

Evaluating thermal resource partitioning

By sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses

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Summary. The field thermal biology of sympatric *Anolis cooki* and *A. cristatellus* were evaluated in January and in August in desert scrub forest at Playa de Tamarindo near Guanica, Puerto Rico. Data on randomly positioned copper models of lizards, each equipped with a built-in thermocouple, established null hypotheses about basking frequency and operative temperatures (T_e) against which the behavior and body temperatures (T_b) of live lizards were evaluated. Both species exhibited non-random hourly basking rates (more marked in *cristatellus* than in *cooki*), and *cristatellus* was virtually inactive during the warm mid-day hours. The relationship between lizards' T_b and randomly sampled T_e differed between the species: *cristatellus*'s mean T_b was 2° to 3° C lower than randomly sampled mean T_e in both months, whereas *cooki*'s mean T_b was slightly higher than mean T_e in January and slightly lower in August. Although *cooki*'s mean T_b was higher than that of *cristatellus* in both months, the T_b 's of the two species overlapped substantially over an annual cycle. Given the similarities in their field active T_b and the low thermal heterogeneity among microsites at Playa de Tamarindo, these species appear not to partition the thermal environment there in a coarse-grained way. Instead, the relatively small differences in their field active T_b probably result from small differences in their use of similar microhabitats within their mutually exclusive territories. Thermal resource partitioning by territorial animals is unlikely unless thermal heterogeneity is coarse-grained in relation to territory size.

Key words: *Anolis* thermal biology – Partitioning thermal resources

1977; Pianka 1986). For more than a quarter century, ecologists have also recognized that the thermal properties of habitats are important to resource partitioning by ectothermic vertebrates (Ruibal 1961; Rand 1964; Schoener 1974, 1977). Magnuson et al. (1979), in a theoretical discussion of environmental temperature as a partitionable (though not consumable) resource, proposed that “animals compete for and partition thermal resources” just as they partition space or food. Roughgarden et al. (1981), Tracy and Christian (1986), and Dunham et al. (1989) subsequently clarified this assertion by identifying space and time as the dimensional units with which to quantify the thermal environment as a resource.

Despite the theoretical discussion, surprisingly few studies have explicitly examined thermal resource partitioning among sympatric reptile species. Mushinsky et al. (1980) concluded that differences in thermal preferences were the basis for resource partitioning by five species of water snakes. Roughgarden et al. (1981) used micrometeorological measurements and biophysical models to identify differences in the thermal characteristics of perch sites used by sympatric *Anolis* lizards in the simple communities of the Lesser Antilles. Both of these studies, however, examined the thermal characteristics of the microhabitats occupied by the animals without sampling the range of thermal environments that were available (see Tracy and Christian 1986; Bakken 1989 for critiques). In addition, neither study examined hourly variations in thermal biology or interspecific differences in daily activity patterns (see Huey 1982).

Here I describe a study in which I used random, independent samples of the thermal environment to evaluate microhabitat use and body temperatures (T_b) of two sympatric sibling species of lizard on Puerto Rico. *Anolis cristatellus* and *A. cooki* are of roughly similar size and habitus (Schoener 1970; Williams 1972) and are commonly sympatric on the arid southwestern coastal plain. Although *cristatellus* is widespread in diverse habitats, *cooki* has a geographically restricted range. Several studies indicate that the two species compete directly for

Studies of reptile community ecology have focused on habitat, food, and time as important dimensions along which species can partition resources (Schoener 1974,

space where their ranges overlap (Williams 1972; Jenssen et al. 1984; Marcellini et al. 1985); that interspecific aggression between the species is common and intense (Ortiz and Jenssen 1982; Jenssen et al. 1984); and that competition from *cratatellus* may be driving *cooki* to extinction (Williams 1972; Marcellini et al. 1985). Some studies report higher T_b in *cooki* than in *cratatellus* (Huey and Webster 1976 [1969 data], Lister 1976), whereas others report no difference in the T_b of sympatric populations (Huey and Webster 1976 [1972 data], Jenssen et al. 1984).

In this paper I compare summer and winter basking behavior and T_b of sympatric *cooki* and *cratatellus* to a random sample of thermal environments available in the habitat. I used a population of copper lizard models, each equipped with a built-in thermocouple thermometer, to measure the operative temperatures (T_e) of microsites directly; T_e is the environmental temperature actually experienced by an animal with a given set of physical attributes (Bakken and Gates 1975; Bakken 1976; Bakken et al. 1985; Bakken 1992). Because *cooki* and *cratatellus* are so similar in size, shape, and color, I assume that they equilibrate to the same T_b if they perch in microsites that provide the same T_e (see Bakken 1992 for rationale); hence, a single set of randomly placed models samples the thermal environment for both species simultaneously. If the basking behavior and T_b of lizards is different from those of randomly positioned models, I conclude that the lizards regulate T_b (i.e., orient nonrandomly to environmental factors that influence T_b , see Huey et al. 1977). The rationale for the experimental design is described more fully elsewhere (Hertz 1992).

To evaluate thermal resource partitioning by sympatric *cooki* and *cratatellus*, I compare their use of available thermal environments just as one compares the use of available food resources in a study of food resource partitioning. Data on T_e distributions are analogous to data on the distributions of available prey types or prey sizes: the distribution of T_e not only defines the range of T_b that the lizards could possibly achieve in a particular environment, but it also reveals whether or not the thermal environment is variable enough to be partitioned. The distributions of T_b that the species actually do achieve are analogous to the distributions of prey type or prey size that they consume; resource partitioning of the thermal environment will be apparent if sympatric species experience little overlap of T_b within the range of achievable T_b (i.e., the distribution of T_e).

I also compare the thermoregulatory behaviors and T_b of *cratatellus* at this desert site to those of *cratatellus* sampled (see Hertz 1992) at a low elevation mesic site (a moderately shaded woodland near San German, 90 m elevation) and at a high elevation mesic site (an open ridgetop with trees and fencerows at Monte Guilarte, 1150 m elevation). Collectively, the three sites represent the elevational and habitat extremes occupied by *cratatellus* on Puerto Rico, and the data provide a more complete portrait of the species' thermoregulatory versatility (see Huey 1974; Hertz 1983) than is currently available in the literature.

Materials and methods

Producing and testing models

Hollow, electroformed copper lizard models with low heat capacity and rapid response time were manufactured according to the methods detailed in Bakken and Gates (1975) and Bakken et al. (1983). Each model had the tip of a type T (copper-constantan) thermocouple built into its thoracic region. Models were fashioned in a realistic posture (four feet, posterior half of the venter, and tail in contact with the substrate) and painted to match the reflectance properties of live lizards (Hertz 1992). Although I created equal numbers of larger "male" and smaller "female" models for use in the field, size had no effect on basking rates or temperatures of the models (X^2 tests for basking rates, t -tests for mean T_b , all P 's > 0.05, see Hertz 1992); hence, data for all models are pooled in this analysis. I tested temperature responses of models against those of restrained live lizards in the laboratory (Hertz 1992); models and lizards equilibrated to nearly the same temperatures ($\pm 1^\circ$ C) under varying combinations of convective cooling and radiant heating.

Field methods

This study was conducted just north of the beach at Playa de Tamarindo (1 km east of the terminus of Rte 333 in the Guanica Forest Reserve, elevation 5 m) on the south coast of Puerto Rico. The terrain at the site consists of large limestone boulders and sparse patches of soil, vegetated by an open canopy desert scrub forest that is commonly occupied by both *cratatellus* and *cooki*. Sampling was undertaken in August 1983 and January 1984, the hottest and coolest months of the year (Calvesbert 1970).

In each month, 60 models were placed at random on woody substrates in the habitat (Hertz 1992): a random numbers table was used to select the trees and shrubs upon which models were mounted as well as each model's height above the ground (at 0.3 m intervals between 0 and 3 m, the range of heights at which these species ordinarily perch [Jenssen et al. 1984]) and compass orientation around the substrate. Because I did not select perches of specific thickness, perch diameter was determined by the structure of the substrate at the randomly selected perch height. Models were attached to substrates with an insulated electrical staple. One set of models established null hypotheses for evaluating the biology of both lizard species.

Two student assistants and I continuously sampled models and lizards for one day (0700 to 1900 h) in August and one in January. The sixty models were each sampled hourly, yielding 11 (January) or 12 (August) records per model, with the following data recorded: identification number; temperature (T_e , with a Bailey [now Physitemp] BAT-12R portable Type T thermocouple thermometer); time of day; "basking status" (i.e., "perched" in full sun, filtered sun, shade under sunny or mixed skies, or shade under overcast skies); and weather (sunny, mixed skies, or overcast).

Lizards were sampled with standard techniques and precautions (Hertz 1981; Hertz and Huey 1981) during continuous walks through the study site. Active (i.e., perched on vegetation, rocks or the ground) subadult and adult lizards were captured by hand or with a noose, and the following data were recorded: species; body temperature (cloacal, T_b , with a Keithley portable Model 870 Type K thermocouple thermometer); time; sex; perch height and diameter; basking status (see above); and weather (see above). Lizards were released at the time and place of capture. Lizard sampling was undertaken with Permit Nos. DRN-83-56 and DRN-84-67 from the Departamento de Recursos Naturales de Puerto Rico.

Statistical methods

Because the experimental design included repeated measures ($N = 11$ or 12) on individual models, I first calculate a basking rate

Table 1. Frequency of lizards perched on rocks and ground, perch heights (m, mean \pm SE), and perch diameters (cm, mean \pm SE) of lizards at Playa de Tamarindo. Sample sizes in parentheses

Species	Elev (m)	Frequency on rocks and ground		Perch height		Perch diameter	
		January	August	January	August	January	August
<i>cooki</i>	5	0.207 (58)	0.088 (68)	0.8 \pm 0.1 (46)	0.9 \pm 0.1 (62)	4.5 \pm 0.5 (46)	7.7 \pm 0.9 (62)
<i>cratatellus</i>	5	0.067 (15)	0.000 (25)	1.1 \pm 0.1 (14)	0.8 \pm 0.1 (25)	10.0 \pm 2.2 (14)	9.4 \pm 1.5 (25)

(i.e., the percentage of observations in sun or filtered sun) and T_e summary statistics for each model; I then compute average basking rates and T_e summary statistics among the models in each month. When sampling lizards, I did not knowingly make repeated measures on individuals; each lizard record is therefore treated as an independent sample, and I calculate basking rates and T_b summary statistics for each month among the lizards of each species.

I evaluate basking behavior of lizards from two perspectives. First, to determine whether or not lizards were basking at random, I use a one-sample z-test to compare the proportion of lizards basking to the distribution of model basking rates; the z statistic (distributed as t with infinite df) estimates the number of standard deviations the lizard basking rate lies from the mean basking rate of models. Secondly, I use logistic regression analysis on the dichotomous contrast "basking versus not basking" to evaluate interspecific and seasonal differences in basking rates at Playa de Tamarindo and to evaluate the effects of elevation and month on the basking rate of *cratatellus*; logistic regression is a technique that predicts a binary dependent variable from a set of independent variables (Norusis 1990).

Body temperatures of lizards are similarly evaluated. I use t-tests and z-tests to compare T_b to T_e , and ANOVA to identify significant effects of species, elevation, and month on T_b . Neither basking rates nor mean T_b differed between males and females in any sample (X^2 -tests on basking rates, t-tests on T_b ; all P 's > 0.05); hence, data are pooled for all analyses.

I use a probability of 0.05 as a standard criterion of statistical significance. However, whenever I use multiple tests on subsets of the data (e.g., a series of t -tests on data from different species and month combinations), I control for an overall Type I error rate of 0.05 by using a sequential Bonferroni correction (Rice 1989).

Results

Perch choice

The frequency with which lizards perched on rocks and the ground did not differ between the species in either month (Table 1; X^2 tests, P 's > 0.05; but see Rivero 1978; Jenssen et al. 1984); I sampled only one *cratatellus* perched on the ground. Male and female *cooki* used rock substrates with equal frequency in both months (X^2 tests, all P 's > 0.05); I did not analyse data for *cooki* on rocks and *cooki* on trees separately because I detected no differences in their basking rates or mean T_b in either month (X^2 tests for basking rates, P 's > 0.35; t -tests for T_b data, P 's > 0.3). Among the lizards perched on vegetation, males and females within each species occupied perches of equivalent height and equivalent diameter (height and diameter analysed separately, Kolmogorov-Smirnov tests, Bonferroni corrected P 's > 0.05). Hence, I com-

bined data for males and females in the following analysis.

Perch heights of *cooki* and *cratatellus* were similar at Playa de Tamarindo, though they were influenced by a species by month interaction (Table 1; ANOVA, $F = 5.444$, $P = 0.021$). In general, *cratatellus* perched on thicker branches than did *cooki* (Table 1; ANOVA; $F = 6.681$, $P = 0.011$), but the latter species used thicker perches in August than in January (Table 1; ANOVA; $F = 4.084$, $P = 0.045$). These data largely confirm Jenssen et al.'s (1984) description of differences in the structural habitats of sympatric populations of these species.

Basking behavior and times of activity

Average sunny weather basking rates of individual models index the relative openness of habitats; in the desert scrub forest both basking sites and shaded microsites were readily available to lizards (average basking rates of individual models were 58% in January and 47% in August). This habitat was more open than the mesic habitats for *cratatellus* (average model basking rates at 90 m: 21% in January, 10% in August; average model basking rates at 1150 m: 31% in January, 29% in August); among all three sites, month and elevation each exerted a significant effect on habitat openness (ANOVA; F 's = 16.262 and 107.107, respectively, P 's < 0.0005).

Sunny weather basking rates of both species (Table 2) were not different from the basking rates of models at Playa de Tamarindo (z -tests, Bonferroni corrected P 's > 0.05); hence, when data are pooled over all hours of the day, both species appear to perch at random with respect to basking sites (but see below). In contrast, *cratatellus* did bask (see Table 2 for lizard basking rates) significantly more often than models (see above) at the

Table 2. Sunny weather basking rates (in full sun and filtered sun) of lizards at various elevations. Sample sizes in parentheses

Species	Elev (m)	Sunny weather basking rate	
		January	August
<i>cooki</i>	5	0.64 (39)	0.54 (61)
<i>cratatellus</i>	5	1.00 (8)	0.61 (23)
<i>cratatellus</i>	90	0.67 (75)	0.56 (59)
<i>cratatellus</i>	1150	0.92 (51)	0.84 (91)

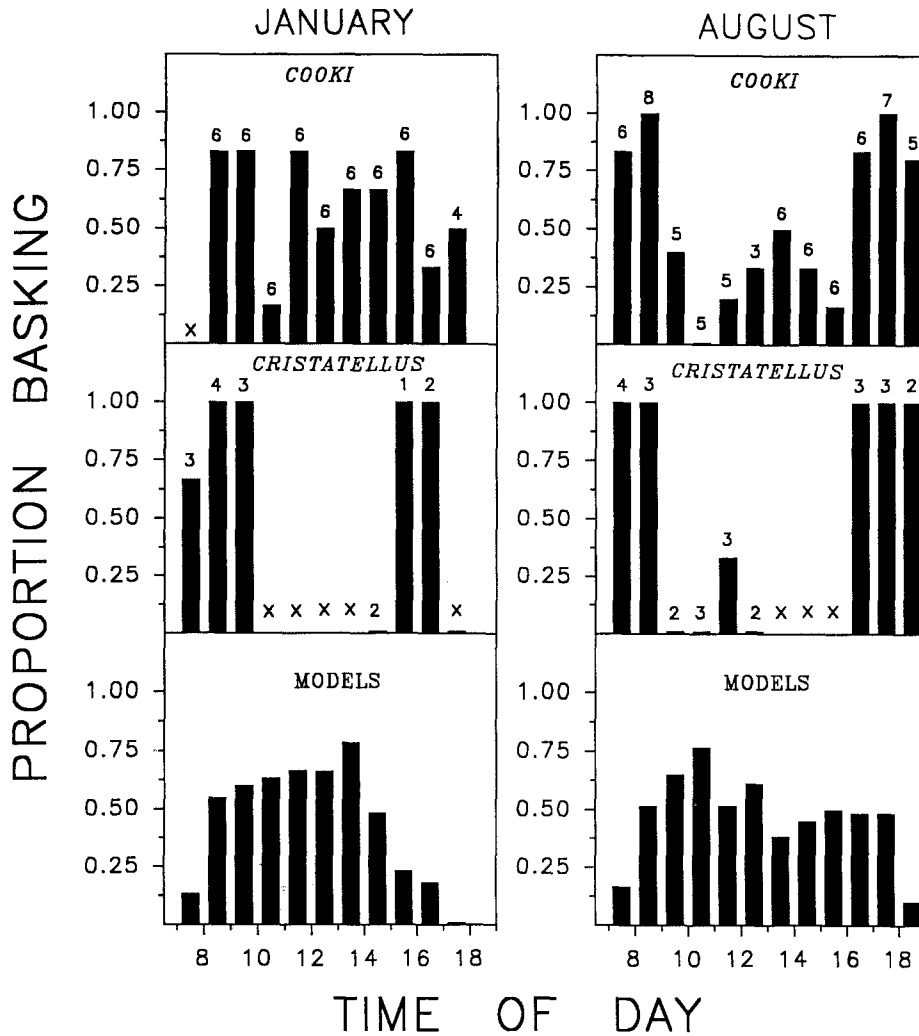


Fig. 1. Hourly basking rates of lizards and models at Playa de Tamarindo. $N=60$ models per hour. Sample sizes for lizards indicated above bars. Activity times indicated by captures of lizard samples; X indicates that no lizards were captured during a sampling hour

mesic sites (z-tests, Bonferroni corrected P 's < 0.05 , Hertz 1992). Using January data for *cristatellus* at Playa de Tamarindo as a baseline in a logistic regression analysis, sunny weather basking rates of lizards did not differ between the two species ($P=0.142$), but they were higher in January than in August ($P=0.011$) and at high elevation relative to the lower elevation sites ($P=0.048$); no significant interactions were detected among these independent variables (all P 's > 0.05).

I could not census times of activity independently of lizard T_b because *cooki* and *cristatellus* are indistinguishable at a distance (Gorman et al. 1968; Marcellini and Jenssen 1983). Nevertheless, because my data are based on an even sampling effort throughout the day, they provide information on the activity periods and relative densities of both species. Activity times of *cristatellus* at Playa de Tamarindo were bimodal (see Fig. 1) and, compared to activity at the 90 m mesic site (Hertz 1992), very much curtailed. In contrast, *cooki* were active throughout the day. In both months, *cooki* outnumbered *cristatellus* in my samples (sample sizes in data on mean T_b , Table 4).

Basking rates (under all weather conditions) and times of activity appeared to be coupled behaviors (see Huey 1982) at Playa de Tamarindo (Fig. 1). Basking was most

Table 3. Temperatures ($^{\circ}\text{C}$) of models (T_m) and lizards (T_b) perched in sun, filtered sun, shade, and those sampled during overcast weather (mean \pm SE, N in parentheses) at Playa de Tamarindo

	January	August
<i>Models</i>		
Sun	34.4 \pm 0.5 (56)	35.3 \pm 0.5 (51)
Filt sun	31.7 \pm 0.2 (240)	33.9 \pm 0.1 (287)
Shade	28.4 \pm 0.2 (265)	31.6 \pm 0.1 (382)
Overcast	26.9 \pm 0.3 (99)	— (0)
<i>cooki</i>		
Sun	30.4 \pm 0.8 (11)	31.7 \pm 0.3 (16)
Filt sun	31.0 \pm 0.3 (25)	31.1 \pm 0.5 (23)
Shade	31.3 \pm 0.7 (14)	33.1 \pm 0.2 (29)
Overcast	30.2 \pm 0.4 (8)	— (0)
<i>cristatellus</i>		
Sun	27.8 \pm 0.6 (6)	29.5 \pm 0.4 (10)
Filt sun	27.6 \pm 1.9 (6)	29.8 \pm 0.8 (6)
Shade	28.1 (1)	32.8 \pm 0.3 (9)
Overcast	24.9 \pm 5.0 (2)	— (0)

Table 4. Operative temperatures (T_e) and lizard body temperatures (T_b) at three elevations in Puerto Rico. $N=60$ models for measurements of T_e . Lizard sample sizes in parentheses. All mean T_b are significantly different from corresponding mean T_e ; see text for explanation

Species	Elev (m)	Mean $T_e \pm SE$		mean $T_b \pm SE$	
		January	August	January	August
<i>cooki</i>	5	29.9 \pm 0.1	32.8 \pm 0.1	30.8 \pm 0.3 (58)	32.1 \pm 0.2 (68)
<i>cristatellus</i>	5	29.9 \pm 0.1	32.8 \pm 0.1	27.3 \pm 0.9 (15)	30.8 \pm 0.4 (25)
<i>cristatellus</i>	90	24.2 \pm 0.1	28.2 \pm 0.1	25.7 \pm 0.4 (115)	28.9 \pm 0.2 (125)
<i>cristatellus</i>	1150	19.0 \pm 0.1	23.4 \pm 0.1	23.5 \pm 0.4 (105)	27.2 \pm 0.3 (159)

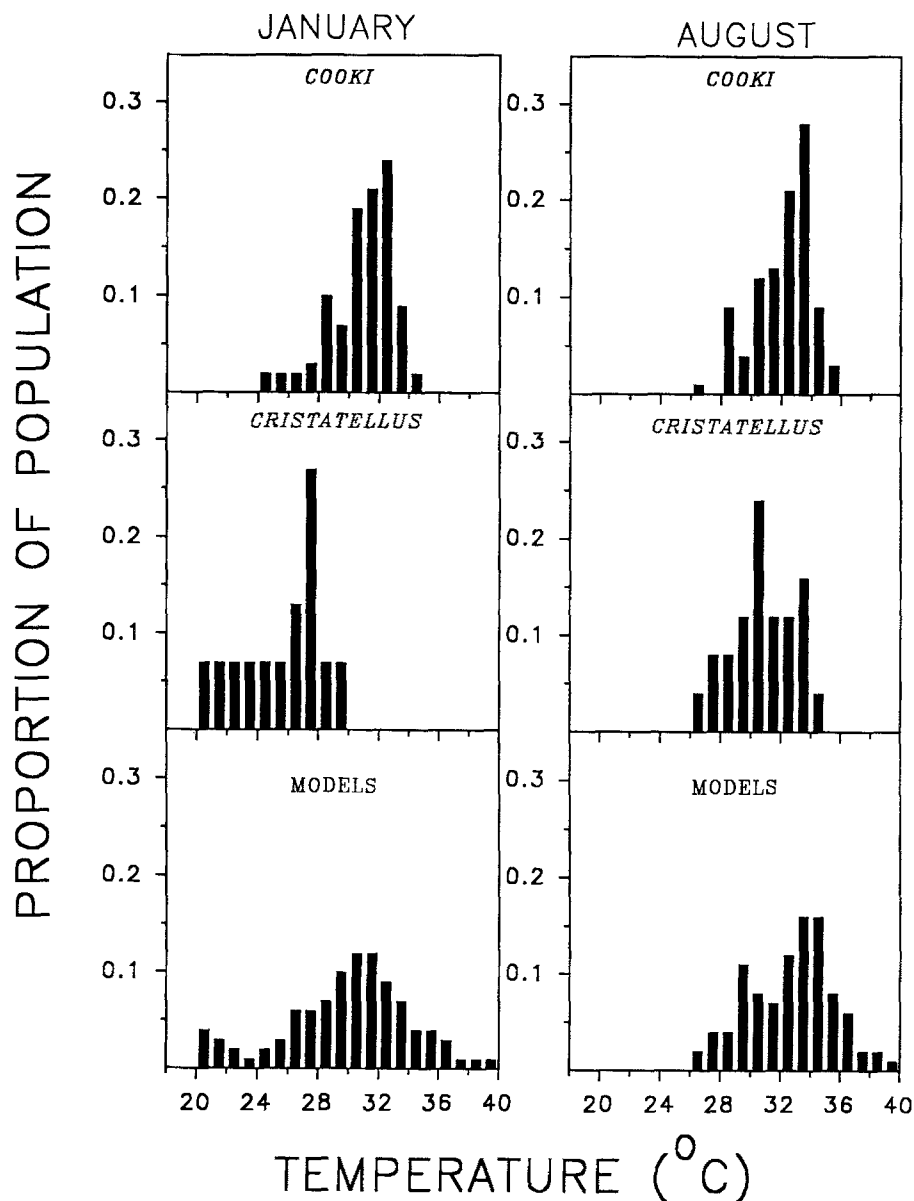


Fig. 2. Distributions of T_b (for *cooki* and *cristatellus*) and T_e at Playa de Tamarindo in January and in August. Sample sizes for lizards in Table 4. Samples of T_e were based upon 11 or 12 repeated measures on each of 60 models; individual T_e readings are plotted here

intense early and late in the day for both species in August and for *cristatellus* in January. In contrast, basking rates of the models (Fig. 1) were either unimodal or uniform. I interpret the difference in these patterns as evidence of behavioral temperature regulation by the lizards (but see Huey et al. 1977): lizards occupied sunny perches at a greater-than-random rate early and late in the day and shaded perches (or reduced activity) at a

greater-than-random rate near mid-day. Unfortunately, hourly samples of lizards were too small for meaningful statistical analysis.

Operative temperatures and body temperatures

Basking status strongly influenced temperatures of models at Playa de Tamarindo in both months (Table 3;

ANOVA's; $F = 88.977$ in January, $F = 59.980$ in August, $P's < 0.00005$): models in sun were warmer than those in filtered sun which were, in turn, warmer than those in shade and those sampled during overcast weather. Although mean T_b did not vary with basking status in either lizard species in January (ANOVA's; $F = 0.652$ for *cooki*, $F = 0.296$ for *cristatellus*, $P's > 0.05$), it did in August: lizards perched in shade were significantly warmer than those perched in full sun or filtered sun (ANOVA's; $F = 15.153$ for *cristatellus*, $F = 8.658$ for *cooki*, Bonferroni corrected $P's < 0.001$; Student-Neuman-Keuls procedure, $P's < 0.05$). This result probably reflects active thermoregulation by the lizards as well as the potential for overheating in the desert (Huey and Slatkin 1976): cool lizards sought basking sites to raise T_b , but warm lizards sought shade (see below).

Mean T_e was influenced by a month by elevation interaction among the three sites (Table 4, ANOVA, $F = 67.566$, $P < 0.0005$), indicating that operative temperatures were highest at Playa de Tamarindo in August and lowest at high elevation in January. The variance in mean T_e among models was very low at all sites in both months (standard errors of mean T_e in Table 4), suggesting low thermal heterogeneity among microsites within each habitat.

Data on randomly sampled T_e provide the statistical yardstick for evaluating lizard T_b . At Playa de Tamarindo, lizard mean T_b differed from mean T_e for both species in both months (Table 4, two-tailed t-tests, Bonferroni corrected $P's < 0.05$). For *cristatellus* mean T_b was 2–3° C lower than mean T_e in both months; in contrast, *cooki*'s mean T_b was slightly higher than mean T_e in January, but slightly lower than mean T_e in August. Interestingly, the mean T_b of *cooki* in January was identical to the mean T_b of *cristatellus* in August. Hence, even though the mean T_b of *cooki* was higher than that of *cristatellus* in both months, a species by month interaction influenced mean T_b (ANOVA, $F = 7.225$, $P = 0.008$). Not surprisingly, the two T_b distributions and the T_e distribution were heterogeneous in both months (Kruskal-Wallis test; $X^2 = 10.704$,

$P = 0.0047$ in January; $X^2 = 17.3529$, $P = 0.0002$ in August), though the interspecific difference in T_b distributions was much more pronounced in January (Fig. 2). Variance of T_b was greater in *cristatellus* than in *cooki* in January (13.22 versus 3.94, $F_{15,58} = 3.35$, $P < 0.001$) but not in August (4.22 versus 3.77, $F_{25,68} = 1.12$, $P > 0.05$).

Hourly mean T_e and hourly mean T_b varied through the day in both months at Playa de Tamarindo (Fig. 3), but the range of hourly mean T_b of both species was smaller than the range of hourly mean T_e . If lizards engage in behaviors that elevate T_b when T_e is low and reduce T_b when T_e is high (see above), one would expect the difference between hourly mean T_b and hourly mean T_e to be negatively correlated with hourly mean T_e (Huey et al. 1977). Although these variables were negatively associated in all four samples, the correlation was significant only for *cooki* ($r_s = -0.842$ in January and $r_s = -0.874$ in August, Bonferroni corrected $P's < 0.05$), the species that was active throughout the day.

In samples of *cristatellus* at both mesic sites (Hertz 1992) mean T_b was significantly higher than mean T_e in January and in August (Table 4, one-tailed z tests, Bonferroni corrected $P's < 0.05$). Elevation and month both exerted significant main effects on lizard mean T_b among the three sites (ANOVA; $F = 28.359$ for elevation, $F = 119.271$ for month, $P's < 0.0005$).

Discussion

Temperature regulation

My analysis of temperature regulation in *cooki* and *cristatellus* provides data on the mechanisms of regulation as well as their effects (Heath 1964; Huey et al. 1977). Although both species exhibited non-random hourly basking rates and reduced activity at mid-day, the data reveal a striking interspecific difference in the relationship between lizards' T_b and randomly sampled T_e (see Fig. 2). The more widespread and eurytopic species, *cristatellus*, experienced T_b 's at the low end of the range of achievable T_b 's in both January and August. In contrast, *cooki*'s T_b 's were more similar to the random sample of T_e in both months. These data collectively suggest that the thermal environment at Playa de Tamarindo is more hospitable for *cooki* than it is for *cristatellus*. A detailed analysis of the extent of temperature regulation in these species will appear elsewhere (Hertz et al. in prep).

The mechanisms of behavioral temperature regulation were also more apparent in *cristatellus* than in *cooki*. The former species' shade-seeking and limited activity during mid-day hours may minimize the risk of overheating in the desert. Mean T_e was above the preferred T_b of both species (approximately 30.0° C, Huey and Webster 1976) from 1000–1600 h in January and from 0900–1700 h in August (Fig. 2); however, my data don't clearly indicate the existence of a critically high mean T_e above which *cristatellus* necessarily seeks shelter. Indeed, avoiding heat stress is only one of several possible explanations for *cristatellus*'s mid-day retreat (Huey 1982):

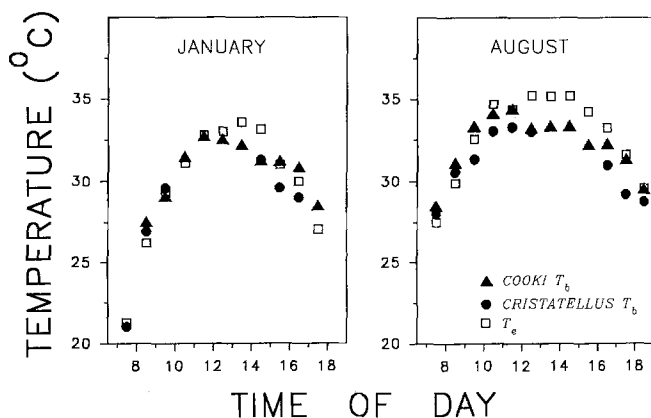


Fig. 3. Hourly mean T_b of *cooki* and *cristatellus* and hourly mean T_e at Playa de Tamarindo. Lizard sample sizes as in Fig. 1. Asterisk (*) indicates that hourly mean T_b of *cooki* was significantly higher than that of *cristatellus* (one-tailed t-tests, Bonferroni corrected $P < 0.05$)

they might limit activity after a period of successful feeding; prey may be less abundant or predators more abundant at these times; or the desert air might be too dehydrating at high T_e (Mautz 1982).

Body temperatures of sympatric anoles

In general, T_b 's of field active anoles are highly correlated with T_e 's at their perch sites ($r=0.982$, $N=35$, $P<0.001$; Hertz and Fleishman, in prep). Because *cooki* and *crisatellus* are of similar size and color, I assume that the T_b 's of both species would be equal if they perched in the same microsite. Hence, *cooki*'s higher mean T_b may have mirrored a difference in the two species' use of space and time (see Roughgarden et al. 1981, Tracy and Christian 1986, Dunham et al. 1989): *cooki* may have been active in warmer microsities than was *crisatellus*. However, analyses of perch sites, basking frequencies, and times of activity provide only equivocal support for that explanation.

Minor differences in the perch heights and perch diameters selected by these species do not explain differences in the T_e 's of the particular microsities that each used. The species reversed their relative perch heights seasonally, but the mean T_b of *cooki* was higher than that of *crisatellus* in both months. Differences in perch diameter certainly don't contribute to the difference in mean T_b : T_e generally increases with increasing perch diameter (Bakken 1989), but at Playa de Tamarindo *cooki* used narrower perches and had higher mean T_b . Indeed, T_e was only weakly related to perch height and perch diameter in the "trunk-ground structural habitat" (Hertz and Adolph, in prep); hence, perch site differences among species will not necessarily facilitate thermal resource partitioning.

Although the overall basking rates of the two species were not significantly different, *crisatellus* basked only infrequently at mid-day, whereas *cooki* was a more active mid-day basker, especially in January. This behavior undoubtedly contributed to *cooki*'s higher overall mean T_b , but it does not explain the apparent interspecific differences in hourly mean T_b at other times of day (Fig. 3).

Differences in times of activity probably also contributed to the interspecific difference in mean T_b , but they cannot fully account for it. Hourly mean T_b 's of *cooki* were at or near maximum levels during the hours when *crisatellus* was inactive. Nonetheless, during those hours when both species were active, the mean T_b of *cooki* was significantly higher than that of *crisatellus* in January ($30.0 \pm 0.4^\circ\text{C}$, $N=30$ for *cooki*; $27.3 \pm 0.9^\circ\text{C}$, $N=15$ for *crisatellus*; $t=2.69$, one-tailed, Bonferroni corrected $P<0.05$) and in August ($31.8 \pm 0.3^\circ\text{C}$, $N=50$ for *cooki* and $30.8 \pm 0.4^\circ\text{C}$, $N=25$ for *crisatellus*; $t=2.03$, one tailed, Bonferroni corrected $P<0.05$). T_e varied markedly through the day at Playa de Tamarindo, and the difference in activity times of the two species may represent incipient temporal and thermal resource partitioning. Additional research on the relationship of their activity

periods to their ecological interactions would be illuminating.

An alternative explanation for the interspecific difference in T_b is that the two species responded differently to microsities with similar thermal properties. Postural (see Muth 1977) and physiological adjustments (see Bartholomew 1982) by both species, thermoregulatory mechanisms that my research does not address, may have contributed to *cooki*'s higher mean T_b in the desert scrub forest at Playa de Tamarindo. However, these mechanisms have not been investigated in any natural population of anoles.

Partitioning the thermal environment

My data show clear differences in the T_b 's of *cooki* and *crisatellus*, and I can at least infer differences in their use of thermal microhabitats. However, because I have no data on allopatric desert populations of these two species, I do not know whether the microhabitat use of each species was constrained by the presence of the other (Schoener 1975). Hence, I cannot argue that interspecific differences in T_b reflect resource partitioning in response to competition rather than differences in microhabitat selection attributable to other causes. Some previous research has documented a shift in *cooki* microhabitat use that is caused by competitive interference from *crisatellus* (Jenssen et al. 1984).

The issue of thermal resource partitioning (Magnuson et al. 1979) or competition for microsities with favorable T_e (Roughgarden et al. 1981; Tracy and Christian 1986; Dunham et al. 1989) is complicated by the phenomenon of territoriality. Territorial lizards each defend a space so much larger than their own dimensions that each territory presents basking opportunities and T_e in a spatial and temporal mosaic (Huey et al. 1977; Roughgarden et al. 1981; Christian and Tracy 1985; Tracy and Christian 1986; Grant 1990; Huey 1991). The ease with which two species might partition these resources depends in part upon the "grain" of the resources in relation to the sizes of the territories held.

If thermal heterogeneity in a habitat is coarse-grained relative to territory size (i.e., low thermal variability among microsities within territories), thermal differences between nearby territories might be profound. Two or more species with different thermal requirements could partition habitats on the basis of T_e differences and experience relatively little spatial overlap. Indeed, Rand (1964) identified such a mechanism of partitioning when he described the distinct "climatic habitats" of different Puerto Rican anoles.

However, if the thermal heterogeneity in a habitat is fine-grained relative to territory size (i.e., high thermal variability among microsities within territories), different territories might offer roughly the same array of T_e . In this case, thermal resource partitioning would require syntopic lizards to experience a great deal of spatial overlap, either non-synchronously (Schoener 1970, 1977; Huey 1982) or by frequently moving into different sets of thermally distinct microsities within the ever-changing

T_e mosaic (Roughgarden et al. 1981). However, even if syntopic lizards used thermally distinct microsites and maintained somewhat different T_b 's, they would still be exposed to the same set of mobile prey items, predators, parasites, and refuges in the shared habitat. Hence, the occupation of thermally distinct microsites would probably not provide much ecological separation of potential competitors in a thermally fine-grained environment (Schoener 1977; Crowder and Magnuson 1983).

Ideally, one could document thermal resource partitioning with detailed maps of the available thermal environments and the ways in which lizards use those microenvironments (Waldschmidt and Tracy 1983; Tracy and Christian 1986; Grant and Dunham 1988, 1990; Grant 1990). The data would describe spatial and temporal variation in available T_e 's, the territorial boundaries of lizards, and the lizards' use of space and time (and, hence, T_e) within territories. One could then define the grain of thermal heterogeneity in relation to territory size and determine how these environments are partitioned. Such studies are needed to understand fully the ecological interactions of *cooki* and *crisatellus*.

Although I have no data on the "grain" of the thermal environment nor maps of lizard territories, my analysis suggests that individual *cooki* and *crisatellus* probably can't partition habitats on the basis of coarse-grained variations in T_e . The interspecific differences in mean T_b of *cooki* and *crisatellus* are no larger than the seasonal variations in mean T_b within species. In addition, both species respond very similarly to high temperature stress (Huey and Webster 1976). [Unfortunately, we have little data on the thermal sensitivity of physiological and performance functions (Huey 1982) in either of these species.] The thermal requirements of *cooki* and *crisatellus* therefore appear to be so similar (Huey and Webster 1976; Jenssen et al. 1984) that their occupation of distinct "climatic habitats" is very unlikely. Moreover, the low variance of mean T_e among models suggests that there is relatively little thermal heterogeneity among microsites at Playa de Tamarindo; hence, there is not much thermal habitat diversity to partition.

Given the similarities in their size, thermal requirements, and perch choices ("structural habitats" *sensu* Rand 1964), it is not surprising that *cooki* and *crisatellus* are interspecifically territorial (Ortiz and Jenssen 1982; Jenssen et al. 1984). Interspecific territoriality provides large scale spatial partitioning of all resources included within the territory boundaries; it therefore supersedes microhabitat partitioning on the basis of fine-grained variations in T_e . Having secured a territory with an acceptable mosaic of available T_e , an individual lizard fine tunes its T_b through microhabitat selection (and postural and physiological adjustments) within its territory (Tracy and Christian 1986). It is probably the sum of these adjustments, rather than large thermal differences between the territories occupied by the two species, that produce the interspecific difference in mean T_b that other workers and I have documented.

Ortiz and Jenssen (1982) found that *crisatellus* dominates in most aggressive encounters between the species,

and Jenssen et al. (1984) described habitat shifts in *cooki* that they attributed to competitive interference by *crisatellus*. These habitat shifts could be interpreted as evidence of coarse-grained habitat partitioning because the presence of *crisatellus* apparently forces *cooki* to perch on vegetation that it does not use where allopatric to *crisatellus*. If local populations of *crisatellus* are as well adapted to the desert environment as *cooki* (Huey and Webster 1976; Hillman and Gorman 1977; Jenssen et al. 1984), the latter species may have few, if any, refuges where it can exist in the absence of competition from its dominant congener. Whether or not these patches of habitat are sufficient to sustain *cooki* populations is presently unknown. However, *cooki*'s numerical predominance in my samples, its daylong activity, and the similarity of its T_b to the available T_e all suggest that *cooki* is physiologically better adapted to the habitat at Playa de Tamarindo than is *crisatellus*. Long-term census data will be needed to confirm Williams' (1972), Jenssen et al.'s (1984), and Marcellini et al.'s (1985) prediction of *cooki*'s impending extinction.

The similarity in the thermal biology of *cooki* and *crisatellus* is in marked contrast to the difference in thermal biology between *crisatellus* and *A. gundlachi*, a behaviorally and ecologically equivalent species that occupies the montane forests of Puerto Rico (Rand 1964; Huey and Webster 1976; Hillman and Gorman 1977; Hertz 1983, 1992). Where they co-occur, *crisatellus* and *gundlachi* occupy different coarse-grained thermal environments (Rand 1964; Schoener and Schoener 1971; Huey and Webster 1976; Hertz 1992).

Thermoregulatory versatility in crisatellus

My analysis, in combination with data in Hertz (1992), offers a comprehensive view of the field thermal biology of *crisatellus* over the range of habitats that it occupies in Puerto Rico. Previous studies of this species (Rand 1964; Heatwole et al. 1969; Huey 1974; Huey and Webster 1976; Hertz 1983) were based on data collected only during summer months and usually for only a few hours at any site. These new data confirm *crisatellus*'s thermoregulatory versatility (Huey 1974; Huey and Webster 1976; Hertz 1983) and its ability to compensate for variations in the thermal environment (Table 4).

This eurytopic species compensates for seasonal and altitudinal variations in the thermal environment by varying its times of activity and basking rates. Comparable altitudinal shifts in these behaviors have been noted in other anoles (Rand 1964; Ruibal and Philibosian 1970; Clark and Kroll 1974; Huey and Webster 1975, 1976; Hertz 1981; Hertz and Huey 1981) as well as in lizards of other genera (see Huey 1982 for review; Adolph 1990). Seasonal shifts in thermoregulatory activity have not been examined systematically in many other anoles, but they are known in other groups (Huey et al. 1977).

In my samples, *crisatellus* did not occupy progressively more open habitats with increasing elevation (see contradictory observations in Rand 1964; Schoener and

Schoener 1971; Huey and Webster 1976). However, the range of acceptable microhabitats is probably greatest at low elevation mesic sites where lizards can attain acceptable T_b whether or not they are able to bask (Huey 1974). At high elevation, *cratatellus* appears to be an obligate basker (Schoener and Schoener 1971; Huey and Webster 1976; Hertz 1992) and probably could not survive in deep forest (Licht and Gorman 1975; Gorman and Hillman 1977; Hertz 1992). Conversely, *cratatellus* probably couldn't survive in the desert habitats in southwestern Puerto Rico without ready access to shade because mean T_b 's frequently exceed tolerable levels (heat resistance data from Huey and Webster 1976).

As a result of its flexible thermoregulatory behaviors, *cratatellus* experienced a range of mean T_b (7.3°C) among sites and seasons that was much smaller than the range in mean T_b (13.8°C). In fact, mean T_b 's overlapped remarkably across sites and seasons. For example, the mean T_b in January at the desert site was virtually identical to the mean T_b in August at high elevation and exactly intermediate between the January and August means for the low elevation mesic site. These data suggest that *cratatellus* populations are unlikely to have evolved large site-specific thermal adaptations because their compensation for environmental variation is so effective (see Hertz 1981, 1983; Hertz and Huey 1981). Indeed, Huey and Webster's (1976) data on resistance adaptation of *cratatellus* from middle elevation rain forest and low elevation desert show minimal divergence of two out of three thermal resistance traits.

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