A Comparison of Maximum Sprint Speed Among the Five-lined Skinks (Plestiodon) of the Southeastern United States at Ecologically Relevant Temperatures

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Abstract.—Three species of Five-lined Skinks (*Plestiodon fasciatus*, *P. laticeps*, and *P. inexpectatus*) are found in the forest of the southeastern United States. They are similar in morphology and habit and are sympatric over the southern portion of their ranges. Field observations suggest that temperatures of preferred natural habitat differ among these species. To determine whole-animal physiological differences associated with thermal aspects of their habitats, we quantified and compared maximum sprint speed at four ecologically significant temperatures. This study is unique among lizard studies due to the high degree of morphological similarity exhibited by these species, thereby allowing direct comparisons of locomotor performance responses to temperature that are not confounded by differences in morphology. As expected with diurnal lizards, the sprint speed of all three species increased significantly at the temperature interval that approximate the elevation of temperature from dawn to mid-day (20 °C to 25 °C). Additionally, *P. inexpectatus* was significantly faster than *P. fasciatus* and *P. laticeps* at the temperatures where these species generally would be active. *Plestiodon laticeps* exhibited a significantly lower sprint speed at 15 °C than the other two species. All species exhibited their fastest sprint speed at the highest experimental temperature. The temperature coefficient (Q_{10}) for maximum locomotor performance across each 5 °C interval follow the same general pattern, with *P. laticeps* exhibiting a significantly higher Q_{10} over the interval of 15 °C to 20 °C. These findings generally correspond to the observed association of *P. inexpectatus* with warmer, open canopy microhabitats and *P. fasciatus* and *P. laticeps* with cooler, closed-canopy microhabitats.

Key Words.—ecology; Five-lined Skinks; *Plestiodon*; sprint speed

Introduction

Since the 1970s, sprint speed has been the predominant means of evaluating whole-animal physiological performance in lizards (Arnold 1983, i.e. Huey and Stevenson 1979; Irschick and Losos 1998). Sprint speed is a particularly appropriate performance measure in studies of actively foraging diurnal species because it relates to both the ability of the lizard to acquire prey and escape predation and is sensitive to changes in temperature (Bennett 1980; Christian and Tracy 1981; Huey and Hertz 1984). Each lizard species has an optimum temperature, or set of temperatures, at which performance is maximized and temperatures outside of this range may result in decreased performance and an associated negative impact on the ability to forage and evade predation (Hertz et al. 1983; Grant 1990). Maximum sprint speed has been used comparatively in both field and laboratory experiments. Studies of the genus *Anolis* (Iguanidae) are particularly well represented in the literature (i.e. Losos and Sinervo 1989; Perry et al. 2004). The current study examines differences in this performance measure among and within three congeneric, morphologically similar species of the family Scincidae at four ecologically significant temperatures.

Three Five-lined Skink species occur in sympatry in the forests of the Southeastern United States. *Plestiodon fasciatus* (Linnaeus), the Common Five-lined Skink, *Plestiodon inexpectatus* (Taylor), the Southeastern Five-lined Skink, and *Plestiodon laticeps* (Schneider), the Broadhead Skink, are phenotypically similar throughout much of their development and were considered a single species prior to the mid 1930s (Taylor 1932 a,b; 1935). While formerly considered a monophyletic species group (Murphy et al. 1983), more recent molecular data (Brandley et al. 2010) suggest that while *P. laticeps* and *P. inexpectatus* are sister species, *P. fasciatus* shares a more recent common ancestor with *P. septentrionalis*, a congener from the interior prairies of the United States and south-central Canada (Conant and Collins 1998).

Fitch (1954) suggested that the measurable phenotypic differences among these species are so slight that they are comparable to differences among sub-species of many other lizards. *Plestiodon fasciatus* is a relatively small lizard (maximum Snout-Vent Length [SVL]: 86

mm) with an unusually broad latitudinal range for temperate lizards, extending from Florida to Canada (Davis 1969; Conant and Collins 1998). The common *P. fasciatus* is found in hardwood forests in the lower extent of its range (Mount 1975; Dundee and Rossman 1989) and open woodlots and fields in the upper extent (Harding and Holman 1997). *Plestiodon inexpectatus* is of comparable size (maximum SVL: 89 mm) and its range is restricted to the southeastern United States (Davis 1969; Conant and Collins 1998). It is found in drier, more open forest habitats, such as the endangered Longleaf Pine Savannah ecosystem, maritime forests, and granite outcroppings (Mushinsky 1992; Watson and Gough 2012). *Plestiodon laticeps* are the largest as adults (maximum SVL: 143 mm), but are comparable in size to the other two species as juveniles and equally difficult to distinguish in the field (Fitch 1954; Davis 1969). *Plestiodon laticeps* is more arboreal and is found in both open and closed habitat (Fitch 1954; Watson and Gough 2012). It exhibits an intermediate northern extent of its latitudinal range compared to the other two species (Conant and Collins 1998).

Variation in sprint speed and its effects on spatial distribution of sympatric congeners has been well documented among Caribbean *Anolis* (Irschick and Losos 1998). However, many of these species exhibit an increase in hind limb length, which is associated with selection for increased speed (a major determinant of maximum locomotor performance; Losos 1990). This mechanical variable is a potentially confounding factor in direct comparisons of the physiological response of sprint speed to differences in temperature. Bonine and Garland (1999) identified a direct relationship with hindlimb length in lizards of the family Phrynosomatidae, with short-limbed lizards exhibiting slower sprint speeds and longer-limbed lizards exhibiting faster sprint speeds. Measures of limb length and relative body length among *P. laticeps*, *P. fasciatus*, and *P. inexpectatus* are similar (Davis 1969), with *P. laticeps* exhibiting a slightly longer forelimb length than the two smaller species. Davis (1969) also stated that hind limb lengths exhibited extensive overlap among these three species. Hind limb length is a cumulative measure whose components have all been shown to significantly affect sprinting ability (Bonine and Garland 1999; McElroy and Reilly 2009). Scincid lizards typically exhibit limited variation in body form, and limb elongation is not generally exhibited in this group (Taylor 1935). One of the hallmarks of the family Scincidae is relatively short limbs, with many species having lost their limbs altogether (Brandley et al. 2008). Comparative studies of sprinting performance in skinks may therefore provide better insight into the evolution of physiological performance independent of complementary morphological adaptations such as increased hind limb length. Our study offers a unique comparison of sprint speed among species with a high degree of morphological similarity.

Watson and Gough (2012), using grey-painted copper tubing outfitted with a temperature data logger to represent skinks, reported mean temperatures in the Longleaf Pine Savannah habitat (where *P. inexpectatus* is generally common) to be 28.69 °C at the Pebble Hill Plantation in southern Georgia in June of 2007 and 29.76 °C at the Lake Ramsay Wildlife Management Area in eastern Louisiana in July of 2007. Watson and Gough (2012) further reported significantly lower mean temperatures for models placed in the adjacent hardwood forests (where *P. fasciatus* is generally common) to be 25.98 °C in southern Georgia and 26.35 °C in eastern Louisiana over the same sampling period. The mean low temperatures of these sites were not significantly different and were approximately 19 °C in southern Georgia and 23 °C in eastern Louisiana. Based upon this *a priori* knowledge, we predicted that *P. fasciatus* would be faster than *P. inexpectatus* at 25 ºC (near the mean daily temperature of closed-canopy hardwood habitats) and *P. inexpectatus* would be faster than *P. fasciatus* at the higher temperature of 30 ºC (near the mean daily temperature of open Longleaf Pine Savannah habitat). *Plestiodon laticeps* should exhibit a sprint speed comparable to both other species because it is found in both habitat types. We further predicted that there would be no interspecific differences at 20 ºC or 15 ºC because none of these animals would be active at these temperatures. Intraspecific differences should be found over the interval between 20 ºC and 25 ºC because all of these species experience this temperature increase as the sun rises and the temperature increases from the overnight low to temperatures equal to or exceeding 25 ºC. These species exhibit a similar preferred body temperature (Fitch 1954; Pentecost 1974; Watson 2008;
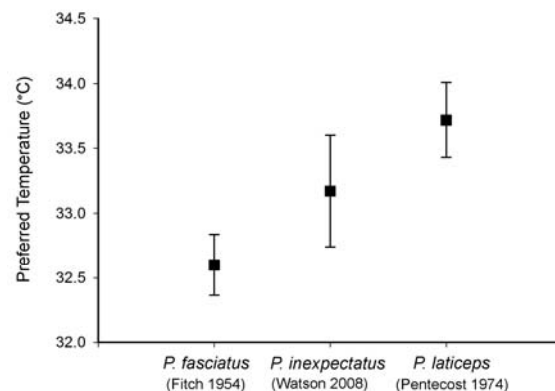
FIGURE 1. Compiled mean preferred temperatures (± 1 SE) of the three Five-lined Skinks (Genus *Plestiodon*) found in the southeastern United States as reported in Fitch (1954), Pentecost (1974) and Watson (2008) using similar methods.

Fig. 1.) and accurate field active body temperatures are not available due to issues associated with capture and handling of small lizards. The thermal differences of these species preferred habitat are measurably apparent (Watson 2008). Therefore, we choose to document and compare the sprint speed of these species at ecologically relevant habitat temperatures derived from the grey copper models rather than actual field-active body temperatures.

MATERIALS AND METHODS

Experimental subjects.—We collected a minimum of 10 lizards of each species from sites in South Carolina. Additional specimens were provided by academic colleagues from areas near Tuscaloosa and Auburn Aabama, Aiken, South Carolina, and Pensacola and Miami, Florida. We maintained experimental subjects in captivity for approximately of one month prior to trials and we provided food (6–10 live juvenile Crickets, *Acheta domestica*) twice weekly and water *ad libitum*.

Sprint speed trials.—To compare whole animal physiological differences among these three species at each of four environmentally relevant temperatures, we used the measure of sprint speed performance adapted from Huey (1982). We placed skinks and their holding enclosures inside a walk-in environmental chamber set at the target experimental temperature ($\pm$ 0.5 ºC). Skinks remained at each temperature for 24 hours prior to testing to ensure that their body temperatures were approximately the same as the ambient temperature. This relationship was confirmed by comparing the cloacal temperature of a specimen of *P. laticeps* not used in the trials. We performed sprint trials following methods adapted from Fieler and Jayne (1998) using a high-resolution video camera (Sony HandyCam DCR-SR42, Sony Corporation, Kōnan Minato, Tokyo, Japan; 30 frames per sec) suspended directly above (~100 cm) the lizard as it sprinted along a 30 cm section in the middle of a 2 m track. The track consisted of a rough-cut piece of dimensional lumber (~10 cm wide) surrounded by aluminum flashing and marked with a line at 10-cm intervals. We hand released each specimen at one end of

the track and we chased them. We analyzed the video frame-by-frame using Sony Vegas Movie Studio 8.0 (Sony Corporation, Kōnan Minato, Tokyo, Japan) and the time that the specimen crossed each line was recorded. From those values, we determined maximum sprint speed for each lizard in each trial.

Losos et al. (2002) criticized many previous studies of sprint speed by pointing out that relatively low samples sizes and a lack of sufficient numbers of trials may provide inadequate data for comparison. Therefore, we used a relatively large sample size (n $\geq$ 10) and performed multiple trials (4) to select the maximum values for statistical comparison and to satisfy these criticisms. *Plestiodon laticeps* is significantly larger than the other two species, so we performed a regression for each species at each temperature between SVL and sprint speed. Despite the greater absolute size of *P. laticeps*, the relationship of size to sprint speed was inconsistently significant (ex: *P. laticeps* at 30 ºC; $F_{1,10} = 2.47$, $P = 0.14$, $R^2 = 0.198$ and at 15 ºC; $F_{1,10} = 5.38$, $P = 0.04$, $R^2 = 0.349$). Due to this and the fact that the largest species consistently averaged the lowest sprint speed, we did not size correct the data. We used a two-way repeated measures ANOVA with species and experimental temperature as main effects to statistically analyze the data. We used pairwise multiple comparisons using the Holm-Sidak method (HSM), which accounts for family-wide type 1 error, as a post hoc means to identify significant differences among and within species at each experimental temperature. For all tests, $\alpha = 0.05$)

Determination of temperature coefficient (Q_{10}).—We calculated temperature coefficient (Q_{10}) values for maximum locomotor performance for each lizard over the temperature intervals of 15–20 °C, 20–25 °C, and 25–30 °C using the van't Hoff equation. We log-transformed these values and statistically analyzed them with a two-way repeated measures ANOVA. We used the Holm-Sidak method (HSM) to identify significant differences among and within species over each interval. For all tests, $\alpha = 0.05$)

TABLE 1. Results of a two-way repeated measures ANOVA for the effects of four ecologically relevant temperatures on the maximum locomotor performance of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps*.

Source of Variation	df	SS	MS	F	P
Species	2	1.95	0.97	11.446	< 0.001
Temperature	3	15.18	5.06	113.174	< 0.001
Species X Temperature	6	1.10	0.18	4.087	0.001
Specimen(Species)	30	2.55	0.09		
Residual	90	4.03	0.04		
Total	131	25.05	0.19		

TABLE 2. Results of the post-hoc pairwise multiple comparisons procedure (Holm-Sidak method, overall significance level = 0.05) applied to the two-way repeated measures ANOVA for intraspecific and interspecific comparisons of *Plestiodon fasciatus, Plestiodon inexpectatus,* and *Plestiodon laticeps* at three environmentally significant temperatures (15 °C, 20 °C, 25 °C, and 30 °C). An asterisk (*) denotes a statistically significant difference.

| Comparison	Difference of Means	t	P	α
Temperature within *Plestiodon fasciatus*				
15°C vs. 20°C	0.085	0.893	0.374	0.025
20°C vs. 25°C*	0.465	4.915	< 0.001	0.017
25°C vs. 30°C	0.035	0.367	0.715	0.050
Temperature within *Plestiodon inexpectatus*				
15°C vs. 20°C*	0.192	2.126	0.036	0.050
20°C vs. 25°C*	0.653	7.244	< 0.001	0.017
25°C vs. 30°C*	0.232	2.577	0.012	0.025
Temperature within *Plestiodon laticeps*				
15°C vs. 20°C*	0.384	4.452	< 0.001	0.017
20°C vs. 25°C*	0.302	3.495	0.001	0.025
25°C vs. 30°C	0.160	1.849	0.068	0.050
Species within 15°C				
P. fasciatus vs. *P. inexpectatus*	0.046	0.452	0.652	0.050
P. inexpectatus vs. *P. laticeps**	0.241	2.460	0.015	0.025
P. laticeps vs. *P. fasciatus**	0.287	2.860	0.005	0.017
Species within 20°C				
P. fasciatus vs. *P. inexpectatus*	0.061	0.596	0.552	0.017
P. inexpectatus vs. *P. laticeps*	0.048	0.489	0.626	0.025
P. laticeps vs. *P. fasciatus*	0.013	0.132	0.895	0.050
Species within 25°C				
P. fasciatus vs. *P. inexpectatus**	0.250	2.437	0.016	0.025
P. inexpectatus vs. *P. laticeps**	0.399	4.085	< 0.001	0.017
P. laticeps vs. *P. fasciatus*	0.150	1.496	0.138	0.050
Species within 30°C				
P. fasciatus vs. *P. inexpectatus**	0.447	4.369	< 0.001	0.025
P. inexpectatus vs. *P. laticeps**	0.472	4.829	< 0.001	0.017
P. laticeps vs. *P. fasciatus*	0.025	0.249	0.804	0.050

RESULTS

Maximum locomotor performance.—We found a significant effect of species, temperature, and their interaction (Table 1). Because the interaction is significant, we cannot interpret main effects individually. This result was expected due to the prediction that temperature influences each species differently. We found that *P. inexpectatus* was faster than the other two species at 25 °C and 30 °C, while *P. laticeps* was slower than the other two species at 15 °C (Table 2). *Plestiodon inexpectatus* exhibited a significant increase in speed across each interval, with *P. laticeps* exhibiting an increase in sprint speed from 15 °C to 20 °C and 20 °C to 25 °C. *Plestiodon fasciatus* exhibited an increase in speed only over the 20 °C to 25 °C interval (Fig. 2)

Temperature coefficient (Q10).—We found a significant effect of species, temperature, and their interaction (Table 3). *Plestiodon laticeps* exhibited a significantly higher Q_{10} over the interval of 15 °C to 20 °C (P < 0.01, HSM). No other interspecific difference was observed. Within *Plestiodon fasciatus*, lizards exhibited a significantly higher Q_{10} over the interval of 20 °C to 25 °C than the interval of 25 °C to 30 °C (P = 0.01, HSM). *Plestiodon laticeps* exhibited a higher Q_{10} over the interval of 15 °C to 20 °C than either of the other two intervals (P = 0.001, P = 0.025, HSM). *Plestiodon inexpectatus* exhibited a higher Q_{10} at 20°C to 25°C than the other two intervals (P = 0.004, P = 0.019, HSM) (Fig. 3).

DISCUSSION

Whole animal functional measures such as sprint speed are excellent parameters to integrate physiology and ecology (Huey and Stevenson 1979). Sprint speed is directly associated with prey acquisition, predator escape, and social interactions. Each of these processes is crucial for survival and reproduction and is subject to selective pressures (Huey and Hertz 1984). Because there is a direct tie to survivorship, such data may be
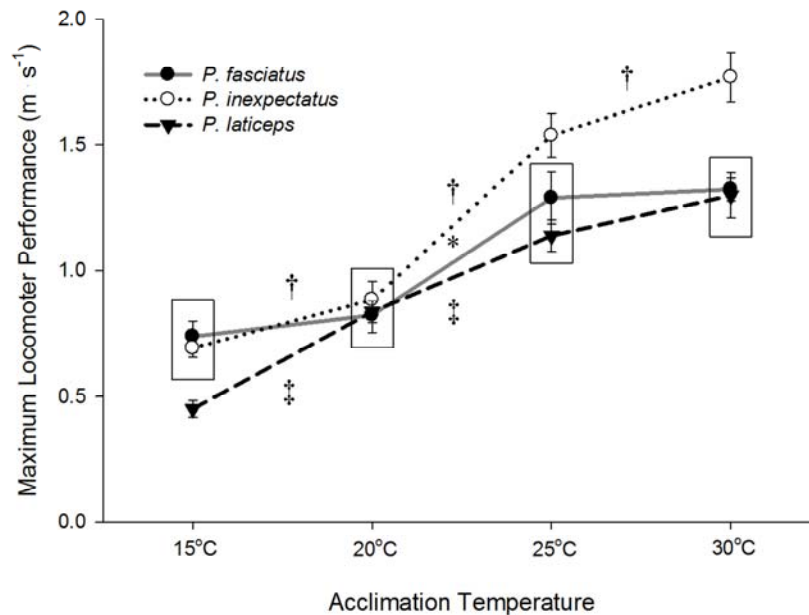
FIGURE 2. Maximum Sprint Speed (± 1 SE) of the common Five-lined Skink (*Plestiodon fasciatus*), the Southeastern Five-lined Skink (*Plestiodon inexpectatus*), and the Broadhead Skink (*Plestiodon laticeps*) at four ecologically relevant temperatures. Values contained within the same box represent statistically indistinguishable interspecific differences (α = 0.05) at each experimental temperature. Statistically significant intraspecific differences (α = 0.05) between consecutive temperatures are indicated for *P. fasciatus* (*), *P. inexpectatus* (†) and *P. laticeps* (‡).

useful in determining the fitness of species within the thermal constraints of different habitats.

Maximum sprint speed is a particularly relevant measure among these skinks because of the apparent cognitive map that each species exhibits over its small home range. Once detected, a skink will run in a straight line to some form of refugia (i.e. a hole in a tree, Fitch 1954; pers. obs.). This suggests that the ability to run very quickly along a straight line may be more beneficial for these species than long-distance endurance or the ability to quickly change direction. Losos et al. (2002) states 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, differences in maximum straight-line speed

are both evolutionarily and ecologically important for these skinks. Each of these species are fastest at the highest experimental temperature (30 °C), which is within 3 °C of their preferred body temperatures (Fig 3.). This finding indicates that these species' preferred temperatures and optimal temperatures may be similar and do not experience the phenomenon of antagonistic coadaptation described in Huey and Bennett (1987) in their study of Australian skinks (Lygosominae).

Plestiodon laticeps, due to its larger size, may not actually be in direct competition with the other two species as adults. In fact, *P. laticeps* is found sympatric with either *P. inexpectatus* or *P. fasciatus*, but almost never with both (Watson and Gough 2012). Without direct empirical evidence of actual fitness advantages associated with performance, concrete

TABLE 3. Results of a two-way repeated measures ANOVA for the effects of three ecologically relevant temperature intervals on the temperature coefficient (Q_{10}) of maximum locomotor performance of *Plestiodon fasciatus*, *Plestiodon inexpectatus*, and *Plestiodon laticeps* (α = 0.05).

Source of Variation	df	SS	MS	F	P
Species	2	0.287	0.143	6.625	0.004
Interval	2	1.466	0.733	8.417	< 0.001
Species x Interval	4	1.323	0.331	3.796	0.008
Individual(Species)	30	0.649	0.022		
Residual	60	5.227	0.087		
Total	98	8.935	0.091		
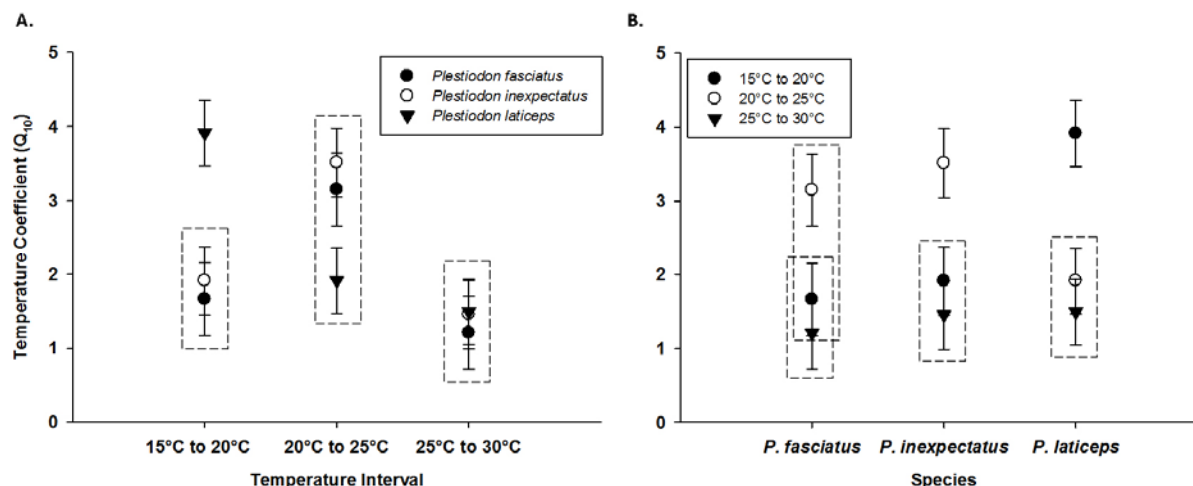
FIGURE 3. Interspecific (A.) and Intraspecific (B.) comparisons of temperature coefficients (Q_{10}) for each 5 °C interval and each species of *Plestiodon* included in the study. Statistically indistinguishable values are contained in dashed boxes.

claims of competitive exclusion and adaptation cannot be supported to describe the distribution of these species. However, the allopatric distribution of *P. inexpectatus* and *P. fasciatus* at the habitat scale may be explained by *P. inexpectatus* having an advantage over *P. fasciatus* in more open habitats that have average daily temperatures at or above 25 °C. However, additional study is required to make definitive claims regarding these species' competitive relationships. No differences in sprint speed between *P. inexpectatus* and *P. fasciatus* were noted at the lower temperatures that are representative of the closed-canopied habitats occupied by *P. fasciatus*. The measured differences between the two smaller species are particularly interesting because they are similarly sized and exhibit more similar limb lengths (Davis 1969). Further field investigations of competitive exclusion with these species are encouraged and may support or refute this speculation.

The increase in maximum sprint speed within all three species over the interval of 20−25 °C is consistent with an increase in diurnal lizard activity from daybreak to mid-day and is also reflected in the significant temperature coefficient increase over this interval for *P. fasciatus* and *P. inexpectatus*. This supports the utility of early-morning basking to rapidly increase the ability of the organism to capture prey and evade predation during these brief times of activity. *Plestiodon laticeps* exhibits a significant increase at 20 °C from a sprint speed that is significantly lower than its congeners at 15 °C. This may be the result of their arboreal lifestyle and associated selection of arboreal refugia (Cooper and Vitt 1994), which may experience lower temperatures due to convective cooling than ground-level refugia that would experience reradiation and the high thermal capacity of moist soils in the same habitat (Kimmins 1987). *Plestiodon laticeps* would thereby resume daily activities from a lower base body temperature than the

mostly terrestrial *P. fasciatus* and *P. inexpectatus* and therefore require a greater increase in performance over the lower interval to attain a similar sprint speed. This phenomenon is further exemplified by the high temperature coefficient, or thermal sensitivity, of the sprint speed of *P. laticeps* over the interval of 15 °C to 20 °C when compared to the other two species (Fig. 3). Additional study as well as quantification of arboreal temperatures within these habitats would be needed to fully substantiate this assertion. Furthermore, significant interspecific differences suggests that there is some evolutionary flexibility in the thermal performance curves in *Plestiodon* that has not been previously detected in comparisons of other aspects of thermal performance such as optimal temperature.

Another curious attribute of the data is that *P. laticeps* never averaged a significantly faster sprint speed value than either congener, even though it is significantly larger. We would expect that these lizards should be absolutely faster due to the much larger size of the adult specimens used in this study. This unexpected finding may be an artifact of the ecology of *P. laticeps* and the evolutionary pressures associated with a more arboreal lifestyle (Fitch 1954; Cooper and Vitt 1994). Further studies that compare sprint performance of these species on an inclined surface may yield different results and identify an additional ecologically relevant variable that affects performance in these species.

The inter- and intra-specific differences among these three morphologically similar congeneric skinks correspond to observed daily activity patterns as well as potential advantages in the ability to evade predation and acquire prey by *P. inexpectatus* in higher-temperature forest habitats, such as the threatened Longleaf Pine Savannah, maritime forests, and granite outcropping ecosystems in which they are found. These data provide measured differences among three species that are

morphologically and behaviorally similar. While we cannot infer adaptation without a much more thorough treatment that includes additional closely related species within a phylogenetic framework (Garland and Adolph 1994), these differences implicate habitat temperature as a potential niche axis by which *P. fasciatus* and *P. inexpectatus* are segregated. These data also provide evidence of physiological differences among morphologically similar species in closely associated, yet thermally distinct, habitats. *Plestiodon laticeps*, which obtains the largest adult size, may maintain its sympatric relationship with the other two species by simply being larger and more arboreal, thereby using resources unavailable to smaller lizards.

Aside from the potential ecological implications, the most unique aspect of this study among comparative studies of sprint speed is the degree of morphological similarity exhibited among these species. Previous *Anolis* studies have highlighted the co-evolution of morphological characters, such as hind limb length, coupled with a greater capacity to rapidly contract muscles to concertedly increase the sprinting ability of some species relative to others (Losos 1990). Observed differences in sprinting speed among these species of *Plestiodon* solely relate to increased or decreased ability to rapidly contract muscles relative to temperature. The significantly faster *P. inexpectatus* at higher temperatures suggest that increased performance can be evolved in morphologically conservative species without an associated change in limb length.

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