The role of temperature in determining distributions and coexistence of three species of Plestiodon

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ABSTRACT

The Common Five-Lined Skink (Plestiodon fasciatus), Southeastern Five-Lined Skink (P. inexpectatus), and Broadheaded Skink (P. laticeps) are all found in forested ecosystems of the southeastern United States and occur in apparent sympatry. No aspect of their ecology has been quantitatively shown to be different. Differences in their natural history, such as northern extent of geographic range, observations of differences in habitat preference, and differing physiological responses to temperature, implicate the thermal environment as a potential niche dimension by which these organisms partition resources. Here we show that the northernmost extent of each species' range can be adequately discriminated by temperature extremes and that their preferred habitats differ in canopy cover, mean temperature, and daily maximum temperatures. These differences are supported by observations in the field. Based upon these findings and observations, we conclude that these species may be able to exist in such close proximity due to differences in their thermal niche, particularly the two like-sized species, P. fasciatus and P. inexpectatus. P. laticeps is a much larger lizard as an adult and functionally coexists with its congeners, potentially by partitioning resources along a different axis.

1. Introduction

The five lined skinks of the southeastern United States are very similar in both habit and habitat. In fact these three lizards were all considered one species (Cope, 1898; Ditmars, 1936) until 1932 when Edward Taylor revived the specific epithet of "laticeps" to denote the large, more arboreal species and formally described Eumeces. inexpectatus from museum specimens (Taylor, 1932a, 1932b, 1935). The morphological differences between these species are so slight that Fitch (1954) noted that those ecological and morphological differences found among these species of Plestiodon (formerly Eumeces; Brandley et al., 2005) are of the degree most often found between sub-species. 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). The most recent phylogeny indicates that P.fasciatus, P. inexpectatus, and P. laticeps are paraphyletic and are not even one another's closest relatives (Brandley et al., 2010).

The ecology of certain populations of P. fasciatus and P. laticeps is relatively well known (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, 1938) 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 typically 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 the ecology of a population of P. inexpectatus.

As P. fasciatus' geographic range extends northward, it inhabits more open habitats, as evidenced, at least anecdotally, by description of its habitat within the southern portion of its range as closed forests (e.g. Dundee and Rossman, 1989; Mount, 1975) and within the northern portion of its range as open fields and meadows (e.g. Harding and Holman, 1997). Quirt et al. (2006)

report that populations of *P. fasciatus* in Canada prefer open, rocky habitats and correlate those preferences with increased temperature and reduced tree cover. *P. laticeps* frequents both edge and deep forests, habitats occupied by either of the other two species (Conant and Collins, 1998).

Currently, there is no indication that *Plestiodon inexpectatus, P. laticeps* 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. *Plestiodon 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 note the similarity in diet between *P. fasciatus* and *P. inexpectatus* from the gut-content analysis 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). Field observation by the author (CMW) indicate that *P. fasciatus* is found in closed canopy hardwood habitats in the south while *P. inexpectatus* is most frequently encountered in longleaf pine, granite outcroppings, and maritime forests (Vitt pers comm; Watson, 2008). *P. laticeps* were encountered in both habitat types in apparent sympatry with either, but never with both.

That very little ecologically differentiates these species is of great interest. Such similar species (phylogenetically, morphologically, and behaviorally) should not be able to coexist under the competitive exclusion hypothesis (Gause, 1934; Pianka, 2000). Upon closer investigation and familiarization with these species in the field, three observations led us to hypothesize that temperature played an important role in determining the ranges and distributions of these three species and could be the primary dimension by which they partition their respective niches. First, these three species exhibit a latitudinally stratified distribution, where all three are sympatric in the south, two species (*P. fasciatus* and *P. laticeps*) have ranges extending northward to the last great glacial boundary, and one species (*P. fasciatus*) has a range extending northward into Canada (Conant and Collins, 1998; Taylor, 1935). The primary climatological variable that changes with latitude is temperature. Secondly, during previous field studies by the author (CMW), *P. fasciatus* and *P. inexpectatus* were never observed in the same habitat in the field. However, *P. laticeps* were routinely found to be sympatric with both. The habitats in which they are typically encountered in the southeastern U.S. (Hardwood-dominated bottomland and Longleaf Pine-dominated upland) appear to differ in canopy cover; therefore, different amounts of solar radiation penetrate to the ground level. Interestingly, the species that has the intermediate northern extent to its range (*P. laticeps*) is also the species that is found in sympatry with the others. Lastly, during transport by the author (CMW) in a cooled container ($\sim$12.5 °C), *P. fasciatus* and *P. laticeps* remained alert and marginally lethargic while specimens of *P. inexpectatus* became still and unresponsive (Watson 2008). This particularly unexpected observation represented a potentially different physiological response to cold temperatures among these species.

We investigated these previously stated qualitative observations by (1) determining how well the the northern extent of each species' distribution can be described in terms of temperature, (2) quantitatively documenting the thermal differences between the two habitats frequented by these species, and (3) comparing canopy cover (as a proxy for the infiltration of solar radiation) between habitats and at point-of-detection among the study organisms. Significant differences in temperature characteristics of their habitat and geographic range would support our hypothesis that these species differ in relation to temperature in their environment and it

would represent a niche axis by which these three lizards may segregate their respective niches and therefore coexist.

2. Materials and methods

2.1. Geographic distribution

We produced 500 range-constricted random points using a web-based random geographic point generator (http://www.geomidpoint.com/random/) that encompassed the latitudinal and longitudinal limits of these three species' natural ranges. Many of these points were in areas uninhabitable by these species (i.e. oceans and lakes) and were excluded from analysis. Presence or absence was determined for each species at each point using published range maps and county records (Conant and Collins, 1998; Conant, 1938; Mount, 1980; Taylor, 1935). Those data were imported into DIVA-GIS in order to append minimum and maximum temperatures to the presence/absence data. DIVA-GIS is a free downloadable Geographic Information System software package (http://www.diva-gis.org/) that, among a variety of other applications, allows the user to analyze data, such as climatic variables and species distributions, on a spatial scale. Discriminate analysis was then used to determine if the ranges of these species could be accurately predicted by temperature extremes.

2.2. Canopy cover

Upon capture and identification of individuals in the field, a value for percent canopy cover at point of detection was established using a concave spherical densiometer (Model-C, Forest Densiometers, Bartlesville, OK). Values for canopy cover for each habitat type 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-detection data was analyzed using a Krustal-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-Wallace test.

2.3. Habitat temperature

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 gray-body models of lizards were placed in ecologically relevant sites within each habitat to represent those areas where lizards were typically encountered. The models consisted of a 10 cm length of 1.9 cm diameter (1 mm thick) copper pipe dipped in ColorPlace© Battleship Gray (#25741) Garage Floor 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 copper pipe and the ends were capped with rubber stoppers.

Fifty data loggers were programmed to log temperature at 20-min intervals for 28 day. iButton© data loggers have a published time constant (τ) of 130 s (Dallas Maxim©, www.maxim-ic.com). While this relatively long response may be inhibitive for studies on a finer time scale, this time constant is permissible given the 20-minute intervals between samples in the present study. Half of these models were placed in an open longleaf pine savannah habitat and half were placed in an adjacent closed-canopy hardwood habitat in southern Georgia (The Pebble Hill Plantation of the Tall Timbers Institute; 30°45′36″N, 84°06′06″W) during the month of

June 2007. This method was repeated for similar habitats in the Lake Ramsey Savannah Wildlife Management Area (30°31′47″N, 90°09′52″W) in eastern Louisiana in late June to early August 2007. Specific sites for data logger placement were chosen within the habitats that represented a microhabitat that skinks would frequent. Such placement allowed for a more relevant sample compared to random placement because, if they were placed in a truly random fashion, some loggers would be placed in sites that skinks do not occur, such as in open fields, ponds, or roads. This methodology allowed us to compare the habitat from the standpoint of the lizard.

These study sites were chosen because they were at similar latitudes within the range of all three species and both sites had an active fire-management plan that maintained longleaf pine savannah habitat. All three species were captured upon the initial visit to each site to validate presence and subsequently released. The daily mean temperature, daily high temperature, daily low temperature, and daily variance (Standard Deviation) for each data logger were recorded and then analyzed using t-tests ($\alpha = 0.05$).

3. Results

3.1. Geographic distribution

Based upon a jackknifed classification matrix derived from the discriminant analysis, we were able to accurately describe presence or absence of each of these three species based upon maximum and minimum annual temperatures (all $> 83\%$; Table 1). *Plestiodon fasciatus*, the most northerly ranging species was restricted by the lowest maximum annual temperature of ~ 14 °C and the highest minimum annual temperature ~ 2 °C (Fig. 1). A maximum annual temperature of ~ 18 °C and a minimum annual temperature ~ 4 °C bound *Plestiodon laticeps*, the species with the intermediate latitudinal range restriction. A maximum annual temperature of ~ 21 °C and the minimum annual temperature of ~ 7 °C. bound *Plestiodon inexpectatus*, the species with the southernmost range restriction.

3.2. Canopy cover

A significant species effect was found among species ($X^2_{(2)}$, $P < 0.001$) in regards to canopy cover at point-of-capture (Fig. 2).

Table 1
Jacknifed Classification matrices for the presence and absence of *Plestiodon fasciatus*, *P. inexpectatus*, and *P. laticeps* based upon maximum and minimum annual temperatures. Actual values for presence and absence in parentheses.

	Absent (%)	Present (%)		Correct (%)
Plestiodon fasciatus				
Absent	58	7		89
Present	32	161		83
Total	90 (65)	168 (193)		85
Plestiodon inexpectatus				
Absent	151	18		89
Present	5	88		95
Total	156 (169)	106 (93)		91
	Absent North (%)	Absent South (%)	Present (%)	Correct (%)
Plestiodon laticeps				
Absent North	126	0	7	95
Absent South	0	5	0	100
Present	12	10	103	82
Total	138 (133)	15 (5)	110 (125)	89

The pair-wise comparisons identified significant differences between all species (Fig. 2). 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)(Fig. 2).

3.3. Habitat temperature

The daily mean temperature for longleaf pine savannah habitat was significantly higher than in 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) ($t_{(16)}= -7.66$, $p < 0.001$). 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 were compared (PHP: $t_{(18)}= -0.39$, $p=0.701$; LRWMA: $t_{(16)}= -.20$, $p=0.84$) (Fig. 3). The mean standard deviation was significantly higher in the longleaf pine savannah than the adjacent hardwood at both sites reflecting a wider range of temperatures over the course of a day.(PHP: $t_{(18)}= -8.92$, $p < 0.001$; LRWMA: $t_{(16)}= -4.58$, $p < 0.001$).

4. Discussion

Classic niche dimensions, such as diet, time, and space, have failed to identify differences between these species. Many qualitative observations, such as the more arboreal nature of *P. laticeps* (Cooper and Vitt, 1994) and the upland habit of a Florida population of *P. inexpectatus* (Mushinsky, 1992) offer indications that there may be some differences among these species, but a comparative study has yet to be undertaken. The findings of the current study offer temperature as a dimension by which *Plestiodon fasciatus* and *P. inexpectatus* partition their respective niches.

The role of temperature in defining local habitat affinities is potentially exhibited by their regional distributions. The northern extent of each species' range can be accurately described by temperature extremes (Table 1, Fig. 1). 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 (Stebbins, 2003). *Anolis* lizards, which were the subject of many early studies in lizard thermal ecology, exhibit a high degree of sympatry and diversity on islands in the Caribbean and their habitat preferences are segregated along gradients among coastal forest, inland forest, and preferred positions in the foliage (Roughgarden, 1995; Huey, 1983). While the continental distribution of these three species of *Plestiodon* is not common to many other closely related species, interpretation of their habitats in terms of temperature may bear some similarities to island distributions. The patchwork distribution of each species' preferred habitat may isolate them from the other species, promote regional biodiversity through niche conservatism and close spatial association of starkly different thermal habitats.

Plestiodon laticeps appears to be more closely aligned with *P. fasciatus* based upon canopy cover values. However, this species is routinely found in the same habitat as both *P. inexpectatus* and *P. fasciatus*. This indicates that *P. laticeps* may actually be choosing more closed canopy areas within the open-canopy habitat of *P. inexpectatus*. Throughout the duration of this study, *P. inexpectatus* and *P. fasciatus* were never observed in the same habitat type, even though they were often collected meters from one another.

Temperature may not be as important to *Plestiodon laticeps* in discriminating its niche from its congeners. The larger adult size of this species may facilitate its coexistence by allowing it to
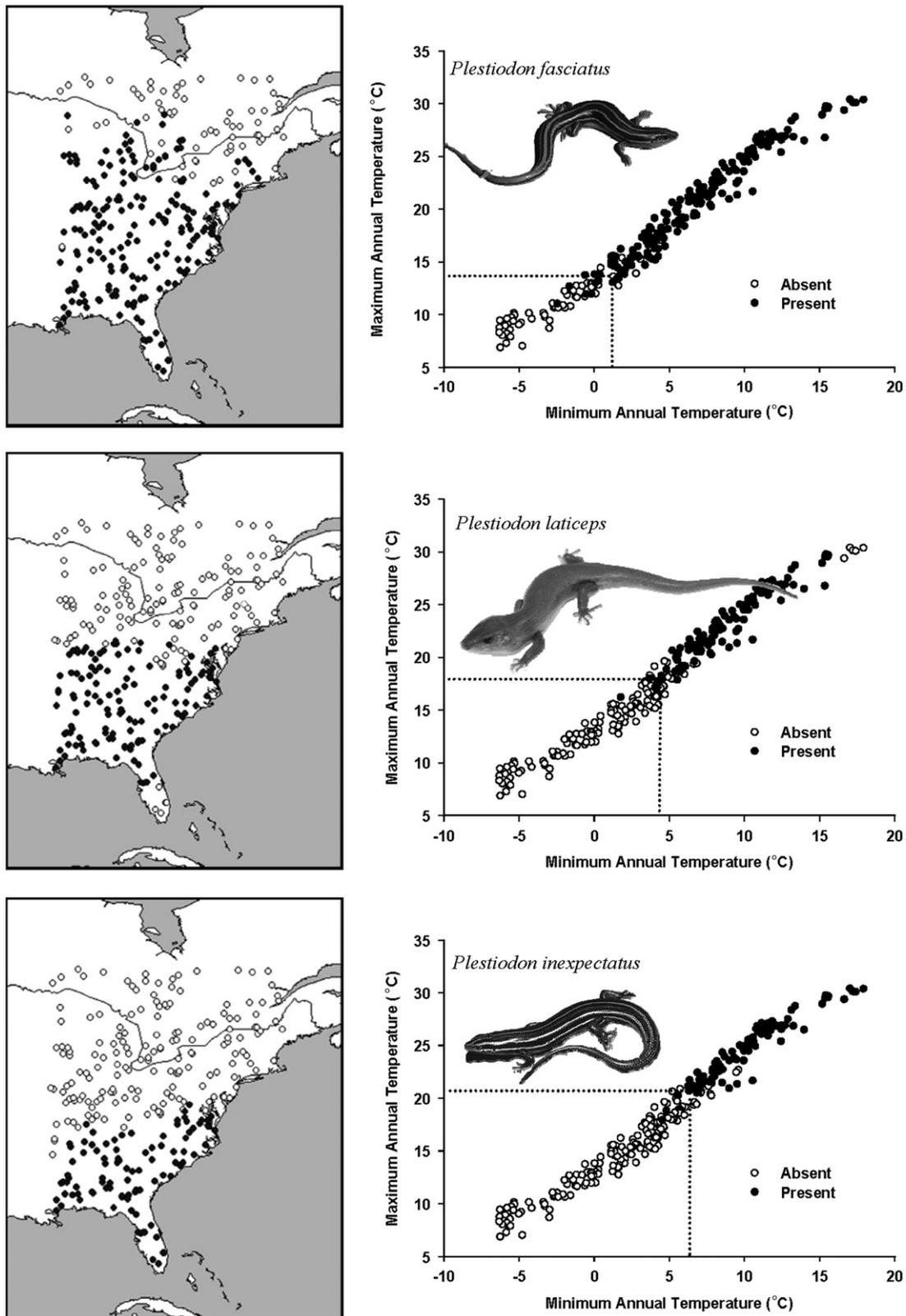
Fig. 1. Presence and Absence data represented geographically and graphically along the axes of maximum daily temperature and minimum daily temperature for each random point for each species of five-lined skink, *Plestiodon fasciatus*, *Plestiodon laticeps*, and *Plestiodon inexpectatus*. Dotted lines represent the temperature value at which 95% of the points represent presence of the corresponding lizard.

utilize different resources, such as larger prey. *Plestiodon laticeps* meets and exceeds Hutchinson's ratio, a theoretical ratio of body size (1:1.3) which would allow coexistence (Hutchinson, 1959),

when compared to the other two similarly sized species (as derived from maximum size estimates reported in Conant and Collins, 1998). This ratio would predict that *Plestiodon laticeps* can
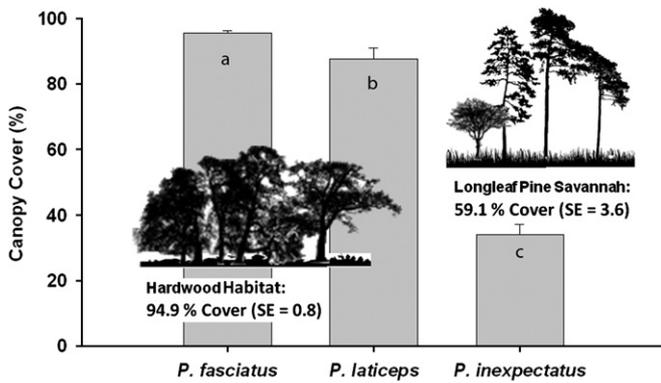
Fig. 2. Point-of-detection canopy cover values for *Plestiodon fasciatus*, *Plestiodon laticeps*, and *Plestiodon inexpectatus* and mean canopy cover values for each of the two general habitat types sampled in this study. Letters indicate significantly different values among species.
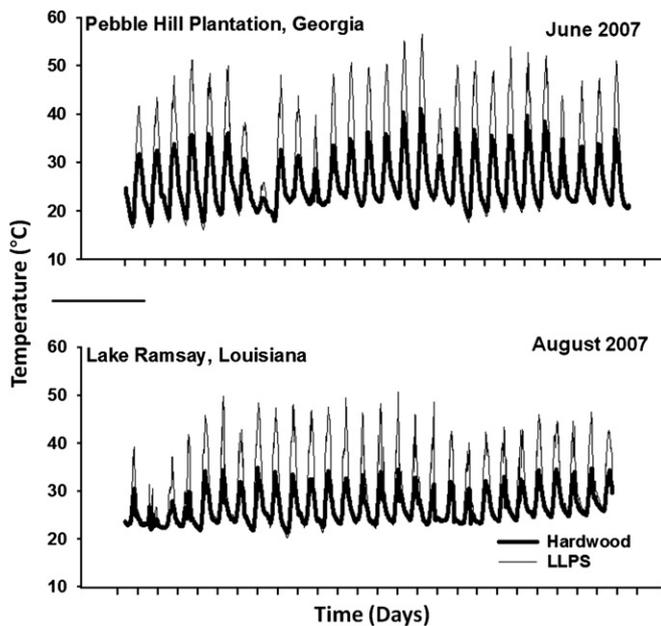

Fig. 3. Daily fluctuations in temperature for Pebbel Hill Plantation in Southern Georgia for the month of June 2007 and The Lake Ramsay WMA in Southeastern Louisiana for August of 2007. Thin lines are derived from copper models placed in Longleaf Pine Savannah Habitat (LLPS) and the thick lines are from adjacent hardwood habitats. Both sites are inhabited by all three species of five-lined skink, *Plestiodon fasciatus*, *Plestiodon laticeps*, and *Plestiodon inexpectatus*.

co-exist with each of the other two species, but they would not coexist with each other. Our field observations are consistent with this prediction.

The findings of this study confirm that *P. fasciatus* and *P. inexpectatus* exhibit an affinity for two closely associated habitats that differ thermally, even though they do use similar food resources and are morphologically very similar. This thermal difference may be the most important axis by which these species partition their niche. Temperature is apparently more important to *P. fasciatus* than other aspects of its habitat based upon the fact that, in northern parts of its range, *P. fasciatus* inhabits open-canopy habitats that our canopy cover data would predict to contain *P. inexpectatus* if the location were further south and therefore warmer.

This study successfully links elements of these species' thermal physiology to field data and illustrates that differences in temperatures across the two preferred habitat types coupled with

a conserved thermal niche can functionally segregate similar species based primarily upon differences in their thermal physiology. Studies aimed to further confirm physiological differences among these species and a better understanding of these species' historic phylogeography might prove enlightening to the nature and origin of these differences.

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