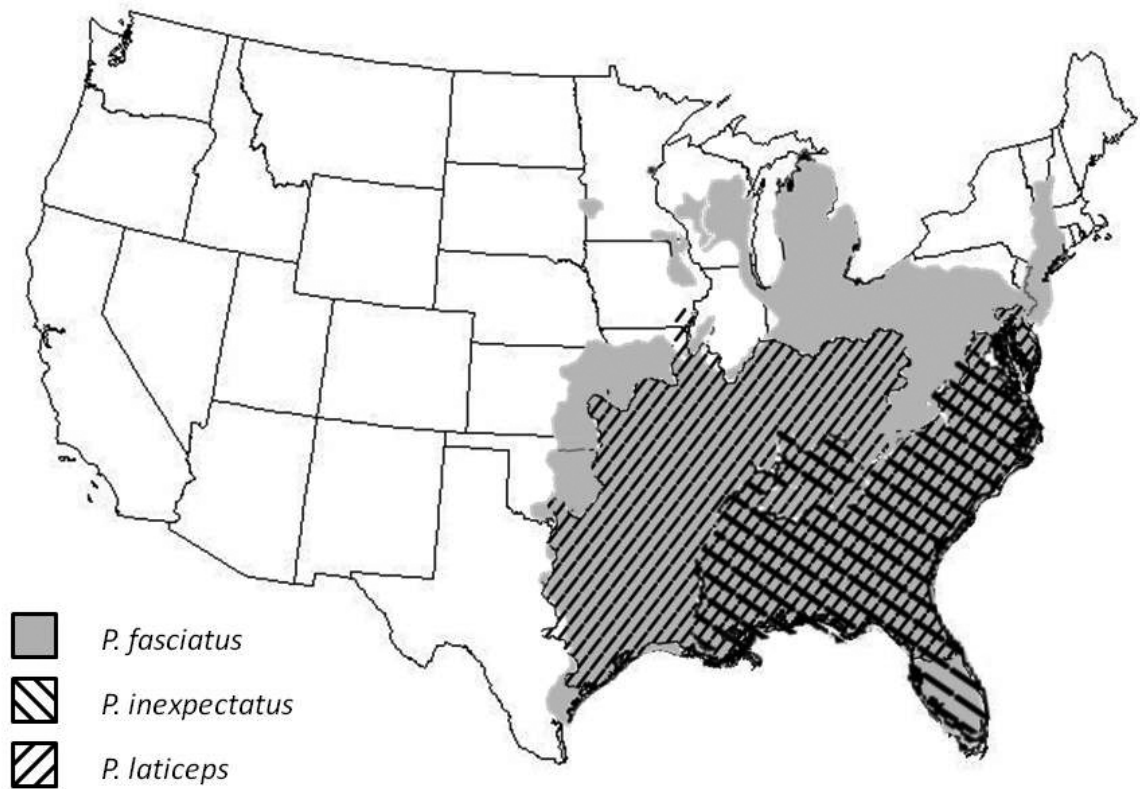


Figure 1.4. Geographic range of *Plestiodon fasciatus*, *P. laticeps*, and *P. inexpectatus*. Modified from Conant and Collins (1998).

1.2.5.3 Habitat

It has been suggested that *Plestiodon fasciatus* prefers moist forests, while *P. inexpectatus* prefers ridges and upland sites (Taylor, 1936; Smith, 1946). *P. laticeps* tends to be more arboreal than the other two species (Conant and Collins 1998; Taylor, 1936), thereby utilizing resources unavailable to the more terrestrial species. *Plestiodon inexpectatus* typically inhabits more open habitats than the other two species (Fitch 1954, Mount 1975, Mushinsky 1992). Such habitats include longleaf pine (*Pinus palustris*) dominated savannas, coastal scrub forest, maritime forests, and granite outcroppings (Vitt pers. comm). Longleaf pine savanna habitat is fire-dependent and has experienced significant decline over the past century due to a

reduced or non-existent fire regime and conversion to timber and agricultural lands (Gilliam and Platt 2006). Therefore, *P. inexpectatus* populations may also be declining over much of its range. *P. fasciatus* are generally found in closed-canopy, hardwood-dominated habitat where its range overlaps the range of *P. inexpectatus*. However, they are present in open longleaf pine forests beyond the western extent of *P. inexpectatus*' range and in open areas along railways beyond the northern extent of *P. inexpectatus*' range (Watson, per obs, Vitt pers comm.). As *P. fasciatus*' geographic range extends northerly, it inhabits more open habitats, as evidenced by southern state field guides describing its habitat as closed forests (e.g. Mount 1975) and northern state field guides describing its habitat as open fields and meadows (e.g. Harding and Holman 1997). Quirt *et al* (2006) found that populations of *P. fasciatus* in Canada prefer open, rocky habitats and correlates those preferences to increased temperature and reduced tree cover. *P. laticeps* frequents both edge and deep forests, inhabiting habitats occupied by both of the other two species (pers obs).

1.2.5.4 Direct Interactions

In a series of studies by Cooper and Vitt (1984, 1985a, 1986a, 1986b, 1986c) dealing specifically with these three species, a chemical mechanism of interspecific discrimination was established. They counted tongue-flick rates of adult specimens when presented with odor-laden cotton swabs. Later studies using a more direct methodology of presenting actual specimens into the same enclosure showed that male *P. fasciatus* and *P. laticeps* did not court or copulate with heterospecific females, but *P. inexpectatus* courted all species and copulated with *P. laticeps* females, but not *P. fasciatus* (Cooper and Vitt 1987). This may be a function of the fact that *P. inexpectatus* may have been completely isolated from *P. laticeps* during some part of its evolutionary history, while *P. laticeps* and *P. fasciatus* were continually or cyclically sympatric, thereby developing this reinforcement mechanism. Nevertheless, these findings cumulatively support the assumption that these three species can identify members of the other species and they generally avoid same-sex interactions while exhibiting relative indifference toward opposite-sexed individuals of the other species (Cooper and Vitt 1984, Cooper and Garksta 1987). These

findings provide a means by which these species can identify and avoid the other species as well as a behavioral barrier to hybridization. While there is no data to indicate if hybridization is mechanically possible, it is generally assumed that, in the very least, these animals can identify conspecifics and exhibit a reproductive affinity toward their own species. Outside of direct reproductive interactions and aggression, large adult *P. laticeps* have been noted to include smaller *Plestiodon* in their diet, including exhibition of cannibalistic behavior (Vitt and Cooper 1986, Hamilton and Pollack 1961).

1.2.5.5 Indirect Interactions

Currently, there is no indication that *Plestiodon inexpectatus* and *P. fasciatus* partition prey resources. In fact, baseline gut-content analyses generally include the same major constituents in the diet of all three species, Coleoptera and Aranea. *P. laticeps*, by virtue of their larger adult size, can take larger prey items including occasional vertebrate species (Hamilton and Pollack 1961). Rundquist and Collins (1974) specifically noted no noticeable difference in diet between *P. fasciatus* and *P. inexpectatus* from the gut-content analysis that they performed on animals in Kentucky. Furthermore, there is no noticeable temporal or microhabitat segregation as *P. inexpectatus* and *P. fasciatus* are both diurnal and they generally utilize low-lying horizontal deadfall as refuge (Watson, pers. obs.). *P. laticeps* is reported to be more arboreal and often utilizes tree hollows as refuge sites (Cooper and Vitt, 1994, Cooper *et al* 1983). These factors indicate that *P. inexpectatus* and *P. fasciatus* may competitively exclude one another while *P. laticeps* persists in true sympatry with both by being more arboreal and satisfying Hutchinson's ratio. This is consistent with the author's field observations that *P. fasciatus* and *P. inexpectatus* are generally mutually exclusive within their respective habitat type, while *P. laticeps* has been observed in both habitats.

1.2.5.6 Biodiversity and Biogeography in Relation to Thermal Ecology

Given these three forest-dwelling species' broadly overlapping ranges, similar prey, and refuge utilization, one must look beyond simple habitat correlates to biogeography and competition to consider other factors that may sway competitive advantages in a differential

manner depending upon latitude and habitat type. This study explicitly investigates differences in thermal ecology among *Plestiodon fasciatus*, *P. laticeps*, and *P. inexpectatus* as an explanation for the range of these species at the continental level and the maintenance of biodiversity within this community at the local level. It is possible, at the local level, that *P. laticeps* may persist in sympatry with *P. fasciatus* and *P. inexpectatus* due to slight differences in resource utilization related to their large size and increased arborality. Therefore, at least at the local level, the most interesting interaction is between the similar-sized *P. fasciatus* and *P. inexpectatus*. These two species are often found in close proximity to one another, often as close as a few meters, but they differ in the characteristics of the forested habitats that they generally inhabit.

At the continental level, the arrangement of these three species is unique in that each species' range is completely nested within the range of the next-most widespread species (Figure 1.4). Therefore, the entire range of the next-most range constrained species represents the interaction zone between the respective species. This provides an opportunity to illustrate how retained physiological adaptations (niche conservatism) and the abiotic landscape (temperature) can affect the biogeography of a closely-related community while promoting biodiversity within broad contact zones by micro-habitat segregation.

1.3 Specific Aims

Using these three phenotypically similar forest-dwelling congeners, this study aimed to draw ecological inferences relative to thermal niche partitioning, the maintenance of biodiversity and extent of their geographic range. The specific aims of this study were as follows:

1.3.1. Thermal Ecology (Chapter 2)

As discussed above, there are many different qualitative accounts of these species' habitat choice across their respective ranges. Some of these differences are consistent with differences in thermal quality of the habitat. This study aimed to quantitatively document the thermal differences among these three species' preferred habitats within their overlapping range by measuring the thermal differences between the two habitats as well as comparing canopy cover data between habitats and among the study organisms. I hypothesized that the two

habitats that these species are most frequently encountered in, longleaf pine savannah and the adjacent hardwood habitat, would differ thermally such that the longleaf pine savannah is warmer throughout the day and the adjacent hardwood habitat would exhibit cooler temperatures. These data provide quantitative, comparable thermal differences between each species' preferred habitats and serve as a basis of comparison for the rest of the study.

1.3.2. *Thermal Choice and Performance (Chapter 3)*

This section aims to determine differences among these species in regard to the thermal ecology established in Chapter 2. Sprint speed and thermal choice were measured in order to compare the response of these species in the context of existing literature. The findings of these experiments were used to draw conclusions on how these species may perform better or worse within the experimental temperatures that represent their microhabitat.

A captive colony was established in order to perform laboratory trials and was maintained in accordance with the UTA IACUC protocols A06.017 and A07.003 as well as the *Guidelines for use of live amphibians and reptiles in field research* set forth by the American Society for Ichthyology and Herpetology and the Society for the Study of Amphibians and Reptiles.

Thermal choice and performance as measured by sprint speed are the typical ecologically interpretable measures found in thermal ecology literature. Thermal choice has been determined through the use of thermal gradient chambers for *Plestiodon fasciatus* and *P. laticeps* (Brattstrom 1965, Pentecost 1974). Using similar methodology, the preference for *P. inexpectatus* was determined for comparison to the established values for the other two species. The use of sprint speed as an indicator of optimal temperatures and thermal performance breadth is well represented in the literature. The rate of increase of sprint speed across four acclimation temperatures was analyzed. The classic measures of critical temperatures were not included in this study because obtaining such values could permanently alter the physiology of individuals, rendering them unfit subjects for other experiments. Furthermore, Hertz *et al* (1983) question the ecological relevance of such measures as body temperatures of lizards almost never reach these temperatures in natural environments.

1.3.3 *Thermal Metabolic Physiology (Chapter 4)*

Studies in metabolic physiology have historically been descriptive in nature. Using such measures as standard metabolic rate, reaction rate, specific dynamic action, and specific dynamic action coefficient, the metabolic reaction to temperature is characterized for each species. How an organism metabolically reacts to changes in temperature (Q_{10}) as well as the amount of energy used at each temperature while at rest (Standard Metabolic Rate: SMR) and the amount of energy used during digestion (Specific Dynamic Action: SDA) all have direct ecological implications. Energy budgets must be maintained for each species and energy consumption is related to temperature in ectothermic organisms. If the cost of digestion exceeds the amount budgeted for such processes at a given temperature, then other processes, such as activity and reproductive endeavors will suffer for the duration of the digestive process (Owen 2001). This could have implications on individual fitness and thermal niche parameters of the species. This study aimed to quantify differences in metabolic rate and establish metabolic optima in the aforementioned terms at three ecologically-relevant temperatures for each of the three species. These data allows for the comparison of these values in respect to the ecological values discussed in Chapter 2.

1.3.4 *Comparative Thermal Biology and the Niche of The Five-Lined Skinks(Chapter 5)*

The data gathered and discussed in Chapters 2-4 were synthesized in order to draw conclusions regarding these three species' thermal biology and related constraints on their thermal niche in respect to the availability of thermally optimal space within the habitats where they are found. Differences in thermal preference, performance, and aerobic metabolism at ecologically relevant temperatures provided a mechanism for differentiation of at least two of these species' thermal niche. Alternative explanations for co-existence and exclusion of these species across their geographic range as also explored.

CHAPTER 2

COMPARATIVE THERMAL ECOLOGY

2.1 Introduction

Species' range and distribution are closely tied to many variables within their preferred habitat. These variables can include prey availability, refuge, and availability of climatic factors that fall within tolerable physiological limits. The most measurable of these climatic factors are rainfall and temperature. The genus *Plestiodon* includes many taxa that inhabit areas that are different in regard to rainfall, temperature, and general habitat (Figure 1.1). The three species involved in the current study exhibit a different pattern that appears to be along a thermal gradient at the continental level. As stated previously, the general trend with these three species is that, in the range of gross sympatry, *Plestiodon fasciatus* inhabits closed-canopy hardwood forests, *Plestiodon inexpectatus* inhabits open habitats, such as longleaf pine savannah and maritime forests, and *Plestiodon laticeps* can be found in both. Over the course of this study this pattern was observed at 100% accuracy. At one site, The Jones Center for Ecological Research in southern Georgia, all three species were found within 100 meters of one another at the interface of these two habitats. *Plestiodon fasciatus* and *P. laticeps* were often found in the same log, while *P. inexpectatus* were observed only as single individuals. These observations were made over the course of two field seasons at various sites across the southeastern United States (Figure 2.1).

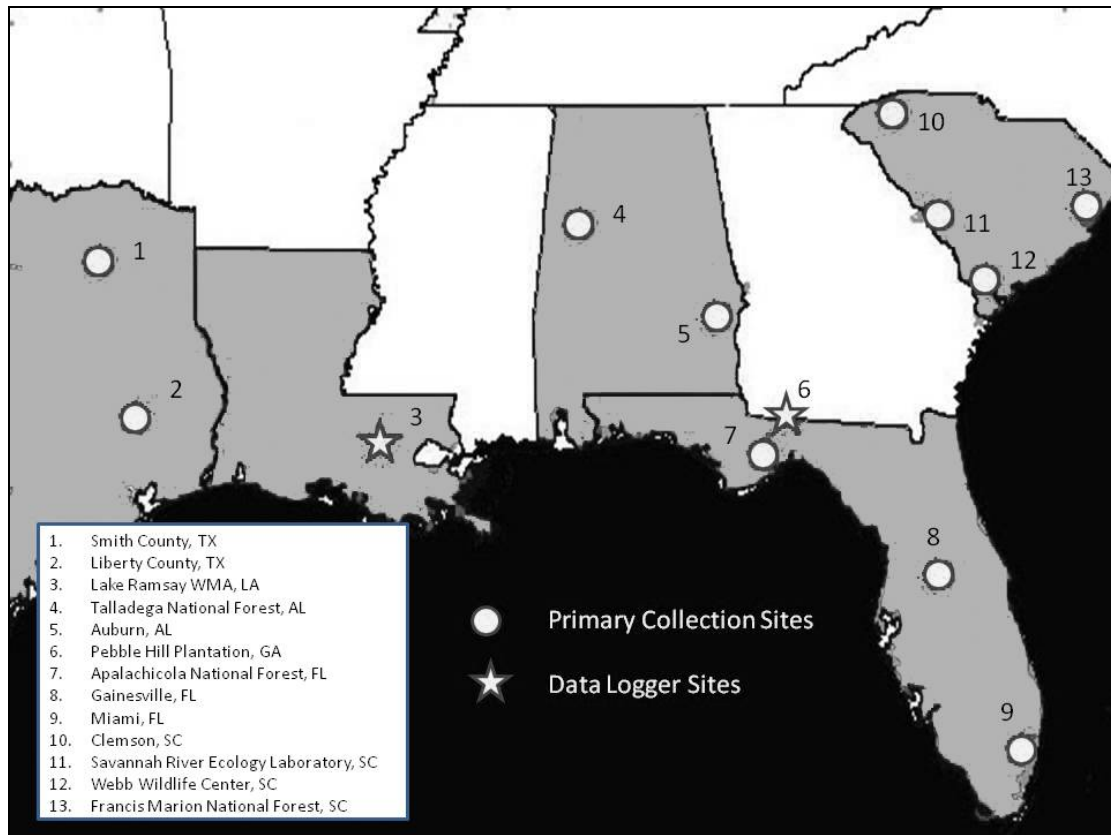


Figure 2.1. Distribution of sites where animals were sampled and data loggers were placed in the southeastern United States.

The fact that these three species have been reported to utilize similar prey resources and exhibit similar color and morphological phenotypes make it unlikely that they strongly partition habitat based upon prey and predation. The most obvious differences between these two habitats (longleaf pine savannah and adjacent hardwood) are temperature and canopy cover, which are intrinsically related (Rauner 1977). There is a positive correlation between canopy cover and temperature at the ground level. This is simply due to the fact that solar radiation penetrates further in open habitats than in closed habitats. The thermal environment becomes more homogeneous as canopy cover decreases (Rauner 1977). Conversely, it is patchy in closed canopy forests with diffuse light and dappling sun flecks, providing limitations on the thermal aspect of space as a resource.

The goal of this study was to describe differences in the thermal aspect of the two habitats where these three species most frequently occur. First, a panel of temperatures was logged in each habitat to determine differences in the thermal environment between longleaf pine savannah and adjacent hardwood habitat. Secondly, canopy cover was measured at the point of capture for each specimen encountered in the field in order to determine whether there are differences among these species in respect to habitat choice associated with openness of the canopy. The following chapters use these findings as a basis for comparison among *Plestiodon fasciatus*, *P. inexpectatus*, and *P. laticeps* in respect to their thermal ecology.

2.2 Habitat Temperature Methodology

In order to document thermal differences between the closed-canopy habitat (hardwood-dominated) and the open-canopy habitat (longleaf pine savannah), temperature data loggers embedded in grey-body models were placed in ecologically relevant sites within each habitat to represent those areas where lizards are typically encountered. The models consist of an approximately 10cm length of $\frac{3}{4}$ " copper pipe dipped in grey paint and fitted with an ibutton© data logger (Dallas Semiconductor, Dallas, TX). The pipe was then filled with nylon filter floss in order to fill the air space and restrict the movement of the data logger. The data loggers were positioned inside of the model so that they did not come in contact with the metal pipe and the ends were capped with rubber stoppers. Data loggers were programmed to log the temperature at 20-minute intervals; 25 were placed in an open longleaf pine savannah habitat and 25 were placed in a closed-canopy adjacent hardwood habitat in southern Georgia (The Pebble Hill Plantation of the Tall Timbers Institute) during the month of June 2007. Specific sites for data logger placement were chosen within the habitats that represent a microhabitat where a skink would likely be seen. Such placement allows for a more relevant sample compared to random placement because, if they were placed in a truly random fashion, some loggers may be placed in sites that skinks would not occur, such as in open fields, ponds, or roads. This method was repeated for similar habitats in the Lake Ramsey Savannah Wildlife Management Area in eastern Louisiana in July 2007. These study sites were chosen for two reasons. First, they are at similar

latitudes within the range of all three species. In fact, all three species were captured upon the initial visit to each site to validate that they were indeed present. All specimens captured at these sites were released because use permits did not include the collection of animals. Secondly, both sites are managed by research-friendly professional biologists and have an active fire-management plan that maintains longleaf pine savannah habitat.

The daily mean temperature, daily high temperature, daily low temperature, and daily standard deviation for each data logger was established. The data were then analysed with a t-test and significance was determined at $\alpha = 0.05$.

2.3 Habitat Temperature Results

The daily temperature for longleaf pine savannah habitat did exhibit a significantly higher mean than the hardwood habitat at both the Pebble Hill Plantation (PHP) ($t_{(18)} = -4.23, p < 0.001$) and the Lake Ramsay Wildlife Management Area (LRWMA) ($t_{(16)} = -7.66, p < 0.001$)(Table 2.1). When daily high temperatures were compared, both sites also exhibited a significantly higher mean value for the longleaf pine savannah than the hardwood habitat (PHP: $t_{(18)} = -4.63, p < 0.001$; LRWMA: $t_{(16)} = -6.97, p < 0.001$), but not when the mean daily low temperatures are compared (PHP: $t_{(18)} = -0.39, p = 0.701$; LRWMA: $t_{(16)} = -.20, p = 0.84$) (Figure 2.1, 2.2). The mean standard deviation from the mean was significantly higher in the longleaf pine savannah than the adjacent hardwood at both sites (PHP: $t_{(18)} = -8.92, p < 0.001$; LRWMA: $t_{(16)} = -4.58, p < 0.001$)(Table 2.1).

Table 2.1. Mean values for comparison between the longleaf pine savannah (LLPS) habitat and adjacent hardwood (HW) habitat for the Pebble Hill Plantation in Southern Georgia and Lake Ramsay Wildlife Management Area in Louisiana. All values are in degrees Celsius.

	Mean	Maximum	Minimum	Standard Deviation
<u>Pebble Hill Plantation</u>				
LLPS	28.69	50.49	19.57	9.09
HW	25.98	38.13	19.36	5.46
<u>Lake Ramsay WMA</u>				
LLPS	29.76	48.18	23.11	7.05
HW	26.35	35.10	23.05	3.06

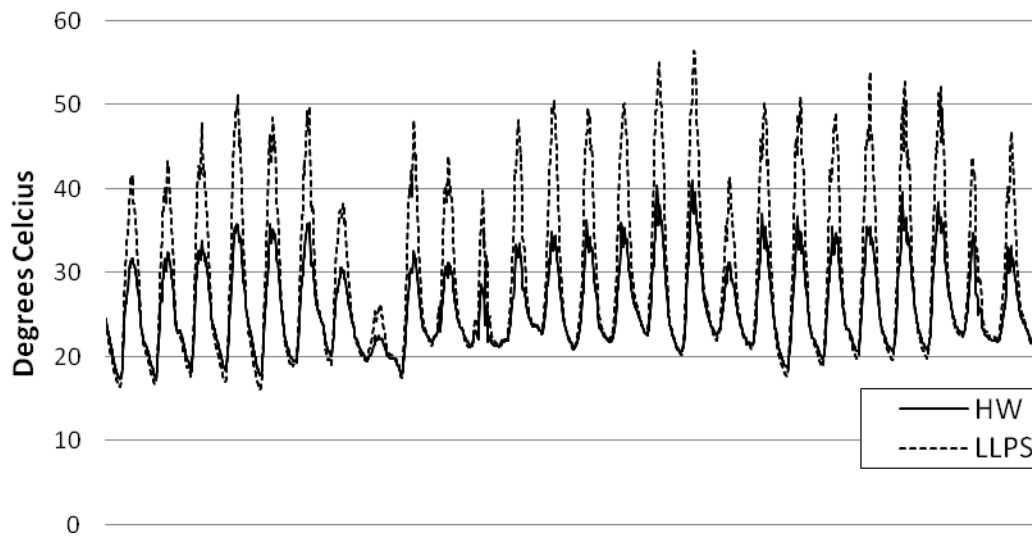


Figure 2.2. Daily thermal fluctuation for June 2007 in Longleaf Pine Savannah (LLPS) and adjoining hardwood forest (HW) in the Pebble Hill Plantation of the Tall Timbers Institute in far southern Georgia.

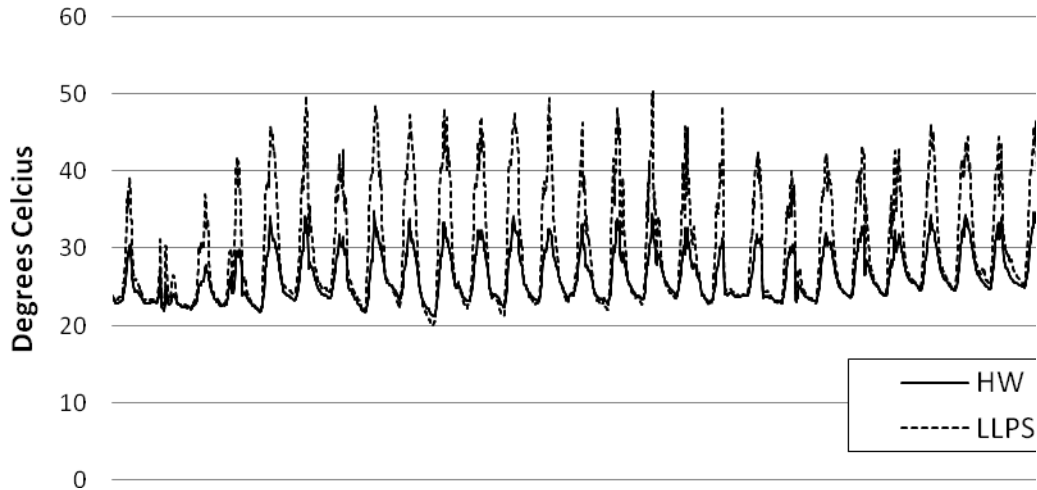


Figure 2.3. Daily thermal fluctuation for July 2007 in Longleaf Pine Savannah (LLPS) and adjoining hardwood forest (HW) in Lake Ramsay Wildlife Management Area in St. Tammany Parish, Louisiana

2.4 Canopy Cover Methodology

Canopy cover data were recorded in order to characterize the two habitats as well as determine if there are observable correlations between where each species occurs and the amount of canopy cover. Upon detection and subsequent capture and identification of individuals in the field, a value for percent canopy cover was established. This was accomplished through the use of a concave spherical densiometer (Model-C, Forest Densiometers, Bartlesville, OK). Values were also gathered along transects within the hardwood and longleaf pine savannah habitat. Due to the non-parametric nature of these data, the point-of-capture data was analyzed using a Kruskal-Wallis test as suggested in Korhonen *et al* (2006). Differences among species were obtained using pair-wise post-hoc Kolmogorov-Smirnov tests. Canopy cover differences between the two habitat types were subjected to a separate Kruskal-Wallis test. The statistical analyses were performed using R.

2.5 Canopy Cover Results

A significant species effect was found among species ($X^2_{(2)}$, $P < 0.001$) (Table 2.1). The pair wise comparisons found that all three species exhibited significant differences between one another (*P. fasciatus* (n=23 \bar{x} =0.96 SD=0.03) X *P. inexpectatus* (n=13 \bar{x} =0.34 SD=0.12): $P < 0.001$, *P. fasciatus* X *P. laticeps* (n=15 \bar{x} =0.88 SD=0.13): $P = 0.015$, *P. inexpectatus* X *P. laticeps*: $P < 0.001$) (Tables 2.2, 2.3). The longleaf pine savannah habitat exhibited significantly less canopy cover than the adjacent hardwood habitat (LLPS: n=25 \bar{x} =0.95 SD=0.04, HW: n=25 \bar{x} =0.41 SD=0.16)(Figure 2.3).

Table 2.2. Kruskal-Wallis One-Way Analysis of Variance results for point-of-capture canopy cover differences among *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps*.

Group	Count	Rank Sum
<i>P. fasciatus</i>	23	829.5
<i>P. inexpectatus</i>	13	91.0
<i>P. laticeps</i>	15	405.5
Kruskal-Wallis Test Stat:		31.9003
$X^2_{(2)}$, P<0.001		

Table 2.3. Kruskal-Wallis One-Way Analysis of Variance results for differences between longleaf pine savannah(LLPS) and hardwood (HW) habitats.

Group	Count	Rank Sum
LLPS	25	948
HW	25	327
Kruskal-Wallis Test Stat:		36.32
$X^2_{(1)}$, P<0.001		

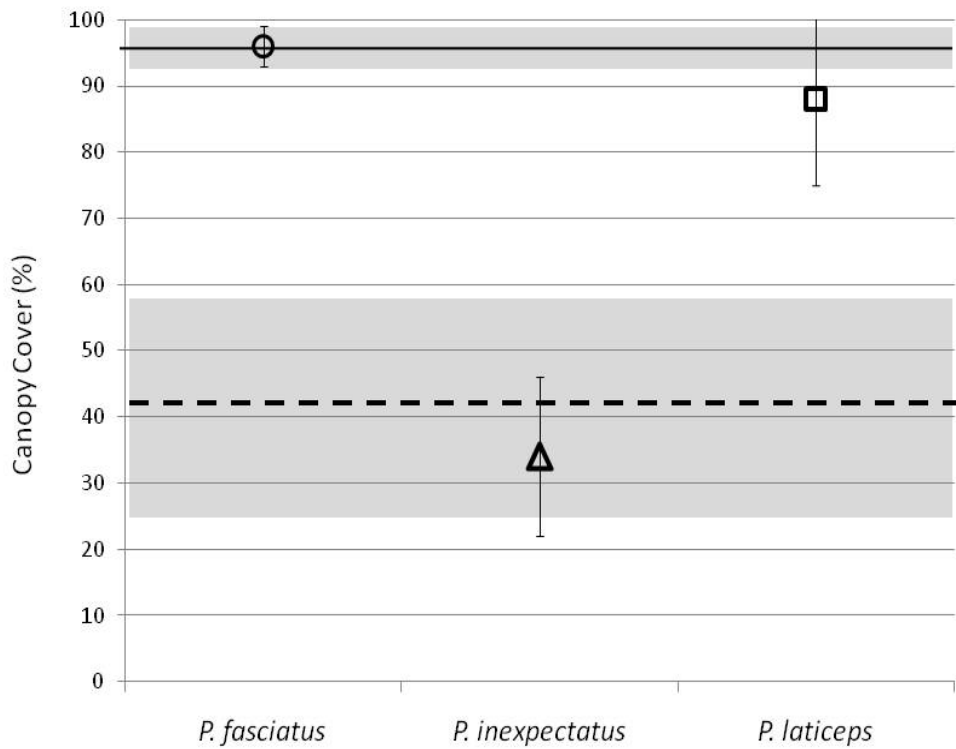


Figure 2.4. Percent canopy cover at point-of capture for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* with canopy cover of sampled habitats (hardwood habitat = solid line (shaded area \pm SD) , longleaf pine savannah habitat = dashed line (shaded area \pm SD)). *P. fasciatus* is typically found in Hardwood forests, while *P. inexpectatus* is typically found in longleaf pine savannah. *P. laticeps* can be found in both habitats.

CHAPTER 3

TEMPERATURE PREFERENCE AND PERFORMANCE

3.1 Introduction

Classic measures used to describe lizard thermal biology are critical thermal limits, thermal preference, and locomotor performance (Huey and Stevenson 1979, Hertz *et al* 1983). Critical thermal limits are the sub-lethal temperatures where an organism loses the ability to function normally yet can recover (Hutchinson 1961). Obtaining these limits experimentally can alter the physiology of the specimen and may be of limited ecological significance, as refuge from thermal extremes are often available. Therefore, these measures were not obtained in this work. Thermal preference provides a temperature value that the organism would “prefer” if given a choice of all temperatures along a gradient (Light *et al* 1966). These measures are, arguably, of limited ecological significance because the temperatures of field-active lizards often are different than these findings, resulting from trade-offs between physiology and ecology (Huey and Stevenson 1979). The third measure, locomotor performance, has been used to describe the thermal optimum associated with whole-animal physiology as an indication of niche breadth and fitness. The application of such measures has also been subject of debate as animals have been found to perform sub-optimally in response to such events as prey acquisition and predator avoidance (Angilletta *et al* 2002) and some works actually indicate that, as temperatures approach a suitable range for natural physiological processes, sprint speed becomes increasingly independent of temperature (Huey 1983).

Locomotor performance is a means to describe thermal optima and is well documented in the literature (i.e. Huey 1982, Hertz 1992, Waldschmidt and Tracy 1983). However, the species that were typically used were *Anolis* lizards and desert Agamas, which exhibit a relatively high

amount of morphological variation among species. It has been shown that limb length exhibits a positive correlation with maximal sprint speed (Miles *et al* 1995). Therefore, morphological characters are influential in the mechanics of sprinting while physiologically constrained by the energy cost of rapid muscle contraction.

Physiological constraints will be intensified at maximum velocity because the energetic cost of locomotion increases as organisms approach this value (Randall *et al* 2002). Skinks are typically short-legged yet notoriously elusive. They also are relatively morphologically conservative, with most species exhibiting the same basic body design. Differences in limb length could be subject to natural selection and could result in different locomotor performance abilities between species with similar physiologies. Genera, such as *Anolis*, that exhibit generally high interspecific variation in morphology make good model species for such studies because variation exists in these characters and locomotor performance can be increased simply by improving mechanics to suit the needs of the thermal habitat. However, a genus that exhibits a high amount of morphological conservatism, such as *Plestiodon*, may provide a better model for physiological differences at different temperatures because they exhibit less variation in limb length among species. Due to the differences in temperature of the habitats where these species are found, I hypothesized that *P. fasciatus* would exhibit a lower temperature preference than *P. inexpectatus*. Also, I predicted that *P. inexpectatus* would perform better than *P. fasciatus* at higher temperatures and *P. fasciatus* would perform better at lower temperatures. I expected *P. laticeps* to exhibit an intermediate preference and performance.

3.2 Temperature Preference Methodology

Thermal preference was obtained using the general methods of Fitch (1954) and Pentecost (1974) for comparison with previous studies. A thermal gradient was established so that one end was significantly cooler than published preferred temperatures of closely-related species and the other end was considerably warmer than the CTmax of closely-related species. The temperature chamber ranged from approximately 23°C on the cold end and over 40°C on the warm end. The elongated fiberglass enclosure was heated with industrial heat tape placed

underneath a sand substrate. Each specimen was released into the chamber and allowed to acclimate for two hours. After two hours, the position of the animal on the substrate was noted and the cloacal temperature of the lizard was measured with a HANNA HI 9063 K-thermocouple Thermometer fitted with a penetration probe. Similar studies have been carried out on *Plestiodon fasciatus* and *P. laticeps* (Fitch 1954, Pentecost 1974), so the present study focused on establishing the thermal preference of *P. inexpectatus* for comparison to the other studies. Fifteen individuals of *P. inexpectatus* were involved in this experiment and the mean and standard error was established for comparison.

3.3 Temperature Preference Results

The mean temperatures of all three species' thermal preference fall within two SE of one another, thereby exhibiting no ecological significance of temperature preference among these species (Figure 3.1).

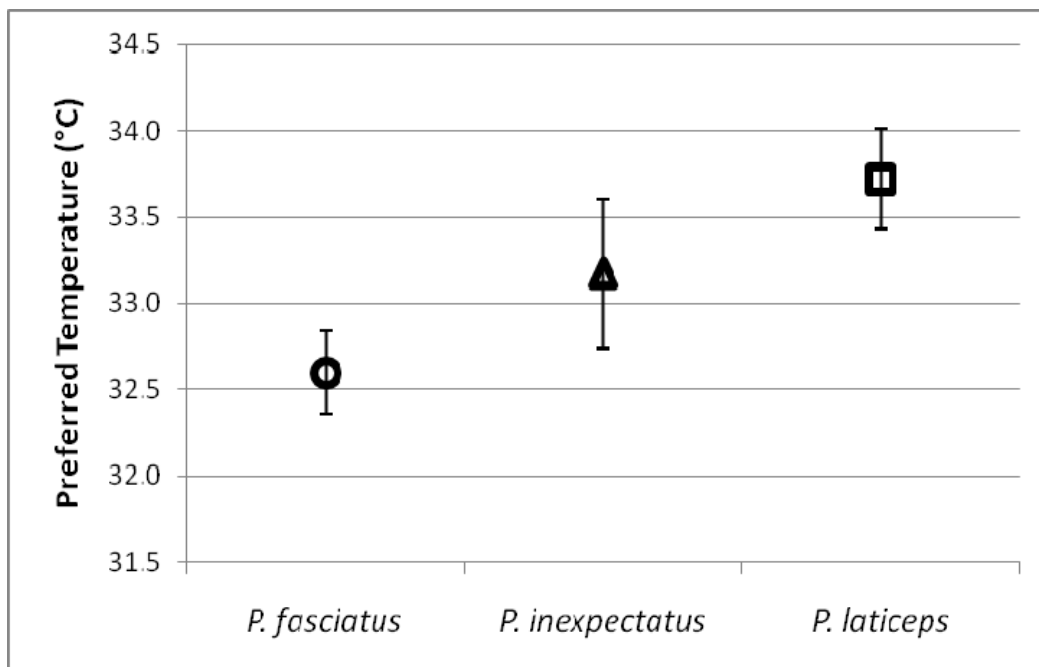


Figure 3.1. Preferred Temperatures (\pm SE) of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* from three studies using similar methodologies (*P. fasciatus* from Fitch (1954), *P. inexpectatus* from present study, *P. laticeps* from Pentecost (1974)).

3.4 Performance Methodology

In order to compare differences in locomotor performance of these three species, I used sprint speed performance as established by Huey (1982). I adapted the methods of Fieler and Jayne (1998) using a high-resolution video camera to capture video of an individual as it sprints along a 30cm section of a 2m track. Each specimen was hand-released at one end of the track and chased along by the investigator. The maximum speed was recorded for each lizard in each trial. Trials were run at 20°C, 25°C, and 30°C because these temperatures represent an approximation of the average low temperature of both habitats (~20°C), the mean temperature of the hardwood habitat (~25°C), and the mean temperature of the longleaf pine savannah habitat (~30°C). Following the suggestions of Losos *et al* (2002), a relatively large sample size (up to 13 *P. fasciatus*, 13 *P. inexpectatus*, and 13 *P. laticeps*) and multiple (4) trials were performed in order to select the highest value for comparison. The slopes of the regression lines for each species was found to be parallel at each temperature, so an ANCOVA using length as a covariate was used at each temperature to determine interspecific differences (Tables 3.2-3.4). A post hoc Tukey test was then applied at temperatures where significance was determined in order to indicate the source of variation. (Table 3.5).

3.5 Performance Results

The ANCOVAs indicated no significant differences among species at 20°C and 25°C, with the only interspecific difference at any one temperature being between *Plestiodon fasciatus* and *P. inexpectatus* at 30°C (Figure 3.2). This indicates that *P. inexpectatus* is faster than *P. fasciatus* at higher temperatures. All species exhibited significant increase in sprint speed between 20°C and 25°C, but weaker differences were observed between 25°C and 30°C (Figure 3.2).

Table 3.1. ANCOVA results comparing maximum locomotor values of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* at 20°C

Source	SS	df	MS	F	P
Species	594.371	2	297.186	1.241	0.302
Length	299.274	1	299.274	1.249	0.272
Error	7,905.730	33	239.568		

Table 3.2. ANCOVA results comparing maximum locomotor values of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* at 25°C

Source	SS	df	MS	F	P
Species	1,687.800	2	843.898	1.636	0.212
Length	621.640	1	621.640	1.205	0.281
Error	15,478.700	30	515.957		

Table 3.3. ANCOVA results comparing maximum locomotor values of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* at 30°C

Source	SS	df	MS	F	P
Species	4,923.200	2	2461.600	4.198	0.024
Length	1,386.400	1	1386.400	2.364	0.134
Error	19,351.600	33	586.412		

Table 3.4. Post-hoc Tukey results for maximum locomotor values of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* at 30°C. * indicates a significant difference ($\alpha=0.05$).

	<i>P. fasciatus</i>	<i>P. inexpectatus</i>	<i>P. laticeps</i>
<i>P. fasciatus</i>	1		
<i>P. inexpectatus</i>	0.018*	1	
<i>P. laticeps</i>	0.755	0.806	1

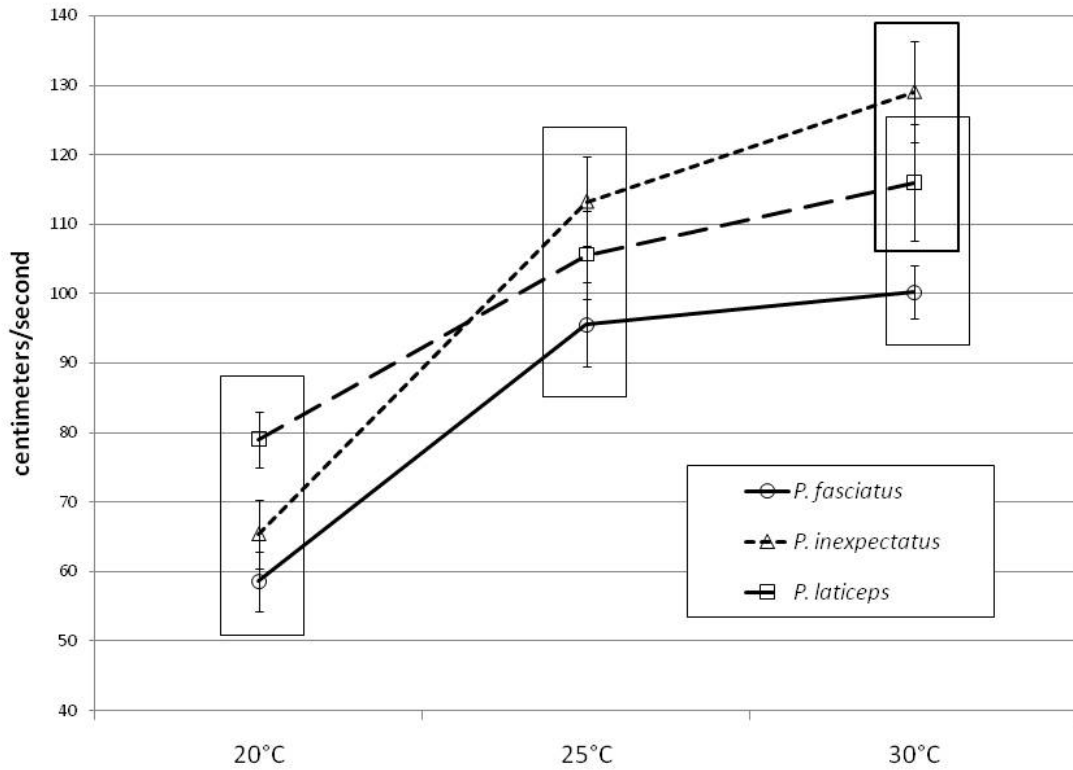


Figure 3.2. Length-adjusted mean maximum sprint speed (\pm SE) at three temperatures (20°C, 25°C, 30°C) for *Plestiodon fasciatus* (n=11, 13, 11), *Plestiodon inexpectatus* (n=13, 12, 13), and *Plestiodon laticeps* (n=13, 12, 13). Values that exhibit no significant differences are contained within the same box.

CHAPTER 4
THERMAL METABOLIC PHYSIOLOGY

4.1 Introduction

Besides the classic measures described in the previous chapter, other measures of physiological response to temperature are common in the literature. Temperature can affect the standard metabolic rate (SMR), reaction rate (Q_{10}), and specific dynamic action (SDA) of ectotherms (i.e. Barrionuevo and Burggren 1999, Secor and Boehm 2006). These measures are typically expressed in terms of oxygen consumption (VO_2) and provide insight into the energetic response of ectotherms at different temperatures. The SMR is the metabolic reaction rate for an animal at rest at a given temperature. This baseline measure allows the investigator to determine the rate of change for a 10°C interval (Q_{10}) and the metabolic response to feeding (SDA). The Q_{10} indicates temperature sensitivity. Animals tend to exhibit higher Q_{10} values at the edges of their metabolic tolerance. Species that exhibit high metabolic response at high temperatures tend to exhibit a low metabolic response at low temperatures, with the same being true in reverse (Nespolo *et al* 2003). Therefore, differences in Q_{10} at different ecologically-relevant temperatures can provide insight into differences among these species and their associated ecological thermal boundaries.

Specific Dynamic Action basically is the energy used to digest a food bolus of a known proportion to the animal's body weight. The raw data for SDA is measured as the amount of oxygen consumed above the SMR for the period that it remains above the SMR (the area under the response curve). Therefore, SDA is influenced by degree and length of the response. An additional measure of potentially greater ecological relevance is the SDA Coefficient. This is calculated by dividing the amount of energy provided by the food item by the whole-animal SDA response. This efficiency measure can be different for different species at different temperatures

(Secor and Boehm 2006). Differences in energetic efficiency at different temperatures can be interpreted as advantageous or disadvantageous. According to optimal foraging theory, an animal should attempt to maximize the amount of energy gained while minimizing energetic expense per unit prey, originally expressed as time (MacArthur and Pianka 1966). The SDA Coefficient provides a measure of this ratio and can be used to predict the optimal temperature interval for feeding.

I hypothesized that *P. fasciatus*, because of its more northern distribution and affinity for cooler habitats, would exhibit a higher resting metabolism (SMR) at lower temperatures and the *P. inexpectatus* would exhibit a lower metabolism (SMR) due to its affinity for warmer habitats. Furthermore, I predicted that each species would exhibit a greater metabolic sensitivity (Q_{10}) to temperature at the intervals that represent the habitat from which they are absent. Lastly, I predicted that each species would exhibit a lower SDA at the temperatures that represent the habitat from which they are found

4.2 Methodology

4.2.1 Measuring O₂ Consumption

In order to determine metabolic rate, oxygen consumption was measured via closed-system respirometry adapted from Barrionuevo and Burggren (1999). Animals were confined to a 500 ml Erlenmeyer flask that was sealed with an air-tight ported rubber stopper. Two ports, an inlet and outlet, were each fitted with glass tubing and a three way stopcock. The flasks were covered with aluminum foil to reduce observer effect. The entire apparatus and animals were placed inside of a walk-in incubator set at the appropriate temperature. These temperatures were also manually monitored during the acclimation time using a standard mercury thermometer immersed in water and placed in the walk-in.

Animals were acclimated for two weeks prior to SMR trials and one week prior to SDA trials. At the end of the acclimation period, each animal was placed into a chamber for one hour with air being pumped through at the rate of 25ml/sec by commercially available aquarium air

pumps. After that period, the barometric pressure (in mmHg) was measured (for establishment of initial PO₂) and the respirometers were closed. Depending on the temperature, animals were left in the closed respirometer for 1-4 hours. This difference in time reflects the differences in reaction rates at different temperatures as crudely established in preliminary trials. At lower temperatures, specimens use oxygen at a slower rate and the O₂ difference in the chamber may not be measurable after 1 hour. Therefore, the duration of the trial is temperature-dependant.

Upon the completion of each trial, a 4ml sample of air from inside of the chamber was drawn from a stopcock with a glass match-numbered syringe and injected across a PO₂ electrode connected to a Radiometer PHM72 gas meter. The value was recorded and subtracted from the initial PO₂ to find the change in PO₂. This value was converted to mlO₂ and divided by the mass of the animal to get the mass-specific O₂ consumption rate (mlO₂/g/h). To determine the SDA, mlO₂ was converted to Joules and plotted across time. The area under the curve was then determined in Joules.

Mean Standard Metabolic Rate was determined and compared among species. This was done by performing a two-way ANOVA on log-transformed values (Table 4.1). A post hoc Tukey test was used to determine significant differences among species.

4.2.2 *Q₁₀ Methodology*

Q₁₀s were determined for each subject using the following formula (Schmidt-Nielsen 1997).

$$Q_{10} = (R2/R1)^{(10/(T2-T1))}$$

R1 is the measured reaction rate at Time 1 (T1), while R2 is the measured reaction rate at Temperature 2 (T2). This gives the amount of increase over a 10°C interval. These measures were log transformed and analyzed using a two-way ANOVA and statistically significant effects were noted for the interaction, but not the main effects (Table 4.2). A post-hoc Tukey test was used to determine significance among species.

4.2.3 *Specific Dynamic Action Methodology*

The specific dynamic action of each species was determined by feeding five specimens of each species a meal equivalent to 2.5% of their body weight. The metabolic response was measured as outlined above at 6hours, 12hours, 24 hours, 48hours, and 72 hours. These data were converted to $\text{J g}^{-1} \text{h}^{-1}$ and plotted along the axis of time. The area under the curve was then measured using the trapezoid rule. These SDA values were log transformed in order to meet the assumption of normality and analyzed using a two way ANOVA (Table 4.3). A post hoc Tukey test was used to determine differences among species.

4.2.4 Specific Dynamic Action Coefficient Methodology

The amount of energy expended to digest the food item was divided by the amount of energy provided by the food item. Juvenile crickets (*Acheta domestica*) provide 5.67 kJ g^{-1} (Secor and Boehm 2006). This was multiplied by the number of grams of cricket that was fed to each lizard. This SDA Coefficient for each species was tabulated at all temperatures, but only 20°C and 30°C were included in statistical analysis. These data were analyzed using a two way ANOVA, with the main effects of species and temperature. A post hoc Tukey test was used to determine differences among species.

4.3 Results

4.3.1 Standard Metabolic Rate

At 20°C , all species exhibited low metabolic rates, while at 25°C *P. inexpectatus*, the species with the most southerly-restricted range and from the highest-temperature habitat, exhibited a significant change. *Plestiodon fasciatus* has one of the largest and most northern ranges among New World lizards. It also happens to be found in the coolest habitat. As expected, at 30°C it exhibited a significant increase from its comparatively moderate SMRs at lower temperatures. *Plestiodon laticeps*, with an intermediate northern range limitation and ability to inhabit both habitats, exhibits a slight increase in SMR across temperatures, but never as dramatic as the other two species (Figure 4.1).

Table 4.1. Two-way ANOVA table for the effects of species and temperature on SMR across all three species and experimental temperatures

Source	SS	df	MS	F	P
Species	11.532	2	5.7659	43.3581	<0.001
Acclimation Temperature	34.589	2	17.2946	130.0510	<0.001
Interaction	4.181	4	1.0452	7.8595	0.001
Error	9.442	71	0.1330		

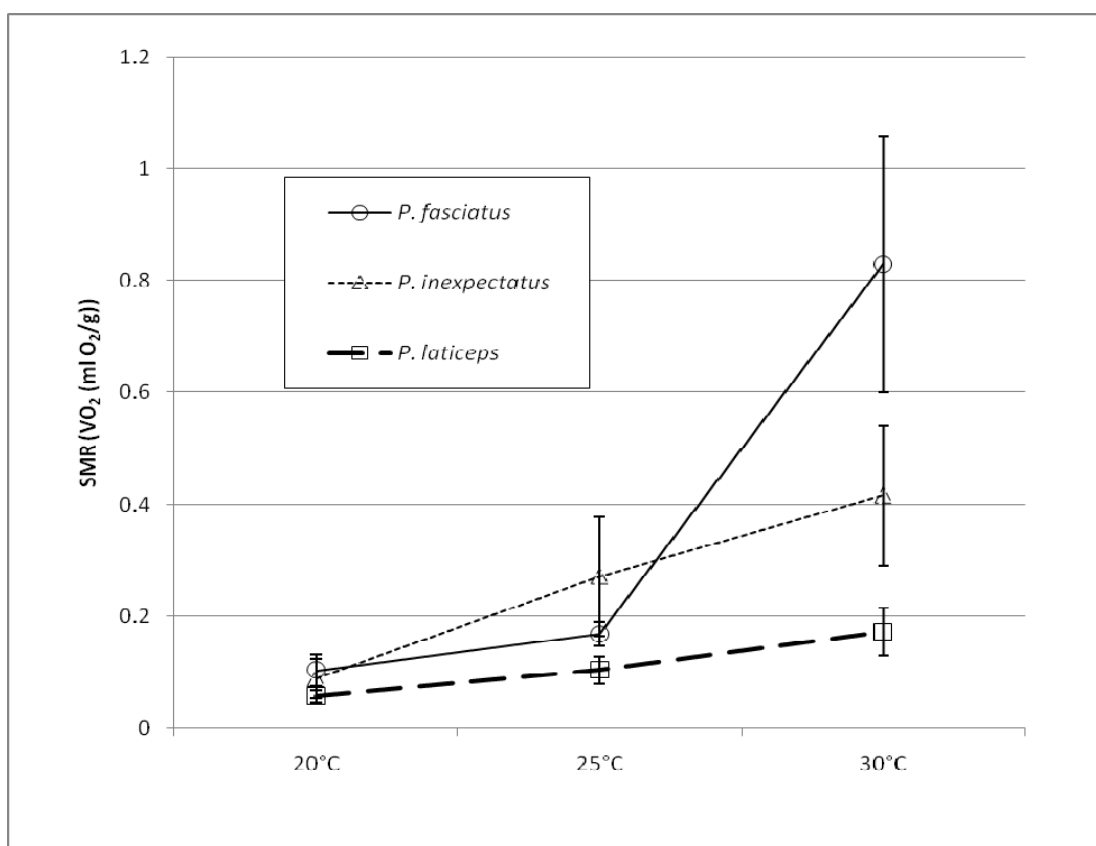


Figure 4.1. Mean Standard Metabolic Rate (SMR) [$\pm 95\%CI$] (ml O₂/g) for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps*.

4.3.2 Q_{10}

As hypothesized, *P. fasciatus* exhibited an elevated Q_{10} at the high interval (25°C-30°C) and *P. inexpectatus* exhibited a high mean Q_{10} at the lower interval (20°C-25°C). *P. fasciatus* was the only species that exhibited a significantly higher Q_{10} value.(Figure 4.2). *Plestiodon fasciatus* exhibited a Q_{10} [$\pm 1SE$] above zero for both intervals and *P. inexpectatus* exhibited a Q_{10} [$\pm 1SE$] above zero at the lower interval, indicating that there is a measurable metabolic reaction to temperature at these intervals. *Plestiodon laticeps* did not exhibit a Q_{10} that exceeded 1SE above zero at either interval. Also, *Plestiodon fasciatus* and *P. inexpectatus* each exhibited two starkly different Q_{10} values for the two intervals. Lastly, as evidenced by the significant interaction effect, species exhibits different effects at the two intervals. The VO_2 values that were measured to obtain R1 and R2 were significantly different (Table 4.1). This is evidenced by the fact that the raw differences in SMR between these temperatures were found to be significant, but the rate of these reactions (Q_{10}) were not. The increased amount of error associated with these values can be partially explained by the properties of having an exponent in the Q_{10} equation.

Table 4.2. Two-way ANOVA table for the effects of species and temperature across all three species and experimental temperatures on Q_{10} .

Source	SS	df	MS	F	P
Species	7.505	2	3.7525	2.1315	0.133
Interval	0.021	1	0.0214	0.0121	0.913
Interaction	26.553	2	13.2765	7.5413	0.002
Error	65.139	37	1.7605		

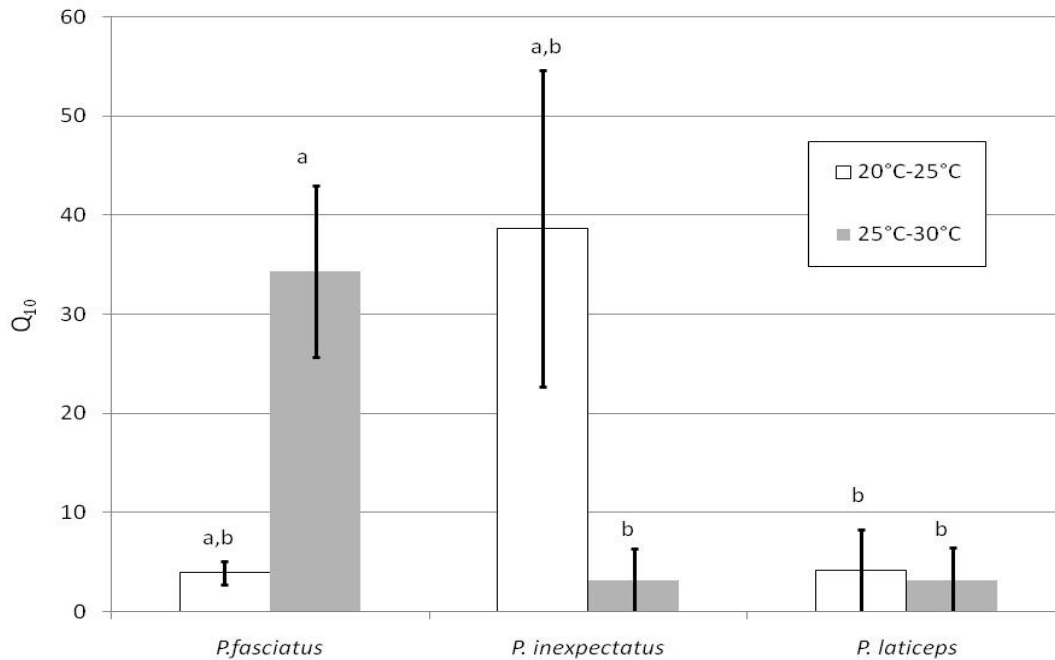


Figure 4.2. Q_{10} (\pm SE) values for the intervals of 20°C-25°C and 25°C-30°C for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps*.

4.3.3 Specific Dynamic Action

In all cases, SDA of *Plestiodon fasciatus* was significantly higher than all other values at 30°C while no other differences were noted (Figure 4.3). In fact, *Plestiodon inexpectatus* and *P. laticeps* did not exhibit an increase in metabolism above 1SE of their SMR and, therefore technically exhibited no SDA response (Table 4.4). *Plestiodon laticeps* continued to exhibit no measurable response across temperatures (Table 4.4). While not all significant, a consistent ranking of SDA means is apparent such that *P. fasciatus* maintains a trend of having a higher SDA response across all temperatures (Figure 4.3).

Table 4.3. Two-way ANOVA table for the effects of species and temperature on Mass-specific SDA for 20°C, 25°C and 30°C for all three species

Source	SS	df	MS	F	P
Species	370621	2	185310.000	6.354	0.004
Temperature	894550	2	447275.000	15.337	<0.001
Interaction	381469	4	95367.200	3.270	0.022
Error	1020720	35	29163.300		

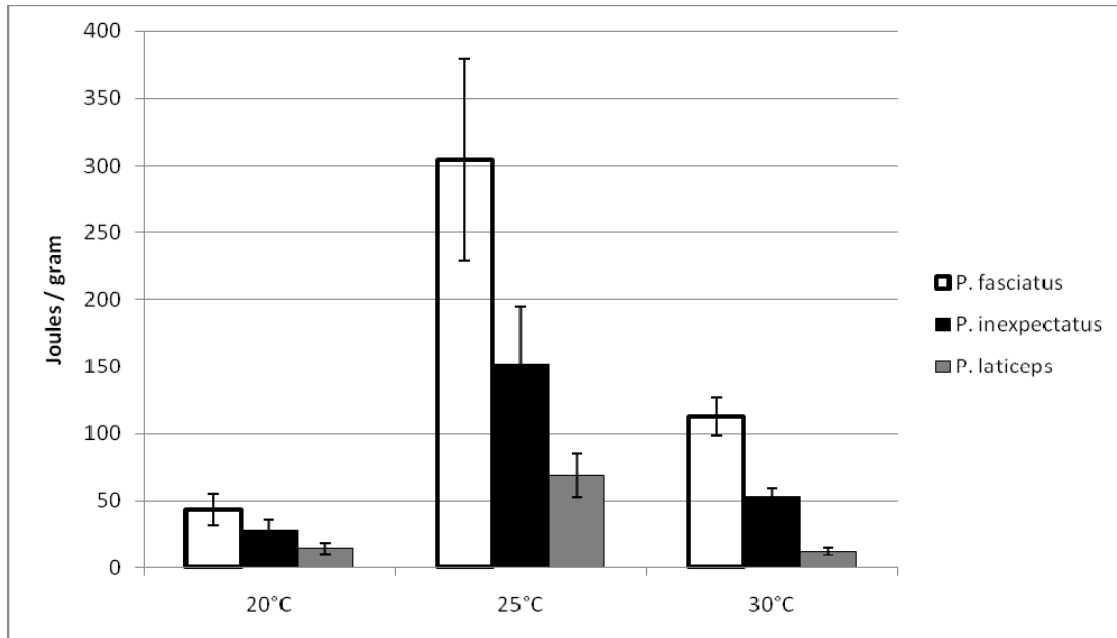


Figure 4.3. Mean Specific Dynamic Action [$\pm 1SE$] for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps*.

4.3.4 SDA Coefficient

The 25°C treatment was omitted from this analysis. This is because the values for this temperature were consistently above 1, resulting in more energy expended per unit food than was taken in. This problematic result was unexpected and may be the result of experimental error, increased activity inside of the chambers or it could simply be a real response that is currently unexplainable and non-interpretable (Secor pers comm.). *Plestiodon fasciatus* exhibited a higher SDA Coefficient at 30°C, indicating that it costs that species more to digest one unit of food than the other two species. However, the maximum VO_2 values measured for *P. fasciatus*

and *P. laticeps* were not significantly higher than the SMR values. Therefore, they did not exhibit a measurable SDA. *Plestiodon inexpectatus* exhibited a high degree of efficiency as evidenced by a lower SDA Coefficient at the same temperature (Figure 4.5).

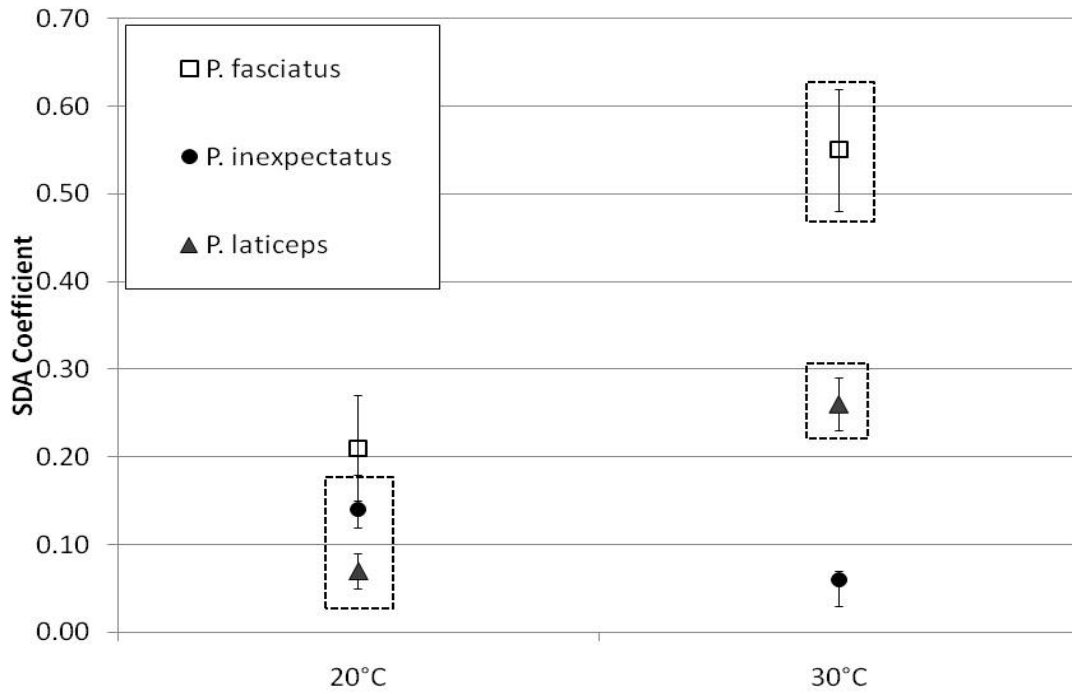


Figure 4.4. SDA Coefficients (Energy required to digest food item/total energy provided by food item) for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* when fed a juvenile cricket with wet mass equivalent to 2.5% of their body weight. Dashed boxes represent responses that did not produce an increase in metabolism greater than the Standard Metabolic Rate (SMR) + 1 SE.

Table 4.4. Comparison of Maximum Specific Dynamic Action (SDA) Response in VO_2 (ml O_2 / gram) and Standard Metabolic Rate for *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* at 20°C and 30°C. (SDA food item: juvenile cricket equaling 2.5% of lizard's body mass)

		<i>P.</i> <i>fasciatus</i>	<i>P. inexpectatus</i>	<i>P.</i> <i>laticeps</i>
Max SDA Response	20°C			
	Mean	0.1872	0.1178	0.0641
	M+1SE	0.2208	0.1341	0.0761
	M-1SE	0.1535	0.1016	0.0522
	30°C			
	Mean	0.9817	0.6822	0.2583
	M+1SE	1.1736	0.8098	0.3001
	M-1SE	0.7898	0.5545	0.2165
	SMR	20°C		
Mean		0.1047	0.1489	0.0567
M+1SE		0.1141	0.1942	0.0608
M-1SE		0.0952	0.1036	0.0526
30°C				
Mean		0.8297	0.4157	0.1724
M+1SE		0.9002	0.4552	0.2231
M-1SE		0.7592	0.3762	0.1217

CHAPTER 5
COMPARATIVE THERMAL BIOLOGY AND THE NICHE OF
THE FIVE-LINED SKINKS

5.1 Discussion

5.1.1 Thermal Ecology and Habitat

Island species of *Anolis* have been shown to partition space based upon such parameters as preferred perch diameter, position in the bush or tree, and general habitat type (Roughgarden 1995). *Anolis cristatellus* from Puerto Rico has specifically been shown to behave differently in respect to thermoregulation and daily activity based upon different temperatures of coastal and inland forests. Huey (1983) found that this species' body temperature is dependent upon which habitat it is in, the time of day, and if it is behaviorally thermoregulating. Populations that live in the open coastal forest are seen basking in the morning and evening, while the deeper forest populations act as thermoconformers and remaining active throughout the middle of the day. Therefore, the thermal aspect of a habitat can alter members of a population's behavior in order to reduce costs associated with thermoregulation. Huey (1983) further noted that these two populations exhibited the same basic thermal preference, but they exhibited sprint speeds that corresponded to temperatures available at different times of day in their respective habitat. The temperature range required for optimal sprint speed in the deep forest is only available in the middle of the day, while the same temperatures are available in the coastal forest only in the morning and evening. Such differences in time of activity could act to isolate two populations in time and potentially lead to speciation.

Observations from the field indicate that *Plestiodon fasciatus* and *Plestiodon inexpectatus* are mutually exclusive in two habitats that differ thermally. Canopy cover data associated with

the capture of *P. fasciatus* allies it with closed-canopy hardwood habitats, while the same data for *P. inexpectatus* suggests that this species prefers more open habitats, such as longleaf pine savannah. *Plestiodon laticeps* is found in both habitats, but the canopy-cover data shows that it is more often found in closed-canopy situations.

These species also behave differently in respect to habitat, with *P. fasciatus* in the closed-canopy hardwood forest often seen basking in sun flecks in the morning and afternoon. *Plestiodon inexpectatus* is often seen actively foraging and is sometimes found feeding under loose bark of standing dead or fallen pine trees regardless of time of day. However, basking behavior by *P. inexpectatus* was never witnessed over the course of this field study. *Plestiodon laticeps* was often seen basking in hardwood habitats, but it was only seen actively foraging in the longleaf pine savannah habitat. These observations correspond with the spatial availability of solar radiation. In the morning and evening, the two forest types warm at the same basic rate until late morning when the hardwood forest habitat levels off and the longleaf pine savannah habitat temperature continues to increase (Figures 2.1, 2.2). *Plestiodon fasciatus* would therefore have to actively increase its body temperature by basking in sun flecks to maintain the preferred body temperature while *P. inexpectatus* could remain active throughout the day and decrease its body temperature by taking refuge from the sun. This type of thermoregulation reduces the cost of predation in an open habitat by allowing the lizard to remain hidden while maintaining the body temperature required for daily activity. It appears that *Plestiodon laticeps* adopts the thermoregulation behavior that is best suited for the habitat that it is in at the time.

Perhaps the most interesting feature of the distribution of *Plestiodon fasciatus* and *P. inexpectatus* is that there are distinct boundaries at the local level that correspond to the two habitat types. Although *P. inexpectatus* is also found in maritime forests and granite outcroppings, the majority of its range overlaps the range of the threatened longleaf pine savannah habitat (LLPS) (Figure 5.1). The longleaf pine savannah habitat was originally decimated by logging and is currently negatively affected by fire suppression. This ecosystem is

characterized as having an overstory of Longleaf Pine (*Pinus palustris*) and a graminoid-dominated understory, all of which are adapted to periodic burning (Beckage *et al* 2006). This arrangement allows a relatively large amount of the sun's radiation to reach ground-level.

This fire-dependant ecosystem once covered around 36,000,000 hectares of the southeastern United States. It currently persists on about 1,000,000 hectares which are only maintained by aggressive fire management through prescribed burning (Beckage *et al* 2006). These remaining sites are usually on lands that are not conducive to agriculture and are thereby conserved rather than being converted to croplands (Peet 2006). Because of this dramatic reduction in range and the reluctance of landowners to periodically burn, this is now designated a threatened ecosystem.

When fire is excluded from the LLPS, it is eventually taken over by hardwoods and exhibits a steep decrease in biodiversity (Frost 2000). A conversion from LLPS to hardwood forest would effectively convert prime *Plestiodon inexpectatus* habitat to *P. fasciatus* habitat. Therefore, in areas where *P. inexpectatus* is dependent upon the open-canopied LLPS, this lizard may be in great peril compared to *P. fasciatus* and *P. laticeps*. *P. laticeps* has been identified as a species that is characteristic of the LLPS, having been featured on a commemorative stamp printed by the US Postal Service promoting LLPS habitat conservation. The findings of my work found that, in reality, *P. inexpectatus* is more consistently associated with LLPS than *P. laticeps* and is the species more deserving of such recognition (Figure 2.3).

If *P. inexpectatus* is as closely tied to LLPS as the data indicate, then it may be of special concern for conservation. This species proved to be the most difficult to locate and capture. This is due in great deal to the unavailability of their preferred habitat. *P. inexpectatus* was locally abundant where found, but appeared to persist in small sub-populations within patches of LLPS. The status of *P. inexpectatus* is of some concern because this habitat continues to disappear. One site, south of the University of Auburn, produced a number of *P. inexpectatus* specimens in the 1960's. However, no specimens were collected when I returned to the site in 2007 and found

that it has since been converted into a large hog lot. This study, while investigating thermal differences among these species may have also identified a species that is in need of conservation efforts, along with the other imperiled species that call the Longleaf Pine Savannah home. The other habitats used by *P. inexpectatus* are also imperiled. The granite outcroppings that it inhabits at the northern extent of its range are not plentiful and the maritime forests are succumbing to the disruption of natural beach erosion and reestablishment processes as well as urbanization of the beachfront (Gehlhausen and Harper 1996).

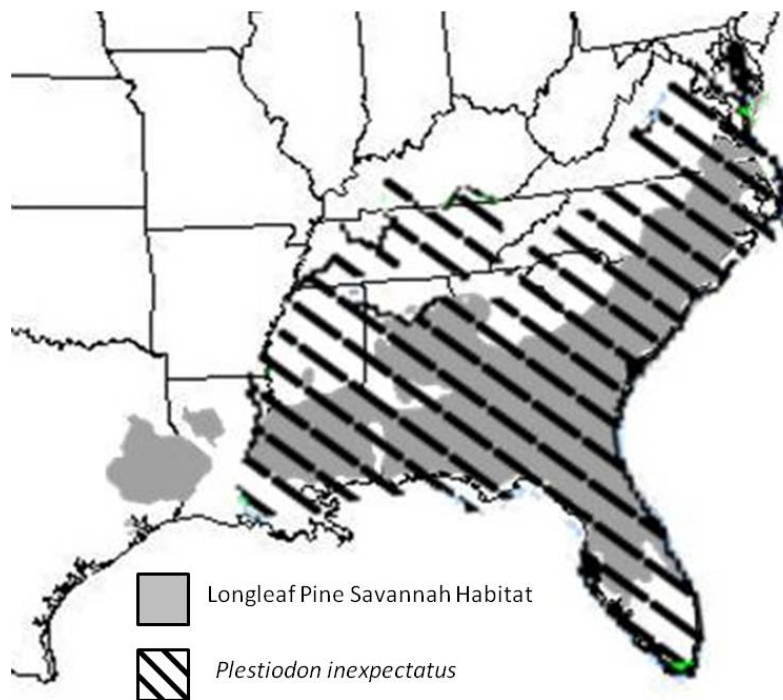


Figure 5.1. Association of the ranges of Longleaf Pine Savannah Habitat and *Plestiodon inexpectatus*. (Adapted from Peet 2006 and Conant and Collins 1998)

Although the evidence strongly indicates that the most important factor in determining habitat associations for two of these three species is temperature, other possibilities must be discussed. The biotic aspect of the two habitats, hardwood and LLPS, are obviously different. The longleaf pine savannah habitat is less dense and lacks a mid-story, which is a major

component of the hardwood habitat. The longleaf pine savannah also exhibits high biodiversity and a high degree of endemism, particularly among plants (Peet 2006). Therefore, there are many plants that would be found at higher densities within the LLPS and would only be sparsely distributed elsewhere. This is also true of the hardwood habitat. Affinities for plants or prey items that use these plants may also cause these species to segregate between habitats. However, the boundaries of these two habitats are not such a hard barrier for small plants, many of which are allied with one habitat and found at the edge of the other habitat. Plants typically found in LLPS, such as Coral bean (*Erythrina herbacea*) were also found well within the edge of the hardwood forest during the fieldwork associated with this study. If these skink species were selecting habitats based upon the plants contained within each habitat, I would expect to see an occasional specimen of *P. inexpectatus* in hardwood habitat or *P. fasciatus* in LLPS, mirroring the local distributions of those plants. Furthermore, due to the insectivorous diet of these species, interactions with plants are typically indirect.

Excluding temperature, perhaps the most stark difference between these habitats is the litter layer. All three of these species forage primarily on arthropods within this layer. In the hardwood habitat, the forest floor is typically covered with broad leaves at various levels of decay. Among and beneath these leaves is a complex community of fungi and arthropods that busy themselves with breaking down the leaves above. The LLPS, on the other hand, has evolved an understory that promotes fire as a means to break down the litter layer. Periodic burning significantly reduces leaf litter arthropod abundance (Coleman and Rieske 2006). Therefore, this habitat harbors the same amount of prey items as the hardwood, and prey availability may be a limiting factor for the species that must maintain a higher resting metabolism, *P. fasciatus*. Instead, the vast majority of arthropods in LLPS are found within standing deadwood (Hanula and Franzrab 1998). I have found both *P. inexpectatus* and *P. laticeps* foraging under loose bark on standing deadwood, but have predominantly found active *P. fasciatus* on top of the bark of horizontal logs.

Even though other factors may affect the local distribution of these three species, it is evident that *P. laticeps* and *P. inexpectatus* are segregating habitats. As previously stated, these animals eat very similar prey and exhibit similar phenotypes. Besides floral assemblage, the most obvious difference between the habitats preferred by these species, particularly *P. fasciatus* and *P. inexpectatus*, is temperature. The following discussions regarding various aspects of the thermal physiology of these species show that they do differ significantly in their response to different temperatures and that these responses correspond to marked differences in their preferred habitat.

5.1.2 Thermal Preference and Performance

Experiments that establish thermal preference typically introduces an individual that has been acclimated to a standard temperature to a thermal gradient that ranges from some temperature below their daily activity temperature to a temperature that greatly exceeds that temperature. The animal is typically given a period of time to acclimate to the chamber and its position in the chamber is marked. The temperature at that position is then determined to be the preferred temperature (e.g. Fitch 1954, Pentecost 1974, Witten and Heatwole 1978) The problem with this method is that it does not take into consideration that a specimen may not choose to be in that position or that temperature all the time. In fact, lizards are often encountered basking on a log or rock that is well above the lethal temperature of that lizard. In this case, preferred temperatures may actually represent an overestimate of the true mean preferred body temperatures of the lizard throughout the day.

Plestiodon fasciatus, *P. inexpectatus*, and *P. laticeps* exhibited no differences in thermal preference. This similar thermal preference data were not surprising because it has been shown with *Anolis* that other lizards may exhibit similar preferred temperatures in the laboratory, but exhibit differences in measures of performance at different temperatures (Huey 1983). Such is the case with these species. At 30°C, *P. inexpectatus* was significantly faster than *P. fasciatus*. However, they exhibited a similar preferred temperature (~33°C) that is well above the highest

tested sprint speed temperature. This corresponds to the mean daily temperature of the habitat (longleaf pine savannah) that *P. inexpectatus* inhabits. This may give *P. inexpectatus* a competitive advantage over *P. fasciatus* at temperatures at or above 30°C which may reinforce the hard boundary observed between the local ranges of these species. In order to better understand this result, sprint speed and the interpretations that can be made from it must first be discussed.

Huey and Stevenson (1979) argue that studies of whole-animal functions, such as sprint speed, are the best measures by which to integrate physiology and ecology. This is because sprint speed has been shown to significantly affect vital life processes such as predation, escape from predators, and social interactions. Each of these processes is crucial to the individual's fitness and is subject to selective pressures (Huey and Hertz 1982). Therefore, sprint speed is often used as a measure of physiological performance relating to ecological variables such as temperature. From these data, predictions regarding fitness of species within the thermal constraints of different habitats can be made.

The application of maximum locomotor ability and preference experiments with this group is the most relevant because of the degree of spatial mapping that each individual exhibits. Once detected, a skink will run in a straight line to a hole in a tree or some other form of shelter. Losos *et al.* (2002) state that because variation in sprint speed associated with prey capture and predator avoidance is paramount for survival, natural selection should operate upon the maximum performance capability of a species. Therefore, maximum straight-line speed is a relevant measure of whole-body physiology in a context that is ecologically relevant for the skinks studied here.

In this case, the sprint speed as maximum locomotor ability was measured and it indicates that *P. inexpectatus* would hold a fitness advantage over *P. fasciatus* in habitats that are above 30°C. These findings therefore indicate that *P. inexpectatus* has an advantage over *P. fasciatus* in the higher temperatures of the longleaf pine savannah. However, no differences in

sprint speed were noted at the lower temperatures that represent the hardwood habitat. This leads to a question of why *P. inexpectatus* does not move into hardwood habitat and sometimes out-compete and displace *P. fasciatus*.

The answer may be found in the metabolic physiology of the individual species. Huey and Stevenson (1979) noted in a short passage of their discussion that maintaining a metabolism is a constant energy drain and elements of a lizard's metabolism may complicate the analysis of sprint speed. This is because other processes such as growth, reproduction, prey digestion, and locomotion are all competing for a finite amount of energy available to the lizard. This energy budget is represented by a number of trade-offs which relate directly to the lizard's metabolism. It is in the metabolic aspect of physiology that the answer to *P. inexpectatus*' inability to colonize cooler habitats becomes clearer.

5.1.3 Thermal Metabolic Physiology

The field of metabolic physiology is predominantly descriptive in nature and few attempts to translate findings to ecology have been made. The most common measure, which serves as the baseline for all other tests in this section, is standard metabolic rate (SMR). This is often referred to as the resting metabolic rate, or RMR. The SMR is the amount of energy that an animal uses to continue basic life processes. This aspect of the animal's energy budget must always receive priority or the animal will perish. Therefore, a lower metabolic rate would be advantageous, especially in areas where there are limitations on prey resources. This is the basis for the "low SMR, low energy" hypothesis set forth by Mautz and Nagy (1988). They contend that if an animal is constrained by energy availability, then natural selection will favor those specimens with a lower SMR.

My results indicate that *Plestiodon fasciatus* maintains a generally higher SMR than the other two species at all temperatures. *P. laticeps* and *P. inexpectatus* both maintained a lower metabolic rate. These findings support the hypothesis that *P. fasciatus*, because of its more northern distribution and affinity for cooler habitats, would exhibit a higher metabolism at lower

temperatures and the *P. inexpectatus* would exhibit a lower metabolism due to its affinity for warmer habitats. This also follows the low SMR hypothesis because *P. fasciatus* inhabits a habitat that is rich in leaf litter arthropods, while *P. inexpectatus* has a more limited fare. *P. laticeps* maintains a larger body, which may require a greater portion of the energy budget. Therefore, a lower SMR would be advantageous in relation to increased size as well.

Another measure of metabolic physiology that is often found in the literature is Q_{10} . This is the factor by which an animal's metabolic processes change over a 10°C interval and is a measure of temperature sensitivity. A species with a high Q_{10} at a given temperature interval would exhibit a relatively rapid increase or decrease across that interval. A high Q_{10} value would indicate a significant disruption from a normal metabolic rate at that interval. Therefore, the temperature interval, and the corresponding habitat, with the highest Q_{10} for each species could be interpreted as the least favorable for that species.

An interesting pattern emerged when Q_{10} was measured and compared to the temperatures within the preferred habitat of each species. This pattern confirmed my hypothesis that each would exhibit a greater metabolic sensitivity to temperature at the intervals that represent the habitat from which they are absent. *Plestiodon fasciatus* exhibited greater metabolic temperature sensitivity (Q_{10}) at higher temperatures, similar to those in the longleaf pine savannah habitat. *Plestiodon inexpectatus* exhibits heightened temperature sensitivity at the cooler tested thermal interval which is similar to the hardwood habitat. This could be a result of an adaptation that allows *P. fasciatus* to obtain the metabolic rate required for field activity while basking less frequently and thereby reducing the risk of being preyed upon that is inherent with basking in the open (Huey 1974). A high sensitivity to higher temperatures may be an adaptation to a generally cooler habitat with dappled sun flecks. With such spatial limitations on availability of direct solar energy, an individual could quickly obtain a metabolic rate sufficient for activity with minimal exposure to such energy. *Plestiodon inexpectatus*, being a warm-adapted species, may not be able to maintain a field-active metabolism in a cooler environment.

However, the high ambient temperature of open habitats such as longleaf pine savannah would likewise reduce the need to bask and also reduce the risk associated with this behavior. In fact, thermoregulation in *P. inexpectatus* may constitute the seeking of colder refuge and cover, which should decrease the probability of detection by predators. The higher sensitivity to lower temperature intervals could simply reflect the species lower physiological threshold. *Plestiodon laticeps* seems to be affected by changes in temperature to a lesser degree. This follows the logic that Q_{10} values would be higher at the temperature intervals that characterize each species preferred habitat. *Plestiodon laticeps* inhabits both habitats and does not exhibit a significantly higher SMR across either interval.

It was hypothesized that each species will exhibit a lower SDA at the temperatures that represent the habitat from which they are found. SDA is defined as the amount of energy beyond the SMR that it takes to digest and assimilate a food item of x% of the animal's body weight (e.g. Secor and Boehm 2006). Also, the SDA coefficient, which is a measure of how efficient each species is at digesting and assimilating food compared to the amount of energy provided by the food. A high SDA Coefficient would indicate that a species is using a large amount of energy per unit food to process that unit of food. It is advantageous to exhibit a lower SDA Coefficient because more energy per unit food item is available for allocation to other parts of the energy budget.

The decreased ability of *P. inexpectatus* to carry on normal physiological processes at lower temperatures was further illustrated by the fact that there was no measurable metabolic response by this species to feeding at low temperatures. *Plestiodon fasciatus* had a measurable response to feeding at low temperatures, where it exhibited a moderate metabolic cost for digestion. *Plestiodon laticeps* exhibited a comparatively low metabolism at all temperatures, which indicates that they are not particularly sensitive to change within the measured temperatures or they simply maintain a generally lower metabolism. If this is true, then *P. laticeps* should be able to carry out daily processes equally in both habitats that the different

acclimation temperatures represent. This is evidenced by the fact that this species is found in both habitats.

At the acclimation temperature that represents the mean daily temperature of the longleaf pine savannah habitat (30°C), *P. fasciatus* exhibits a comparatively low efficiency in digesting prey as compared to *P. inexpectatus*. In fact, *P. inexpectatus* is nearly 10X more efficient than *P. laticeps* at these higher temperatures. This is because *P. fasciatus* is maintaining such a high metabolic rate at higher temperatures, and more food is required just to maintain the standard metabolic rate. *P. inexpectatus* and *P. laticeps* did not actually exhibit a measurable response to feeding at the lowest temperature (20°C). In fact, *P. laticeps* did not exhibit a measurable metabolic response at any temperature. This is potentially due to the fact that they are a larger species and a prey item that makes up a greater percentage of their body weight may be needed to illicit a measurable response. *P. inexpectatus*, on the other hand, only exhibited this phenomenon at the lowest temperature, signifying that they may not be able to properly digest prey at such a low temperature. This may be the key to why *P. inexpectatus* is not superior to *P. fasciatus* in all habitats. At colder temperatures, *P. inexpectatus* exhibits a high degree of thermal sensitivity, exhibiting a rapid reduction in its metabolism below 25°C. Furthermore, *P. inexpectatus* does not appear to be able to effectively digest prey at 20°C while *P. fasciatus* proved quite efficient at doing so at the same temperature. The relative efficiency of *P. inexpectatus* at digesting prey coupled with its relatively low metabolic rate at 30°C further illustrates that it is well-suited for warmer habitats. The thermo-physiological basis of habitat segregation is supported throughout these findings, and I am confident that these underlying metabolic reactions to temperatures that are representative of each species' habitat is of great importance to the maintenance of species local range boundaries and overall distribution.

5.1.4 Local and Regional Distribution

The local distribution patterns found in this study suggest possible explanations for regional distributions of these three species. The field data indicate that *Plestiodon fasciatus* and

P. inexpectatus are not sympatric at the local scale. In fact, they inhabit distinctly different habitats. Therefore, they do not violate competitive exclusion hypothesis or Jordan's Law (Jordan 1908). It is clear that the two habitats that were sampled are thermally different and exclusive to either *P. fasciatus* or *P. inexpectatus*, that each exhibit metabolic adaptations that best suit their environment. *Plestiodon laticeps* appears to be more of a generalist, at least in respect to the thermal differences in habitat. This species appears to physiologically react to temperature in similar ways across all experimental temperatures. This explains how it can inhabit both habitats that are dealt with in this study. Therefore, on the local scale, this group of species exhibit physiological adaptations that best suit their microhabitat. *Plestiodon fasciatus* is found, at least in the southern portion of its range, in closed-canopy hardwood forest, *P. inexpectatus* is found in open habitats, such as longleaf pine savannah, and *P. laticeps* is found in both.

Due to the findings that many physiological variables appear to be in conflict with maintaining proper energy budgets at 30°C and the fact that they occur in open northern habitats and closed-canopy southern habitats, I conclude that *P. fasciatus* may not be well suited for the habitat often inhabited by *Plestiodon inexpectatus*. Likewise, the inability of *P. inexpectatus* to exhibit a digestive response at 20°C coupled with the fact that it is very temperature sensitive at lower thermal intervals suggest that this is a warm-adapted species that requires the higher temperatures found in open habitat to maintain field-active metabolism and digest prey. Again, these findings support the general hypothesis that, in light of the fact that these species are not locally sympatric, elements of their metabolic physiology are better suited for each species' preferred habitat.

These local habitat affinities are reflected in their regional distributions. At this scale these species are sympatric, but obviously different. Their latitudinal distribution appears to be limited by each species' ability to deal with lower temperatures, or at least longer durations of low temperatures. *Plestiodon inexpectatus*, having the most southern distribution is limited due to its physiological inability to maintain daily life processes at low temperatures. Likewise, *Plestiodon*

fasciatus is probably able to tolerate longer durations of colder temperatures due to the fact that it is well adapted for cooler temperatures. *Plestiodon laticeps* exhibits an intermediate distribution and may be limited by the availability of prey or some other resource in more northern localities. Therefore, a thermal explanation for the distributions of these species is supported by their underlying physiology.

The nested nature of these closely-related species' ranges is relatively unique among lizards. The *Plestiodon skiltonianus* complex in western North America exhibit range overlap, but only along small contact zones (Conant and Collins 1998). The Anolis lizards that were the basis for many early studies in lizard thermal ecology are often found on islands with their habitat preference either being coastal forest or deep inland forest (Roughgarden 1995, Huey 1983). While the continental distribution of these species is not generally exhibited by many other closely-related species, another interpretation of the habitats at the local and regional scale may bear some similarities to island distributions. The patchwork distribution of each species' preferred habitat may isolate them from the other species and promote regional biodiversity through niche conservatism and close spatial association of starkly different microhabitats.

5.1.5 Implications for the Niche

The findings of this study confirm that two of these species exhibit an affinity for two closely-associated habitats that differ thermally. Furthermore, they exhibit differences in their thermal physiology that correspond to these thermal habitat differences. Even though they do use similar food resources and are nearly morphologically identical, they are able to co-occur in regional sympatry by segregation along habitat boundaries that are thermally different. This thermal difference may be the most important axis by which these species partition space. This is evidenced by the fact that, in northern parts of its range, *P. fasciatus* inhabits open habitats that would be predicted to contain *P. inexpectatus* if the location were further south and therefore thermally suitable. *Plestiodon laticeps* appears to not be affected by temperature to the same extent that the other two species are. The larger size of this species may facilitate its coexistence

by allowing it to utilize different resources. *Plestiodon laticeps* meets and exceeds Hutchinson's ratio of 1:1.3 when compared to the other two species, which are much more similar in size. This would theoretically allow it to co-exist with each of the other two species (Hutchinson 1959). However, since the other two species do not meet or exceed this ratio, they would not be predicted to co-occur and my work indicates that in fact they do not. *Plestiodon laticeps*, due to its larger size, may partition its niche along axes independent of temperature. This conclusion is drawn from the fact that if a temperature response was noted for this species at all, it was not significantly different from the other two species.

In light of the segregation of habitats based upon thermal differences, these species do not have to partition food or refuge resources because these species do not occupy the same space. Therefore, they cannot compete for the resources associated with that space. These differences in the thermal niche were probably more important at the dawning of these new species and the subsequent re-establishment of overlapping ranges.

The distributions of these species are well defined once these thermal differences are taken into consideration. The habitat that each species inhabits is predictable and obviously not a subject of chance. If this were so, then *P. fasciatus* would inhabit the local habitats that they just happen to get to first and *P. inexpectatus* would do the same. I hypothesize that speciation and distribution of *P. fasciatus* and *P. inexpectatus* are a result of vicariance biogeography, with *P. inexpectatus* evolving on Floridian islands formed during the Holocene glacial retreat and *P. fasciatus* inhabiting more closed-canopy forest habitat than its closest relative, *Plestiodon septentrionalis*. Biodiversity after continental contact of *P. inexpectatus* and *P. fasciatus* may have been maintained due to conserved niches driving these two species to inhabiting habitats that most closely resemble those in which they evolved. *Plestiodon inexpectatus* can still be found as the most common lizard in southeastern maritime forests (Steiner 1986).

In closing, this study successfully links elements of these species' thermal physiology to field data and effectively shows that differences in temperatures across the two habitat types that these species are most commonly found within, coupled with a conserved thermal niche can functionally segregate similar species based primarily upon differences in their thermal physiology.

REFERENCES

- Amaya C. C., P. D. Klawinski, and D. R. Formanowicz. 2001. The Effects of Leg Autotomy on Running Speed and Foraging Ability in Two Species of Wolf Spider, (Lycosidae) *The American Midland Naturalist* 145(1). pp 201-205.
- Angilletta M. J., P. H. Niewiarowski and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27(4). pp 249-268.
- Auffenberg W. and T. Auffenberg. 1988. Resource partitioning in a community of Philippine skinks:(Sauria: Scincidae). *Bulletin of the Florida State Museum* 32(2). 68 pp.
- Barrionuevo W. R. and W. W. Burggren. 1999. O₂ consumption and heart rate in developing zebrafish (Danio rerio): influence of temperature and ambient O₂. *American Journal of Physiology/ Regulatory, Integrative and Comparative Physiology* 276(2).pp R505-R513.
- Begon M., J. L. Harper, C. R. Townsend. 1996. *Ecology: Individuals, Populations and Communities*. 3rd ed. Blackwell Publishing, Cambridge MA. 1068 pp.
- Brandley M., A. Schmitz, and T. Reeder. 2005. Partitioned Bayesian Analyses, Partition Choice, and the Phylogenetic Relationships of Scincid Lizards. *Systematic Biology* 54(3). pp 373-390.
- Brattstrom B. H. 1965. Body Temperatures of Reptiles. *American Midland Naturalist* 73 (2). pp. 376-422.
- Brown J. H. and M. V. Lomolino, 1998 *Biogeography* 2nd ed. Sinauer Associates, Sunderland, MA. 560 pp.

- Brown W. L. and E. O. Wilson. 1956. Character Displacement. *Systematic Zoology*, 5(2). pp. 49-64
- Bush G. L. 1969. Sympatric Host Race Formation and Speciation in Frugivorous Flies of the Genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* 23(2). pp. 237-251
- Campbell N. A., and J. B. Reece. 2002. *Biology* 6th ed. Benjamin Cummings. San Francisco, CA. 1247pp.
- Chase J. M. and M. A. Leibold. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press. Chicago, IL. 221 p.
- Coleman T. W. and L. K. Rieske. 2006. Arthropod response to prescription burning at the soil–litter interface in oak–pine forests. *Forest Ecology and Management* 233(1) pp. 52-60
- Conant R. 1951. The Reptiles of Ohio. Indiana. *Amer Midl Naturalist* p284
- Conant R and J. T. Collins. 1998. *A Field Guide to Reptiles and Amphibians of Eastern Central North America*. Houghton Mifflin Co. New York, NY. 616pp
- Cooper, W. E., Jr., and Garstka, W. R.. 1987. Aggregation in the broad-headed skink *Eumeces laticeps*. *Copeia* 1987. pp. 807-810.
- Cooper, W. E., Jr., and Vitt, L. J. 1984. Detection of conspecific odors by the female broad- headed skink, *Eumeces laticeps*. *Journal of Experimental Zoology* 229. pp. 49-54.
- Cooper, W. E., Jr., and Vitt, L. J. 1985a. Response of five-lined and broad-headed skinks (*Eumeces fasciatus* and *E. laticeps*) to airborne conspecific odors: Further appraisal. *J. Herpetology* 19. pp.481-486.
- Cooper, W. E., Jr., and Vitt, L. J. 1985b. Blue tails and autotomy: Enhancement of predation avoidance in juvenile skinks. *Ethology* 70. pp. 265-276.

- Cooper, W. E., Jr., and Vitt, L. J. 1986a. Thermal dependence of tongue-flicking and comments on studies of tongue-flicking as an index of squamate behavior. *Ethology* 71. pp. 177-186.
- Cooper, W. E., Jr., and Vitt, L. J. 1986b. Interspecific odour discrimination by a lizard (*Eumeces laticeps*). *Animal Behaviour* 34. pp. 367-376.
- Cooper, W. E., Jr., and Vitt, L. J. 1986c. Lizard pheromones: Behavioral responses and adaptive significance in skinks of the genus *Eumeces*. In: *Chemical Signals in Vertebrates IV: Ecology, Evolution, and Comparative Biology*, D. Duvall, D. Muller-Schwarze and R. M. Silverstein, eds. pp. 323-340. Plenum Press, New York.
- Cooper, W. E., Jr., and Vitt, L. J. 1987. Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces*: Pheromonal recognition of conspecific sexual competitors. *Herpetologica* 43. pp. 7-14.
- Cooper, W. E., Jr., and L. J. Vitt. 1994. Tree and substrate selection in the semiarboreal scincid lizard *Eumeces laticeps*. *Herpetological Journal*. 4. pp. 20-23.
- Cooper, W. E., Jr., Vitt, L. J., Vangilder, L., and Gibbons, J. W. 1983. Natural nest sites and brooding behavior of *Eumeces fasciatus*. *Herpetological Review* 14. pp. 65-66.
- Cope E.D. 1898. The *Crocodylians, Lizards and Snakes of North America* in the *Annual Report of the Smithsonian Institution, U.S. National Museum*. Government Printing Office, Washington D.C. pp. 153-1270.
- Cott H.B. 1966. *Adaptive coloration in animals*. Methuen and Co., London. 508 pp.
- Cowles R. B., and C. M. Bogert. 1944. *A preliminary study of the thermal requirements of desert reptiles*. Bulletin of the American Museum of Natural History 83(5). pp. 261-296.

- Cunha A. A., and M. V. Vieira. 2004. Two bodies cannot occupy the same place at the same time, or the importance of space in the ecological niche. *Bulletin of the Ecological Society of America*. 85(1). pp. 25, 26.
- Darwin C. 1859. *On the Origin of Species by Means of Natural Selection*. Murray. London.
- Davis D. 1968. A study of the variation in North American lizards of the *fasciatus* group of the genus *Eumeces* (Scincidae). PhD Dissertation. Duke University
- Ditmars R. L. 1936. *The Reptile of North America*. Doubleday, Page, and Co., New York. NY. 476pp.
- Duméril & Bibron (1839): *Érpetologie Générale ou Histoire naturelle complète des reptiles*, Vol. 5. Libraire Encyclopedique de Roret. Paris France. 860 pp.
- Elkins N. 1989. Species richness and the energy theory. *Nature*. 340:350.
- Elton C. 1927. *Animal Ecology*. Sidgewick and Jackson Ltd. London, UK.
- Fargione J, CS Brown, and D Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceeding of the National Academy of Sciences* 100. pp. 8916-8920
- Fitch H.S. 1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. *University of Kansas Publications of the Museum of Natural History* 8. pp 1-156.
- Frost, C.C. 2000. *Studies in landscape fire ecology and presettlement vegetation of the southeastern United States*. Ph.D. dissertation, University of North Carolina, Chapel Hill.
- Gause G.F. 1934. *The Struggle for Existence*. William and Wilkins. Baltimore, MD.

- Gehlhausen S. and M. G. Harper. 1996. Management of Maritime Communities for Threatened and Endangered Species. U.S. Army Corps of Engineers. *USA CERL Technical Report 98/79*. 49pp.
- Gilliam F. S. and W. J. Platt. 2006. Conservation and restoration of the *Pinus palustris* ecosystem. *Applied Vegetation Science* 9(1) pp. 7–10
- Grinnell J. 1917. The Niche-Relationships of the California Thrasher. *The Auk* 34(4) pp. 427-433
- Grover J.P. 1997. *Resource Competition*. Chapman and Hall. New York, NY. 342 pp.
- Grover, J. P. Professor, The University of Texas at Arlington. Arlington, TX
- Hamilton W.J. and J. A. Pollack. 1961. The Food of Some Lizards from Fort Benning, Georgia *Herpetologica*. 17(2) pp. 99-106
- Hanula, J. L. and K. E. Franzreb. 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. *Forest Ecology and Management* 102. pp. 89-102.
- Harding J.H. and J.A. Holman. 1997. *Michigan Turtles and Lizards*. Michigan State University Cooperative Extension Service, East Lansing, MI. 94 pp.
- Heath JE. 1970. Behavioral regulation of body temperature in poikilotherms. *Physiologist* 13(4). pp. 399-410.
- Hengeveld, R. 1990. *Dynamic Biogeography*. Cambridge University Press. Cambridge UK. 249pp.
- Hertz P. E. 1992. Evaluating thermal resource partitioning. *Oecologia* 90(1). pp. 127-136.

- Hertz P. E., R. B. Huey and E. Nevo. 1983. Homage to Santa Anita: Thermal Sensitivity of Sprint Speed in Agamid Lizards. *Evolution* 37(5) pp. 1075-1084
- Hubbell S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton Monographs in Population biology, Princeton University Press. Princeton, NJ. 375 pp.
- Huey R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184. pp. 1001-1003.
- Huey R. B. 1982. Temperature, physiology, and the ecology of reptiles. pp. 25-91, In: C. Gans and F. H. Pough, eds., *Biology of the Reptilia Vol. 12, Physiology (C)*. Academic Press, London.
- Huey R. B. 1983. Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*), pp. 484-490. In: A. G. J. Rhodin and K. Miyata, eds., *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Museum of Comparative Zoology, Cambridge, Mass.
- Huey R. B. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51. pp. 363-384
- Huey R. B. and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* 19. pp. 357-366
- Huey R. B., E. R. Pianka, and T. W. Schoener, eds. 1983. *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, Cambridge MA. 501 pp.
- Hutchinson G.E. 1944, Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake waters. *Ecology* 26: 3-26
- Hutchinson G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22. pp. 415-427
- Hutchinson, G. E. 1959. "Homage to Santa Rosalia or why are there so many kinds of animals?" *American Naturalist* 93. pp. 145-159.

- Hutchison V. H. 1961. Critical thermal maxima in salamanders.
Physiological Zoology 2(34) pp. 92-125.
- S Iglesias S. , M.B. Thompson, F. Seebacher 2003. Energetic cost of a meal in a frequent feeding lizard. *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* 135(3). pp. 377-382
- Jordan D. S. 1908. The law of germinate species. *The American Naturalist* 42(494). pp. 73-80.
- Klopfer P. H. and R. H. MacArthur. 1960. Niche Size and Faunal Diversity. *The American Naturalist* 94(877) pp. 293-300
- Klopfer P. H. and R. H. MacArthur. 1961. On the Causes of Tropical Species Diversity: Niche Overlap. *The American Naturalist* 95(883). pp. 223-226
- Korhonen L., K. T. Korhonen, M. Rautiainen and P. Stenberg. 2006. Estimation of Forest Canopy Cover: a Comparison of Field Measurement Techniques. *Silva Fennica* 40(4). pp. 577-588
- Levins R. 1963. Theory of Fitness in a Heterogeneous Environment. II. Developmental Flexibility and Niche Selection. *The American Naturalist* 97. pp. 75
- Light P., W. R. Dawson, V. H. Shoemaker and A. R. Main. 1966. Observations on the Thermal Relations of Western Australian Lizards *Copeia*. 1966(1). pp. 97-110
- Losos, J.B. 1992. The evolution of convergent community structure in Caribbean Anolis communities. *Systematic Biology* 41. pp. 403-420.
- Losos, J.B. 1990. A phylogenetic analysis of character displacement in Caribbean Anolis lizards. *Evolution* 44. pp. 558-569.
- Losos, J.B., D.A. Creer, and J. Schulte, II. 2002. Cautionary comments on the measurement of maximum locomotor capabilities. *Journal of Zoology* 258. pp. 57-61.
- Losos, J.B., S. Naeem, and R.K. Colwell. 1989. Hutchinsonian ratios and statistical power. *Evolution* 43. pp. 1820-1826.
- Lotka A. J. 1925. *Elements of Physical Biology*. Williams & Wilkins. Baltimore MD.
- MacArthur R. H. 1972. *Geographical Ecology*. Harper and Row. New York, NY. 269 pp.

- MacArthur R. H. and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *The American Naturalist* 101. pp. 377-385
- MacArthur R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* 100. pp. 603-609.
- MacArthur R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton, NJ. 203pp.
- Magnuson J.J., L. B. Crowder , and P. A. Medvick. 1979. Temperature as an Ecological Resource *American Zoologist* 19. pp. 331-343.
- Mongold, J. A., A. F. Bennett, and R. E. Lenski. 1996. Evolutionary adaptation to temperature. IV. Adaptation of *Escherichia coli* at a niche boundary. *Evolution* 50. pp.35-43.
- Mautz W. J. and K.A. Nagy. 1988. Xantusiid lizards have low field metabolic rates. *American Zoologist* 28. P. 103
- Mavarez J., C. A. Salazar, E. Bermingham, C. Salcedo, C. D. Jiggins and M. Linares. 2006. Speciation by hybridization in *Heliconius* butterflies. *Nature* 441. pp. 868-871
- McGill B.J. 2003. A test of the unified neutral theory of biodiversity. *Nature*. 422(6934). pp. 881-5
- Miles D. B., L. A. Fitzgerald and H. L. Snell 1995. Morphological correlates of locomotor performance in hatchling *Amblyrhynchus cristatus*. *Oecologia* 103(2). pp. 261-264.
- Milstead W. W., Ed. 1967. *Lizard Ecology. A symposium*. University of Missouri Press, Columbia, MS. 300 pp
- Mount, R. H. 1975. *The Reptiles and Amphibians of Alabama*. Auburn University Agricultural Experiment Station, Auburn, AL. 347 pp.
- Murphy R. W., William E. Cooper, Jr. and William S. Richardson 1983. Phylogenetic Relationships of the North American Five-Lined Skinks, Genus *Eumeces* (Sauria: Scincidae). *Herpetologica* 39(3). pp. 200-211
- Mushinsky, H. R. 1992. Natural history and abundance of southeastern five-lined skinks, *Eumeces inexpectatus*, on a periodically burned sandhill in Florida. *Herpetologica* 48. pp. 307-312

- Nespolo, R. F., Lardies, M. A., Bozinovic, F. 2003. Intrapopulation variation in the standard metabolic rate of insects: repeatability, thermal dependence and sensitivity (Q_{10}) of oxygen consumption in a cricket. *Journal of Experimental Biology* 206. pp. 4309-4315
- Odum E. P. 1960. Organic Production and Turnover in Old Field Succession *Ecology* 41(1). pp. 34-49
- Owen S.F. 2001. Meeting energy budgets by modulation of behaviour and physiology in the eel (*Anguilla anguilla* L.). *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* 128(3). pp. 629-642
- Peet, R.K. 2006. Ecological classification of longleaf pine woodlands. In: *Longleaf pine ecosystems: ecology, management, and restoration*. S. Jose, E. Jokela and D. Miller. (Eds.) Springer, NY. pp 51-94.
- Pentecost E. D. 1974. Behavior of *Eumeces laticeps* Exposed to a Thermal Gradient. *Journal of Herpetology* 8(2). pp. 169-173
- Peterson A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of Ecological Niches in Evolutionary Time. *Science* 285(5431). p. 1265.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist* 100. pp. 33-46
- Pianka, E. R. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50. pp. 498-502
- Pianka, E. R. 1975. Niche relations of desert lizards(Chapter 12) in M. Cody and J. Diamond (eds.) *Ecology and Evolution of Communities*. Harvard University Press. Cambridge MA. pp. 292-314
- Pianka, E. R. 1986. Ecological phenomena in evolutionary perspective. (Chapter 16) in N. Polunin (ed.) *Ecosystem Theory and Application*. Wiley and Sons. pp. 325-336
- Pianka, E. R. 2000. *Evolutionary Ecology*. Sixth Edition. Benjamin-Cummings, Addison-Wesley-Longman. San Francisco, CA. 528 pp.
- Popper K. 1963. *Conjectures and Refutations: The Growth of Scientific Knowledge*. Routledge, London UK. 688 pp.

- Poulton E. B. 1890. *The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects*. Appleton and Co. New York, NY. 360 pp.
- Prosser C. L. 1991 (Ed.). *Environmental and Metabolic Animal Physiology*, Wiley-Liss, New York, NY. 578 pp.
- Quirt K., G. Blouin-Demers, B.J. Howes and S.C. Lougheed. 2006. Microhabitat selection of five-lined skinks in northern peripheral populations. *Journal of Herpetology* 40. pp. 337-344
- Randall D., W. Burggren, and K. French. 2002. *Eckert Animal Physiology: Mechanisms and Adaptations*. Fifth Edition. W. H. Freeman. New York, NY. 752 pp.
- Rauner, Y. L. 1977. *Heat Balance of the Plant Cover*. Amerind Publishing Co., New Delhi, India. 219 pp.
- Richmond J. Q. 2006. Evolutionary basis of parallelism in North American scincid lizards. *Evolution & Development* 8(6). pp. 477-490.
- Richmond JQ, Reeder TW (2002) Evidence for parallel ecological speciation in scincid lizards of the *Eumeces skiltonianus* species group (SQUAMATA: SCINCIDAE). *Evolution* 56(7) pp. 1498–1513
- Roughgarden J. 1995. *Anolis Lizards of the Caribbean: Ecology Evolution, and Plate Tectonics*. Oxford University Press. New York, NY. 200 pp.
- Roughgarden J., W. Porter and D. Heckel. 1981. Resource partitioning of space and its relationship to body temperature in Anolis lizard populations. *Oecologia* 50(2). pp. 1432-1939.
- Rubner M. 1885 Calorimetrische Untersuchungen. *Zeitschrift fur Biologie*, 21. p. 319.
- Rundquist E.M. and J.T. Collins. 1974. Distribution and life history notes on the southeastern five-lined skink, *Eumeces inexpectatus* Taylor, in Kentucky. *Transactions of the Kentucky Academy of Science* 35. Pp. 79-80.
- Schmitz, A., P. Mausefeld, and D. Embert. 2004. Molecular studies on the genus *Eumeces* Wiegmann, 1834: Phylogenetic relationships and taxonomic implications. *Hamadryad* 28(1&2). pp. 73-89.

- Schoener T. W. 1967. The Ecological Significance of Sexual Dimorphism in Size in the Lizard *Anolis conspersus*. *Science* 27. pp. 474-477
- Secor, S. M. Associate Professor: The University of Alabama, Department of Biology.
- Secor, S.M., and M.C. Boehm. 2006. Specific dynamic action of ambystomatid salamanders and the impact of meal size, meal type, and body temperature. *Physiological and Biochemical Zoology* 79. pp.720-735
- Segraves K. A. and J. N. Thompson. 1999. Plant Polyploidy and Pollination: Floral Traits and Insect Visits to Diploid and Tetraploid *Heuchera grossulariifolia*. *Evolution* 53(4). pp. 1114-1127
- Simberloff D. and W. Boecklen. 1981. Santa Rosalia Reconsidered: Size Ratios and Competition. *Evolution* 35(6). pp. 1206-1228
- Simberloff D. and E.O. Wilson. 1969. Experimental Zoogeography of Islands. A Two-Year Record of Colonization. *Ecology* 51(5). pp. 934-937
- Smith H. M. 1946. *Handbook of Lizards. Lizards of the United States and Canada*. Comstock Publishing Company. Ithaca, NY. 557 pp.
- Stebbins R. 2003. *A Field Guide to Western Reptiles and Amphibians*. Second Edition, Revised. Houghton Mifflin Company, Boston, MA. 336 pp.
- Steiner, T. M. 1986. *Eumeces inexpectatus* Taylor. Southeastern five-lined skink. Catalogue of American Amphibians and Reptiles 385. pp. 1-2
- Taylor, E. H. 1932a. *Eumeces inexpectatus*: A new American lizard of the family Scincidae. *The University of Kansas Science Bulletin* 20. 251-258.
- Taylor, E. H. 1932b. *Eumeces laticeps*: a neglected species of skink. *The University of Kansas Science Bulletin* 20. pp. 263-272.
- Taylor, E. H. 1935. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *The University of Kansas Science Bulletin* 23. pp. 1-643
- Turner, J. R. G., J.J.Lennon and J. A. Lawrenson. 1988. British bird species distributions and the energy theory. *Nature* 335. pp. 539-541.

- Volterra V. 1926. Fluctuations in the Abundance of a Species considered Mathematically. *Nature* 118(2972). pp. 558-560
- Vitt, L. J., and W. E. Cooper, Jr. 1986. Foraging and feeding habits of a diurnal predator (Lacertilia: Scincidae: *Eumeces laticeps*) feeding on hidden prey. *Journal of Herpetology* 20. pp. 404-411
- Vitt, L. J., and E. R. Pianka (Eds). 1994. *Lizard Ecology: Historical and Experimental Perspectives*. Princeton University Press. Princeton, NJ. 403pp.
- Vitt L.J. George Lynn Cross Research Professor. Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma. Norman, OK
- Waldschmidt S. and C.R. Tracy 1983. Interactions between a Lizard and Its Thermal Environment: Implications for Sprint Performance and Space Utilization in the Lizard *Uta Stansburiana*. *Ecology* 64(3). pp. 476-484
- Wang, T., M. Zaar, S. Arvedsen, C. Vedel-Smith and J. Overgaard. 2002. Effects of temperature on the metabolic response to feeding in Python molurus. *Comparative and Biochemical Physiology: A Molecular and Integrative Physiology* 133(3). pp.519–527
- Wiens J. J. and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* 19(12). pp. 639-644
- Wiens J. J. and C. H. Graham. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics*. 36. pp. 519-539
- Williams E. E. 1969. The Ecology of Colonization as Seen in the Zoogeography of Anoline Lizards on Small Islands. *The Quarterly Review of Biology* 44(4) p. 345
- Witten G. J. and H. Heatwole. 1978. Preferred temperature of the agamid lizard *Amphibolurus nobbi nobbi*. *Copeia* 1978(2). pp. 362-364

BIOGRAPHICAL INFORMATION

Charles Matthew Watson was born on a stormy August night in 1976. He grew up in the forests of southeast Texas and was able to interact directly with nature from an early age. Matt, as generally known by friends and family, attended Hull-Daisetta High School where he excelled in both academics and athletics. From there, he traveled to Nacogdoches, Texas to pursue a degree in Forestry from Stephen F. Austin State University. He became more and more interested in ecology while at SFA and ultimately earned a degree in Wildlife Science in 1998 under the direct influence of Dr. Robert Fleet and Dr. Fred Rainwater.

Upon graduation, Matt worked at The Ellen Trout Zoo in Lufkin, Texas and later moved to The Dallas Zoo. He ultimately became the Supervisor of Herpetology with The Dallas Zoo. While there, he traveled to the Philippine Islands and Amazonian Peru for conservation and research purposes. He returned to academics as a part-time student at The University of Texas at Arlington under the advisement of Dr. Daniel Formanowicz, ultimately earning a Master of Science in Biology in 2004 with the work that he performed regarding prescribed burning and the ground skink, *Scincella lateralis*. This experience began his interest in scincid lizards and he ultimately returned to them for his doctoral work. Matt left the zoo behind to pursue his Ph.D. in Quantitative Biology from The University of Texas at Arlington under Dr. Laura Gough, a plant ecologist who was not at all scared to take on a “herp guy” as a student. This work is the culmination of his Ph.D. research.

Matt currently resides in Rowlett, Texas with his beautiful wife, Rebbekah, and step-son Aiden. They are anxiously awaiting a new child in October of this year and they look forward to a life full of love, happiness, and fulfillment. Matt hopes for a successful academic career as an evolutionary ecologist. His soul continuously seeks the forests of his youth.