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Author

McElroy, Matt T

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THERMAL ECOLOGY AND HABITAT SELECTION OF TWO CRYPTIC SKINKS (SCINCIDAE: *EMOIA CYANURA*, *E. IMPAR*) ON MO'OREA, FRENCH POLYNESIA

MATT T. MCELROY

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. I studied the habitat selection and thermal biology of two cryptic South Pacific skinks (*Emoia cyanura* and *Emoia impar*) in order to determine whether or not differences in thermal preference affect habitat partitioning. I measured sun exposure and thermal characteristics of microhabitats selected by each skink, and then quantified preferred substrate temperatures and preferred body temperatures in a laboratory thermal gradient. Compared to *E. impar*, *E. cyanura* inhabited areas with open canopy cover, and selected significantly warmer substrates in the field and lab setting. *E. cyanura* also had a significantly higher preferred body temperature than *E. impar*. Furthermore, *E. cyanura* had significantly less variability in preferred body temperature than *E. impar*. These findings up hold Huey and Slatkin's (1976) theory on the costs and benefits of lizard thermoregulation, and support the hypothesis that differences in thermal preference provide *E. cyanura* and *E. impar* with a mechanism for habitat partitioning.

Key words: lizards, skinks, microclimate, microenvironment, resource partitioning, thermoregulation, thermal preference, thermal specialist, thermal generalist, substrate selection, Squamata

INTRODUCTION

Morphologically similar species often share ecological and physiological characteristics (Pianka 1973). Where such species occur in sympatry, limited resources will drive species to niche partitioning in order to reduce competition. Competing lizards partition resources along at least one of three axes: habitat, food, and time of activity (Pianka 1975). While lizard ecology has generally been considered in terms of niche partitioning and biotic interactions, few studies have been done on the relationship between thermoregulatory needs and habitat selection (Adolph 1990, Grover 1996)

As ectotherms, lizards must maintain a preferred body temperature in order for optimal physiological function (Bennet 1980, Huey 1982, Ji et al. 1996). Lizards are known to accomplish this by shuttling between sunny and shady substrates, changing their position in relation to the sun, and limiting their activity to times of day when the appropriate thermal environment is present (Grant 1988, Heath 1970). Furthermore, for small lizards with little thermal inertia, there is likely an increased importance to select substrates with temperatures approaching their preferred body temperature (Bartholomew 1982). Thus, lizards may finely partition

habitat based on thermal microenvironments, reducing competition in sympatric assemblages of morphologically and ecologically similar species.

Recently, the Brown-Tailed Copper-Striped Skink (*Emoia cyanura*) was split into two cryptic species, *E. cyanura* and the Blue-Tailed Copper-Striped Skink (*Emoia impar*), based on morphological (Ineich and Zug 1991) and biochemical (Bruna et al. 1995, Guillaume et al. 1994) analysis. The two species occur in sympatry on many islands in the South Pacific, but quantitative data shows that *E. cyanura* occurs primarily in open canopy habitat (beach and disturbed) while *E. impar* prefers closed canopy habitat (coastal and interior forest) (Bruna et al. 1996, Schwaner and Ineich 1998). This distribution pattern could result from competitive exclusion interactions between the species, or from differences in thermal preferences (Bruna et al. 1996). Furthermore, if physiological requirements influence *Emoia* distributions, it is unclear whether sympatric assemblages of *E. cyanura* and *E. impar* result from physiological similarities in thermal requirements that force individuals to converge on one habitat type (Adolph 1990), or whether the two species are finely partitioning the microhabitat based on

differences in thermal preference (Roughgarden 1981, Hertz 1992.)

In this study, I explored the relationship between microhabitat selection and preferred body temperature of two closely related, morphologically similar skinks, *E. cyanura* and *E. impar*, on the island of Mo'orea, French Polynesia. First, I measured the thermal properties of microhabitats selected by each species in sympatric assemblages. Then, I quantified each species' selected substrate temperature and preferred body temperature (T_{pref}) in a thermal gradient in the laboratory. Using these data, I aim to (i) see if there are differences in thermal physiology between *E. cyanura* and *E. impar*, (ii) investigate the thermal properties of field substrates selected by each species, and (iii) determine whether or not such interspecific physiological differences provide a mechanism for habitat partitioning.

METHODS

Study site

Experiments were conducted on Mo'orea, French Polynesia (17° 30'S, 149° 50'W) from October 16 to November 14, 2007. Mo'orea, a volcanic island located in the Society Archipelago, encompasses an area of 134 km² and has many high peaks, including the highest, Mt. Tohivea (1207 m). The interior of the island is comprised of mountains and valleys covered in closed canopy forests with vegetation including Tahitian Chestnut (*Inocarpus fagifer*), Hibiscus (*Hibiscus tiliacius*), African Tulip Tree (*Spathodea campanulata*), Screw Pine (*Pandanus tectorius*), Tree Fern (*Angiopteris evecta*), and a variety of other ferns. Vegetation in open canopy and agricultural areas along the coast include Coconut (*Cocos nucifer*), Indian Almond (*Terminalia catappa*), Hibiscus, and a variety of ferns and grass.

Habitat characteristics and field substrate selection

Patches of skinks were observed along the Three Coconut Trail at the Belvedere, Mare Mare Kellum's property at PK 17.5, the Hati'tia center at PK 11.5, and in coastal coconut groves near Vaiare. Patches were selected based on lizard abundance and accessibility. At each patch I recorded i)

landscape (interior forest, forest trail, coastal forest, agricultural area), ii) vegetation present, iii) percent substrate present (leaf litter, rocks, fallen branches), iv) sun conditions (overcast, direct sun, filtered sun), and v) percent canopy cover. Percent canopy cover was determined using a canopy densiometer.

During sunny days from 900-1500 sites were observed and digital photographs (200mm focal length, D40x, Nikon Inc.) were taken during a 10-minute scan for sun basking skinks within each patch. Following each scan, substrate temperatures of both shaded and sun exposed rocks, logs, and leaf litter were taken using a non-contact laser thermometer (MiniTemp6, Raytek, USA). Each photograph provided information for skink identification, substrate selection, sun exposure (sunny or shaded), and time of day. Substrate temperatures taken following scans were matched with photographs of skinks, and the photographs from each site were used to determine the species composition present there. Skinks in photographs were identified based on three visible characteristics: 1) absence or presence of an epiphyseal eye, 2) fused or unfused mid-dorsal scales, and 3) bluish or greenish tail color (Bruna, 1995). Because of individual variation, at least two of the three characteristics needed to be visible in order to identify a skink to species.

Thermal profiles of substrates used by skinks were created using a non-contact laser thermometer on rock, log, and forest floor leaf litter where skinks were sighted. Surface temperatures were recorded every 15 seconds at noon for at least five minutes to show variability in substrate surface temperature.

Preferred laboratory temperatures

During the field study, 40 skinks (*E. cyanura*: n = 20, svl = 48.4 ± .84 mm, weight = 2.29 ± .12 g; *E. impar*: n = 20, svl = 45.05 ± .64 mm, weight = 1.68 ± .06 g,) were captured both by hand and by strategically placed Victor rat glue traps. Upon capture, skinks were removed from traps using vegetable oil (Bauer 1992), and transported back the laboratory at the Richard B. Gump Station. Skinks were placed in a terrarium (80 cm x 43 cm x 52 cm) with gravel, leaf litter, and drinking water to imitate natural habitats. Skinks were kept overnight, and lab test were performed the following

morning. Two 100 W light bulbs were suspended 15 cm above a separate terrarium (57 cm x 41cm x 38 cm) with gravel, basking rocks, and leaf litter to create a thermal gradient of 25-60°C. The day following capture, individual skinks were placed in the thermal gradient, and observed during a 10-minute focal watch. Substrate temperatures in the cage were taken using a Rayetet Mini non-contact laser thermometer and were matched up with substrates each individual selected during the focal watch. Following the focal watch, body temperature was taken using a Schultheis quick-reading cloacal thermometer within 30 seconds of the initial re-capture attempt. If the body temperature could not be taken within the allotted 30 seconds, the skink was allowed five minutes in the cage to readjust to its preferred body temperature before a second attempt was made. Each specimen was then identified to species and photographed. Individuals were measured for SVL with calipers, weighed using a 10 g Pesola, and sexed via hemipene inversion.

Statistical analysis

All statistics were performed using JMP v5.1.2. The relationship between canopy cover and community ratio (*E. impar* : *E.*

cyanura) was analyzed with regression. The Rank Sum Test was used to test for differences between species for all field substrate temperatures, and for preferred body temperatures. Five tests (O'Brien, Brown-Forsythe, Levene, Bartlett, and F Test 2-side) were used to test for differences between species in variance of preferred body temperature. The difference between species for selection of thermal substrates in the lab were compared with means.

RESULTS

Habitat selection, microenvironment, and substrate selection

Linear regression indicates that the ratio of *E. impar* : *E. cyanura* in assemblages of skinks responds to percent canopy cover. As canopy cover approached 100 percent, *E. impar*'s representation within the assemblage increased dramatically. The regression equation for % *E. impar* is $y = 1.1463x - 20.414$ ($R^2 = .5226$, $P = .0079$). Similarly, as canopy cover decreased, *E. cyanura*'s representation within the assemblage decreased in a reciprocal manner (Figure 1).

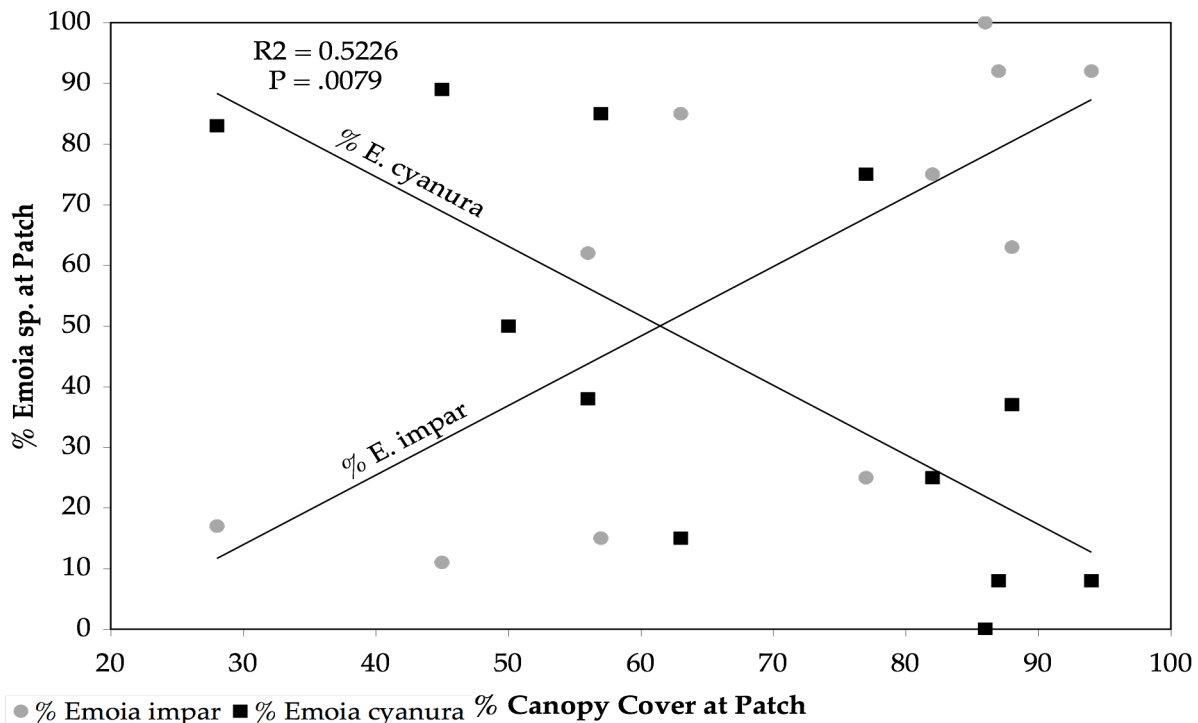


Figure 1. The ratio of *E. impar* : *E. cyanura* at lizard patches in relation to the percent canopy cover.

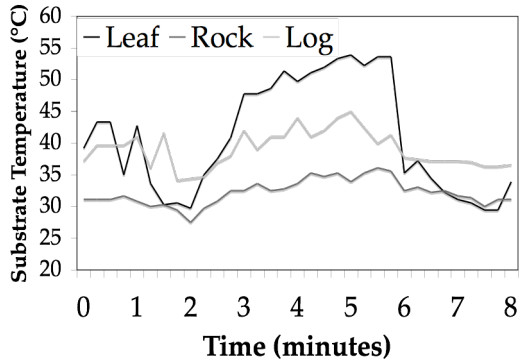


FIG. 2. Substrate temperature variability in response to sun exposure and shade. Upward temperature spikes result from brief sun exposure do to passing clouds. Between minutes two and six there was relatively constant sun exposure, and between minutes six and eight there was constant cloud cover.

A thermal profile of substrates selected by *Emoia* skinks, indicates that various substrates heat up and cool down differently when exposed to sun (Figure 2).

Substrate selection differed between species (Table 1). *E. impar* was more likely to select sunny leaf litter than shaded leaf litter, and more likely to select shaded logs and rocks, than sunny logs and rocks. *E. cyanura* had no preference between sunny or shaded leaf litter, and sunny or shaded logs.

Preferred temperatures in the field

A Rank Sum test indicates significant

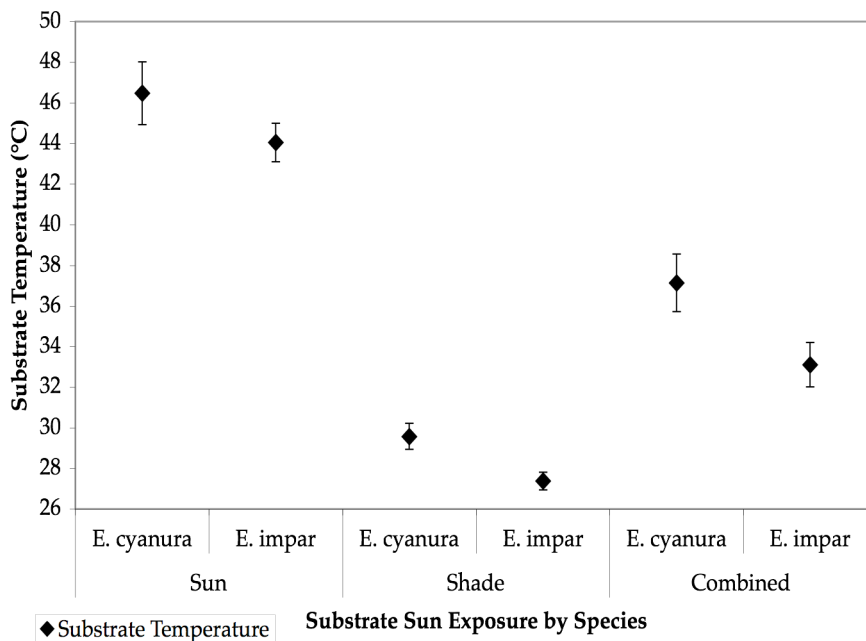


FIG. 3. The mean field substrate temperature selected by *E. cyanura* and *E. impar*. Selected temperatures are grouped by sunny substrates, shaded substrates, and both sunny and shaded substrates combined. Error bars represent ± 1 standard error.

Table 1. The frequency that sun exposed and shaded substrates were selected by *E. cyanura* and *E. impar*.

Substrate	Exposure	Species	
		<i>E. c.</i>	<i>E. i.</i>
Angiopteris	sun	1	0
	shade	0	5
Coconut	sun	6	1
	shade	1	0
Leaf Litter	sun	10	20
	shade	9	9
Log	sun	17	10
	shade	16	26
Rock	sun	0	2
	shade	3	6

differences in temperatures of substrates selected by *E. cyanura* and *E. impar* in the sun (T_{sun}), shade (T_{shade}), and overall ($T_{substrate}$) (T_{sun} : $Z = 1.9626$, $P = .0497$; T_{shade} : $Z = 2.6724$, $P = .0075$; $T_{substrate}$: $Z = 2.6251$, $P = .0087$). Substrate temperatures selected by *E. cyanura* were significantly higher than those selected by *E. impar* for all three categories (Figure 3) (T_{sun} : *E.c.* = 46.67 ± 1.55 °C, *E.i.* = 44.05 ± 0.95 °C; T_{shade} : *E.c.* = 29.57 ± 0.64 °C, *E.i.* = 27.38 ± 0.43 °C; $T_{substrate}$: *E.c.* = 37.14 ± 1.4 °C, *E.i.* = 33.11 ± 1.09 °C).

Preferred temperatures in the laboratory

The temperature of substrates selected by *E. cyanura* were quite different than those

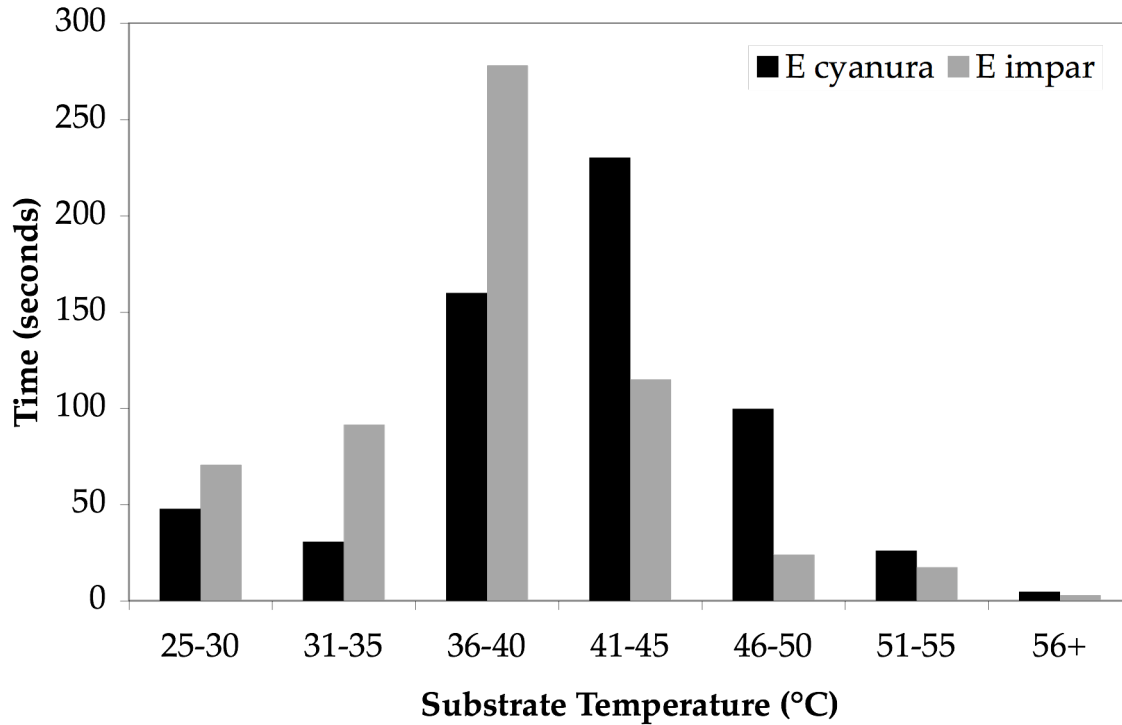


FIG. 4. This chart represents a mean 10-minute focal watch and shows the average time that each species spent on substrates of each temperature group within the gradient.

selected by *E. impar*. *E. cyanura* preferred substrates with temperatures ranging from 36-50 °C with substrate selection peaking between 41-45 °C while *E. impar* preferred substrates with temperatures between 31-45 °C with substrate selection peaking from 36-40 °C (Figure 3). The mean temperature

selected by *E. cyanura* was 41.53 °C, and the mean for *E. impar* was 38.34 °C.

A Kruskal-Wallis test indicated that preferred body temperatures (T_{pref}) differed between species ($Z = 3.861$, $P = .0001$). T_{pref} for *E. cyanura* was significantly higher than that of *E. impar* (*E. cyanura*: 36.6 ± 0.12 °C; *E. impar*: 35.08 ± 0.35 °C). Five tests confirmed that *E. cyanura* and *E. impar* had significant differences in variance of body temperature (Bartlett's: $P = .0001$; F-test 2 ways: $P = .0001$).

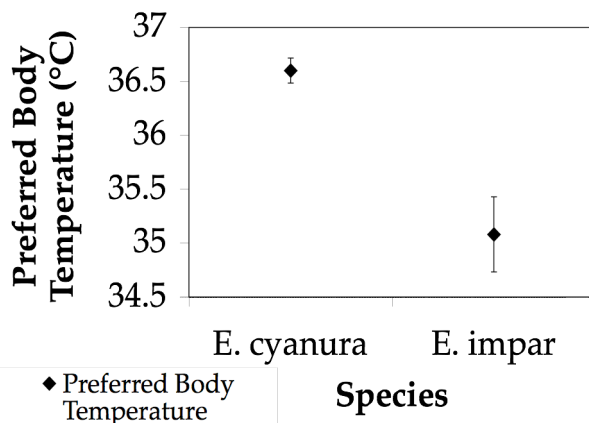


Fig. 5. Mean preferred body temperatures of *E. cyanura* and *E. impar*. The error bars represent one standard error.

DISCUSSION

Emoia cyanura and *E. impar* are very similar in morphology and ecology and are syntopic on Mo'orea, French Polynesia. On Mo'orea, the species appear to partition the landscape based on canopy cover and sun exposure, such that *E. cyanura* prefers open canopy areas, and *E. impar* closed canopies. Similar *Emoia* distributions are known to occur on other islands in the South Pacific (Bruna et al 1996, Schwaner and Ineich 1998). However, the ratio of *E. cyanura* to *E. impar* within skink assemblages may be more responsive to percent canopy cover at a given location than the general landscape (Fig 1). Within the Belvedere, the species

ratio of lizard assemblages varied widely depending on the canopy cover, even though the general landscape was closed canopy interior forest. Both species could be found throughout the forest, but *E. cyanura* tended to congregate at piles of fallen branches along trails where the canopy was disturbed and sun exposure was direct. Assemblages predominated by *E. impar* could be found just 10 meters off the trail, where the canopy was generally >90% and sun light was heavily filtered.

Studies have shown that sympatric lizard assemblages may use microhabitat features differently to reduce competition (Grover 1996). Behaviors and substrate selection differed between *E. cyanura* and *E. impar* (Table 1). These differences likely result from habitat differences and sun exposure. In closed canopy areas, where the thermal environment is highly variable, *E. impar* behaved differently than *E. cyanura* did in more open areas. When passing clouds allowed for sun exposure, *E. impar* was observed rushing down from inconspicuous perches on *Angiopteris* and fallen logs to bask in small sun patches on forest floor leaf litter. After some time (usually less than 30 seconds), the skink would scamper off to presumably search for food, or even cool down. When clouds blocked out the sun, *E. impar* was usually found on rocks, fallen branches, and logs, but not leaf litter. Table 1 shows that *E. impar* is twice as likely to use sun exposed leaf litter than shaded leaf litter, and is twice as likely to use shaded logs than sun exposed logs for basking. Thermal data collected on substrates show that leaf litter is a very responsive heat pad, and will heat up/and cool down rapidly in response to sun exposure, while logs appear to be less responsive than leaf litter to sun exposure, but maintain heat during periods without direct sun exposure (Fig. 2). Therefore, *E. impar* appears to shuttle between shaded logs and sunny leaf litter when weather conditions allow for such behavior. The data shows that *E. cyanura* did not use sun exposed leaf litter more than shaded leaf litter. Furthermore, they did not use shaded logs more than sunny logs, indicating that *E. cyanura* does not perform such shuttling behavior. Since *E. cyanura* generally inhabits areas with more constant sun exposure, sun patches and substrate heat are not a fleeting and limited resource, so such behavior is not necessary.

Across landscape types and levels of sun exposure, *E. cyanura* appears to select hotter substrates than *E. impar* (Fig 3). Since both species are small lizards, temperatures of selected substrates likely correlate closely with their actual field body temperature due to their low thermal inertia (Bartholomew 1982). Such findings indicate that thermal characteristics of substrates may in fact provide a resource for microhabitat partitioning. However, no physiological studies have been done on *E. cyanura*, or *E. impar*, and biotic interactions, such as competitive exclusion between species, could also influence *Emoia* habitat selection in the field. One survey showed that on the fourth day of a removal experiment of *E. cyanura* from a transect, the number of *E. impar* increased from two of 18 skinks on the first day, to seven of 15 (Zug 1991).

In laboratory settings, where such competition and biotic interactions are removed, *E. cyanura* still appears to select warmer substrates than *E. impar*. During ten-minute focal watches of individually caged skinks, *E. cyanura* spent more time basking on the warmest substrates than did *E. impar* (Fig. 4). Furthermore, preferred body temperatures (T_{pref}) for *E. cyanura* were significantly high than those for *E. impar* (Fig. 5). These findings strongly suggest that physiological differences between *E. cyanura* and *E. impar* influence both habitat and substrate selection, and provide a mechanism for microhabitat partitioning.

The theory on costs and benefits associated with lizard thermoregulation helps describe *Emoia* distribution and habitat selection. From variability in T_{pref} it appears that *E. cyanura* is a thermal specialist while *E. impar* is a thermal generalist (Fig 5). Theory states that a thermal specialist should benefit from a high energetic gain or increased physiological function when maintaining an optimal body temperature. A thermal generalist likely experiences less energetic gain from maintaining such an optimum body temperature, but is able to benefit nominally across a wider range of temperatures (Huey and Slatkin 1976). Furthermore, the energetic cost (locomotion) for a thermal specialist attempting to maintain a specific body temperature in highly variable thermal environments (i.e. closed canopy forest) might be too great, and therefore the costs associated with inhabiting such an environment would out weight the benefits.

A thermal specialist should seek environments with low thermal variability (open canopy areas) in order to maintain T_{pref} . In such an environment, a thermal specialist would not need to expend large amounts of energy performing excessive shuttling behavior, because thermal resources are not as scarce and fleeting. A thermal generalist, however, should have little difficulty in environments with high thermal variability, since a wide range of temperatures are energetically beneficial. Based on the theory of the cost and benefits of lizard thermoregulation we could predict that *E. cyanura* (a thermal specialist) should inhabit open canopy areas, while *E. impar* (a thermal generalist) would inhabit closed canopy habitats. The theory provides insight into *Emoia* habitat selection and helps us to understand possible competitive interactions.

Zug's (1991) removal experiment took place in a relatively open canopy area. Since *E. cyanura* are slightly larger than *E. impar* and require open areas for proper thermoregulation, it is likely that to some extent they do competitively exclude *E. impar* from such habitats. Furthermore, since *E. impar* is a thermal generalist, it makes sense that they should be able to inhabit a variety of thermal environments, including relatively open areas, yet they tend not to. It would be unlikely, however, that a removal experiment of *E. impar* from a closed canopy habitat would result in an increase in *E. cyanura*. While *E. impar* may be limited to closed canopy areas due to biotic interactions with *E. cyanura*, *E. cyanura* is likely limited to open canopy areas because of abiotic and thermal constraints.

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