

THERMAL BIOLOGY OF A SOLITARY LIZARD: *ANOLIS MARMORATUS* OF GUADELOUPE, LESSER ANTILLES¹

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Abstract. To describe the thermal biology of *Anolis marmoratus*, a species living without congeners, we obtained 29 samples of air and body temperatures. Mean body temperatures (range 9.9°) differ from locality to locality, among habitats within localities, and during the day. Strong correlation of mean body with mean air temperatures among samples suggests that these lizards are routinely passive to ambient conditions. Indeed, short-term thermoregulatory behaviors such as basking and regulation of times of activity are rarely used by individuals in most populations. Nonetheless, evidence of habitat selection at one locality suggests that these anoles have long-term thermal preferences. The broad thermal niche of *A. marmoratus* seems primarily due to individual eurythermy rather than to populational differentiation. The general passivity of this and some other anoles may be an adaptation to life in tropical forests, where careful thermoregulation is disadvantageous.

Key words: *Anolis*; eurythermy; habitat selection; niche breadth; thermoregulation; tropics.

INTRODUCTION

The West Indian radiation of the iguanid lizard genus *Anolis* has produced faunas varying from 1 to more than 30 species per island. Anoles in complex faunas are thought to have relatively narrow niches resulting from ecological interactions among congeners; in contrast are the solitary species of *Anolis*, whose relatively broad niches are possibly the result of ecological release in the absence of congeners (Williams 1969, Ruibal and Philibosian 1970).

Our understanding of the thermal biology of solitary anoles is, however, based primarily on only two species (Ruibal and Philibosian 1970, 1974, McManus and Nellis 1973). Both *A. oculatus* on Dominica and *A. acutus* on St. Croix are generally passive to ambient conditions and apparently have broad thermal niches. Here we describe the thermal biology of another solitary anole, *Anolis marmoratus*, of Guadeloupe, Lesser Antilles. This species is widely distributed on Guadeloupe, an island with considerable diversity of topography, climate, and habitat (Stehle 1936, Beard 1949). *Anolis marmoratus* has differentiated into several very distinctive morphological races which geographically correspond with major habitat formations (Lazell 1964, 1972).

We address ourselves to three questions. First, does *A. marmoratus* have a broad thermal niche like other solitary anoles? Second, what are the associated behaviors? Third, what is the explanation of such a thermal biology?

Our data are from field observations on thermo-

regulatory behavior and on its immediate consequence, body temperature. We obtained a temporal and spatial series of samples to ascertain the ranges of both the thermal environments and the behavioral responses of this species. If individuals of *A. marmoratus* are passive, thermoregulatory behaviors should rarely be witnessed, the correlation of mean body and mean air temperatures should be strong, and the range of mean body temperatures should be large (Ruibal and Philibosian 1970). If individual lizards are eurythermal (i.e., have the ability to be active over a wide range of body temperatures), then the amount of variation in body temperature within a population should be a large proportion of the total for the species.

MATERIALS AND METHODS

During late July and early August 1971, we captured over 600 *A. marmoratus* from nine localities by hand or by noose with a minimum of pursuit and handling. For each lizard we recorded (1) body (cloacal) and air (shaded bulb, 1 cm above substrate) temperatures with a Schultheis thermometer, (2) sex, and (3) snout-to-vent length (SVL). For each sample the Appendix gives the subspecies studied, the locality and dates, and habitat descriptions.

The body temperature of a lizard is primarily influenced by radiation, wind, air temperature, and humidity (Porter and Gates 1969). Nonetheless, for simplicity we used shaded air temperatures as indicators of ambient heat loads for these predominantly shade-inhabiting anoles. For lizards in open habitats with complex thermal inputs, this approximation may underestimate ambient heat loads.

Since mean body temperatures (MBT's) of males

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TABLE 1. Body temperature and air temperature data for various populations of *Anolis marmoratus* on Guadeloupe, July 1971, including correlation coefficients ($r_{BT,AT}$) between body and air temperatures. Appendix gives subspecies, exact localities, habitats, dates, and times of samples

Locality and sample (Time)	N	Body temperature °C		Air temperature °C		$r_{BT,AT}$	MBT- MAT
		$\bar{x} \pm s_x$	Range	$\bar{x} \pm s_x$	Range		
1 (1200-1305 h)	44	29.92 ± .21	28.0-31.5	28.42 ± .12	27.0-29.8	.279	+1.50
2 (1415-1520)	44	31.21 ± .13	29.1-33.7	30.41 ± .08	29.4-32.0	.678**	+0.80
3a Shade trees (0940-1115)	32	28.21 ± .25	27.5-29.9	27.87 ± .08	27.1-28.7	.688**	+0.34
3b Palms (0940-1115)	24	29.21 ± .30	28.3-30.0	28.26 ± .12	26.8-29.5	.133	+0.95
3c Open bananas (1140-1235)	20	31.39 ± .24	29.7-35.0	29.63 ± .15	28.4-31.4	.537*	+1.76
3d Shade trees (1247-1310)	17	28.41 ± .10	27.4-28.9	27.98 ± .10	27.3-28.7	.367	+0.43
3e Shade trees (0550-0605)	10	26.18 ± .07	25.7-26.5	25.86 ± .09	25.1-26.1	.662*	+0.32
3f Palms (0605-0618)	10	26.04 ± .09	25.3-26.3	25.99 ± .08	25.7-26.5	.483	+0.05
3g Shade trees (0659-0714)	11	27.14 ± .11	26.6-27.8	26.92 ± .09	26.4-27.4	.827**	+0.22
3h Palms (0714-0730)	10	27.51 ± .22	26.9-29.1	26.83 ± .06	26.7-27.3	.450	+0.68
3i Shade trees (0805-0820)	11	27.44 ± .09	27.1-28.1	27.06 ± .11	26.6-27.9	.083	+0.38
3j Palms (0820-ca. 0835)	10	28.82 ± .39	27.4-31.0	28.16 ± .22	27.3-29.1	.899**	+0.66
3k Shade trees (1015-ca. 1030)	10	29.16 ± .23	28.5-30.7	28.44 ± .16	28.0-29.6	.708**	+0.72
3l Palms (ca. 1030-1100)	11	32.12 ± .18	30.6-32.7	30.17 ± .21	28.5-30.8	.798**	+1.95
3m Shade bananas (1130-1210)	11	30.68 ± .09	30.2-31.2	29.71 ± .13	29.3-30.8	.245	+0.97
3n Open bananas (1130-1210)	15	32.67 ± .16	31.9-33.9	31.10 ± .15	30.5-32.3	.260	+1.57
3o Shade trees (1215-1230)	10	29.91 ± .12	29.3-30.4	29.15 ± .18	28.4-29.7	.198	+0.76
3p Palms (1228-1245)	11	31.15 ± .21	30.4-32.4	29.86 ± .18	29.0-31.2	.111	+1.29
3q Shade trees (1405-1420)	9	29.73 ± .38	29.0-32.5	29.08 ± .14	28.6-30.0	.820**	+0.65
3r Palms (1420-1439)	11	30.74 ± .22	29.4-31.5	29.36 ± .16	28.6-30.3	.696*	+1.38
3s Shade trees (1600-1617)	12	28.04 ± .19	27.5-29.8	27.66 ± .14	27.3-29.1	.898**	+0.38
3t Palms (1617-1630)	13	28.72 ± .15	28.2-29.8	27.74 ± .12	27.3-28.6	.810**	+0.98
4a Road edge (1519-1730)	22	30.48 ± .29	26.6-32.8	22.87 ± .20	21.4-24.4	.155	+7.61
4b Forest (1519-1730)	11	22.73 ± .14	21.9-23.5	22.13 ± .18	21.2-23.0	.743**	+0.60
5 (1055-1155)	44	31.48 ± .15	30.0-34.1	30.45 ± .09	29.4-31.7	.703**	+1.03
6 (0950-1115)	48	30.96 ± .18	29.1-35.4	30.03 ± .13	28.1-32.1	.668**	+0.93
7 (1545-1633)	44	28.32 ± .07	27.4-29.6	28.08 ± .06	27.0-28.7	.486**	+0.24
8 (1655-1745)	52	29.68 ± .15	27.9-32.0	28.49 ± .07	27.4-29.6	.240	+1.19
9 (1520-ca. 1630)	44	31.15 ± .09	30.0-33.2	29.50 ± .13	26.3-31.2	.252	+1.65
Summary statistics	638	29.75 ± .08	21.9-35.4	28.50 ± .08	21.2-32.3	.894 ^a	+1.10

^a Rank correlation of means; see text.

* Significant at 0.05 level.

** Significant at 0.01 level.

and females did not differ significantly within any sample (t -tests, P 's > .05), we pooled BT's of males and females for this analysis. We used Pearson product-moment (r) tests for correlations of individual temperature records, nonparametric Spearman rank (r_s) tests for correlations of means or variances, t -tests for paired comparisons, Student-Newman-Keuls tests for comparisons among several means, and Kolmogorov-Smirnov tests for comparisons of SVL distributions. Our minimum criterion for statistical significance is a probability of 0.05.

Although we sampled with replacement in our all-day study at Locality 3, we ignored possible effects of recapture on statistical analyses. It is unlikely that any lizard was recaptured in the open-banana or shaded-banana plant habitats (hereafter open or shaded bananas) as the former habitat was very extensive and the latter was sampled only once. We also believe that few lizards in the open-palm and shade-tree habitats were recaptured because of high densities of lizards, because no tree was visited more than a few times, and because lizards are often more evasive after initial capture.

RESULTS

In our survey of the thermal biology of *A. marmoratus*, we gathered 29 samples representing nine localities (Appendix). The mean body temperature (MBT) of all 638 lizards collected is $29.75 \pm 0.08^\circ$ with a corresponding mean air temperature (MAT) of $28.50 \pm 0.08^\circ$ (Table 1).

Populations from a wide variety of thermal environments contribute to these results. For all samples the range of MAT's is 9.0° , and the range of MBT's is 9.9° (Table 1). MBT's are strongly correlated with MAT's ($r_s = .894$, $P < .01$) and differ from them by an average of only $+1.1^\circ$. In 16 of 29 samples, BT is significantly correlated with AT (Table 1, P 's < .05). Among samples variance in BT is correlated with variance in AT ($r_s = .741$, $P < .01$). These data suggest that *A. marmoratus* passively tolerates broad ranges of air and body temperatures without conspicuous thermoregulation. However, basking was observed occasionally, and habitat discrimination at a lowland locality suggests that these lizards do have a thermal preference despite being generally passive.

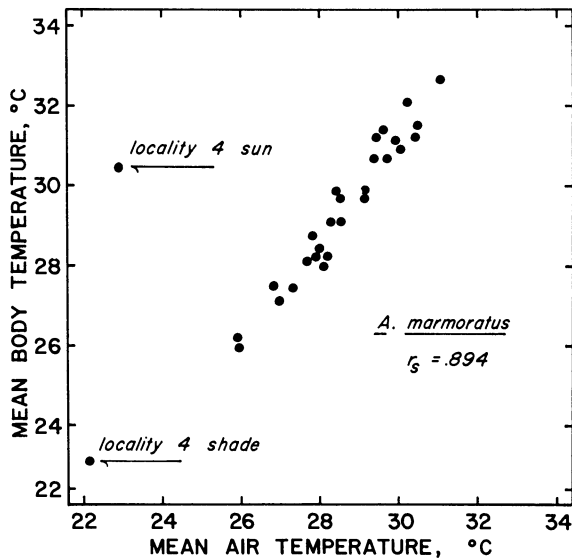


FIG. 1. Mean body temperature vs. mean air temperature of 29 samples of *Anolis marmoratus* on Guadeloupe, Lesser Antilles.

A montane population (A. marmoratus near alliaceus)

At our montane forest locality, lizards on exposed, sunny perches (along a road edge) had a MBT 7.7° higher than lizards on deeply shaded perches (usually on trees within the forest), even though MAT's differed by only 0.6° (samples 4a and 4b of Table 1, Fig. 1). Because shade was readily available to all exposed lizards along the road edge, they were showing a preference for high BT's. Activity was not, however, dependent on elevated body temperatures. For example, we observed an adult male in the forest with a BT of 21.7° feeding (AT = 21.4°) and a second male feeding and headbobbing (AT = 21.5°).

Thermal habitats at a lowland locality (A. m. marmoratus)

At Locality 3 we sampled three contiguous vegetational habitats: shade trees, palms, and open bananas. MAT's differed significantly among the habitats (Table 1, samples 3a to 3c; P 's < .01) and had a range of 1.8°. The lowest MAT was in the shade trees, and the highest was in the open bananas. Since samples 3a (shade trees) and 3b (palms) were taken simultaneously (Appendix), differences between MAT's of these habitats were determined by vegetation, not time of day. MAT's of two shade-tree samples (3a and an early afternoon sample, 3d) did not differ significantly ($P > .40$).

MBT's of lizards differed significantly among these habitats (P 's < .01) and had a range of 3.8°. MBT's were identically ranked with MAT's: lizards were coolest in the shade trees and hottest in the open

TABLE 2. Kolmogorov-Smirnov one-tail tests for differences in SVL (Fig. 3) among *A. m. marmoratus* ♂♂ and ♀♀ in different habitats at Locality 3. Habitat with larger individuals listed first

Paired comparison	♂♂		♀♀	
	χ^2	P	χ^2	P
Palms vs. shade trees	21.7	< .001	1.9	> .15
Palms vs. open bananas	37.4	< .001	13.5	< .001
Palms vs. shade bananas	3.5	> .05	3.5	> .05
Shade trees vs. open bananas	15.3	< .001	11.1	< .001
Shade bananas vs. shade trees	1.9	> .15	2.5	> .10
Shade bananas vs. open bananas	5.9	< .05	3.5	> .05

bananas. MBT's of the two shade-tree samples did not differ significantly (3a and 3d, $P > .50$). All lizards collected were on shaded perches, and BT's were significantly correlated with AT's in two of the samples (Table 1). These observations indicate that differences in body temperature of lizards among habitats are a consequence of behavioral passivity in thermally distinct environments.

A few days later we resampled these habitats (Table 1, samples 3n to 3p) and confirmed the previous pattern (differences among MAT's and among MBT's were significant, P 's < .02). Again MAT and MBT were highest in the open bananas and lowest in the shade trees. In addition, lizards collected on the few shaded bananas (sample 3m, Appendix) had BT's and associated AT's significantly cooler than those of lizards in the adjacent open bananas (P 's < .001) and intermediate between those of lizards in the shade trees and palms.

At a locality where habitats vary in quality, one would expect the most socially dominant individuals to occur in the most desirable situations. Body size, an indicator of social dominance (Rand 1967), should thus vary directly with quality of habitat. Sex ratios should be biased toward females in preferred habitats, both because females have generally smaller territories than males (Rand 1967, Jenssen 1970, Stamps 1973) and because males should exclude only other males from their territories. Hence

TABLE 3. χ^2 -tests for differences in sex ratios of *A. m. marmoratus* between habitats at Locality 3 (see Fig. 3). Habitat with fewer ♂♂ listed first

Paired comparisons	χ^2	P
Palms vs. shade trees	6.1	< .02
Palms vs. open bananas	15.6	< .001
Palms vs. shade bananas	0.2×10^{-3}	> .98
Shade trees vs. open bananas	26.4	< .001
Shade bananas vs. shade trees	1.1	> .20
Shade bananas vs. open bananas	5.3	< .025

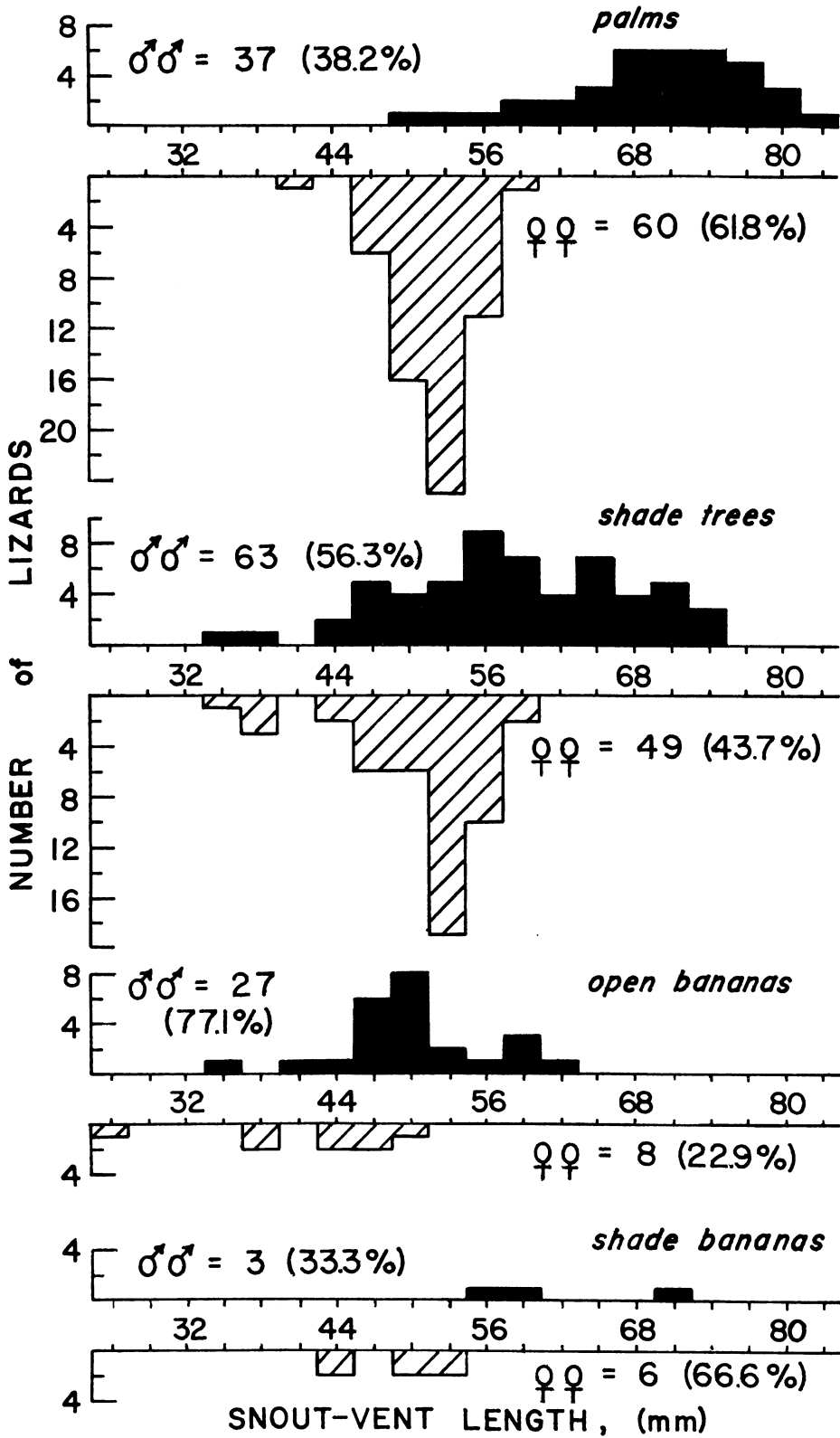


FIG. 2. Histograms of SVL for *A. marmoratus* ♂♂ and ♀♀ in four habitats at Locality 3. Sample sizes and sex percentages included for each habitat.

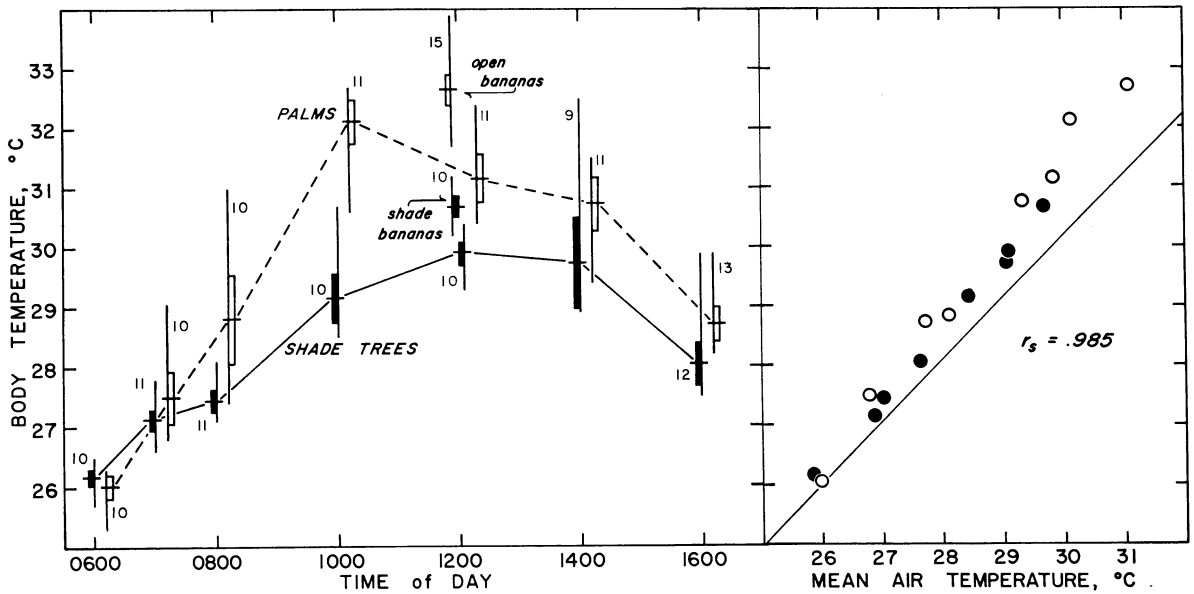


FIG. 3. For several habitats at Locality 3, mean body temperatures vs. time of day (left) and vs. mean air temperatures (right), as obtained in a 1-day census. Vertical lines represent ranges, horizontal lines represent means, boxes represent ± 1 SE, and associated numbers are the sample sizes. Circles are records from seven palm and one open-banana samples; dots represent seven shade-tree and one shade-banana samples.

we use male size, female size, and sex ratio as indirect evidence of habitat preferences at Locality 3 (Fig. 2, Tables 2 and 3).

In the palms, males (but not females) are significantly larger than in the other two major habitats, and females are proportionately more common. Males and females on shade trees are larger than those on open bananas, and females are more common. Thus, palms seem to be the most favored of the three major habitats, shade trees are of intermediate desirability, and lizards would prefer to be almost anywhere else than in the open bananas.

A possible basis for this habitat discrimination is the intermediate thermal environment of the palms (i.e., on the average, anoles find them neither too cool nor too warm). If this explanation is valid, one would expect lizards in the shaded bananas to be more similar in SVL and sex ratio to lizards in the palms and shade trees than to lizards in the open bananas. This trend is evident (Fig. 3): indeed, sex ratios and male SVL's for lizards in shaded bananas differ significantly from those of lizards in open bananas (Tables 2 and 3).

The consistency of these patterns suggests that palms are favored because of an intermediate thermal regime. However, sizes or abundance of prey might also influence habitat preference. Physical structure of habitat is an unlikely basis for discrimination as shaded bananas attracted larger and proportionally fewer males than did open bananas. Also, if there are ontogenetic changes in thermal preferences, they

are not monotonic: at least some of these lizards may shift from hot (bananas) to cool (shade trees) to intermediate (palms) habitats during their lifetimes.

Diurnal variability at a lowland locality

To determine the extent of diurnal variation in BT of *A. marmoratus* in two of the habitats at Locality 3, we censused lizards in the shade trees and palms during a full day (Table 1, samples 3e to 3l and 3o to 3t; Fig. 3). For these samples MBT's are strongly correlated with MAT's (Fig. 3, $r_s = .982$, $P < .01$). BT is correlated with AT in 9 of 14 samples.

Except for the first two morning censuses, MAT's and MBT's were significantly higher ($P < .05$) in the palms than in the shade trees. MAT's had 3.3° and 4.2° ranges during the day in the shade tree and palm habitats, respectively; MBT's had corresponding 3.7° and 6.1° ranges. Both AT's and BT's were significantly less variable in the shade trees than in the palms (*F*-tests, P 's $< .025$). If thermal conditions are primarily responsible for the discrimination between these two habitats, then the relatively constant thermal regime of the shade trees appears less desirable than the more variable, but warmer, regime of the palms as discussed in the previous section.

Although habitat selection may be influenced by thermal conditions and thus represent long-term thermoregulatory behavior, lizards appear to be tolerant of and passive to a broad range of ambient

temperatures within habitats during the day. (Some lizards were on sunny perches and presumably basking in the palms during the 0820 census, yet the MBT of this sample was not noticeably elevated (Table 1, sample 3j).) At all times and in all habitats, individuals were feeding or interacting socially. Therefore, behavioral tolerance limits were not reached despite the broad range of temperatures experienced.

DISCUSSION

Thermoregulation is generally considered adaptive in enabling lizards both to avoid hazardous temperatures and to achieve some control over metabolic processes (Cowles and Bogert 1944). Many lizards carefully regulate body temperature within narrow ranges by coordinated behavioral (Heath 1965) and physiological adjustments (Templeton 1970). Solitary *Anolis* lizards, however, are seemingly eurythermal and passive to many environmental conditions. The evidence comes not only from *A. marmoratus* but also from *A. oculatus* (Ruibal and Philibosian 1970) and to a lesser extent from *A. acutus* (McManus and Nellis 1973, Ruibal and Philibosian 1974). After elaborating on characteristics of the thermal biology of solitary anoles, we evaluate alternative explanations for the evolution of eurythermy and passivity.

Species niche breadth

As a species *A. marmoratus* occurs in a broad range of habitats (Lazell 1964, 1972) and is active at a wide range of temperatures (MBT range = 9.9°). In a complex fauna this range of habitats would be shared by several species differing principally in climatic preference (Williams 1969). *Anolis oculatus*, a close relative of *A. marmoratus*, also occupies a variety of habitats and has an observed 7.3° range in MBT's (Ruibal and Philibosian 1970). Though less well studied, *A. acutus* on St. Croix similarly appears to have a broad species niche (McManus and Nellis 1973, Ruibal and Philibosian 1974).

Using the range of MBT's to index thermal niche breadth of a species, Ruibal and Philibosian (1970) contrasted *A. oculatus* with five of the Cuban species (maximum MBT range = 3.0°, *A. sagrei*, Ruibal 1961) to document that this solitary anole is broad niched relative to anoles in complex faunas. Our data on the solitary *A. marmoratus* and the limited data on *A. acutus* (McManus and Nellis 1973, Ruibal and Philibosian 1974) support the generalization that solitary anoles are broad niched. However, we need comparable data for more species to verify narrow thermal niches of anoles in complex faunas, particularly since *A. cristatellus* in the complex Puerto Rican fauna is broad niched (Huey 1974b).

While the ranges of MBT's of these solitary anoles seem large, lack of similar data precludes comparisons with other groups of lizards. However, variances of body temperatures of these anoles, another possible index of thermal niche breadth, are in fact smaller than those of many desert lizards from North America and Australia (Pianka and Pianka 1970). Such comparisons may well be invalid since variance in body temperature can be influenced by the heterogeneity of thermal environments sampled (Soulé 1963, this report) and since the thermal regimes in temperate zone deserts are far more variable than those on tropical islands.

Components of broad species niches

The broad thermal niche of a species may be due to individual eurythermy and/or to populational differentiation. In determining the contribution of individuals to the observed broad range of a species, we have assumed that intrapopulational differentiation, even though suspected in lizards (Stebbins 1961), is relatively unimportant. (Habitat discrimination at Locality 3 supports this assumption: were phenotypic differentiation a major component of the niche breadth of the population, the observed correlations of size class and sex ratio with habitat would not occur). Thus, if the range of temperatures tolerated within populations is large relative to the total range for the species, then individual eurythermy is the major contributor to the niche width of the species. Conversely, if the range is small, then populational differentiation is predominant.

Broad habitat and thermal tolerances within a population apparently exist at Locality 3, our most intensively studied locality. MBT's differed by as much as 3.2° for lizards in adjacent habitats at similar times and as much as 6.1° within one habitat during a day. We found an even more extreme range at Locality 4, where MBT's of lizards on exposed and on shaded perches differed by 7.7°. Because the observed range of MBT's within a population accounted for as much as 80% of the total range observed for the species, we infer that individual niche width is large and that eurythermy makes the dominant contribution to the overall niche breadth of *A. marmoratus*.

At single localities on Dominica, individual *A. oculatus* are found in diverse structural and thermal habitats, and populations show a corresponding broad range in MBT's. Thus individual *A. oculatus* also seem eurythermal (Ruibal and Philibosian 1970).

The differentiation of *A. marmoratus* and *A. oculatus* into distinctive races (Lazell 1972) suggests that populational differentiation could also contribute to the overall niche breadths of these species. The

montane *A. m. alliaceus* and *A. o. montanus* undoubtedly experience lower average body temperatures than the other races, particularly the arid coastal forms (*A. m. girafus* and *A. o. cabritensis*). Nonetheless, morphological variation and differences in ambient conditions do not necessarily imply physiological variation and adaptation (Brown and Feldmeth 1971). Indeed, color patterns of some races of these anoles seem related to camouflage (Lazell 1972). Additional field work supplemented by laboratory studies of physiological tolerance limits and thermal preferences would be relevant.

Behavioral correlates

Since many lizards thermoregulate behaviorally by shuttling between sun and shade (Cowles and Bogert 1944), by modifying posture (Heath 1965), and by regulating activity to times of suitable conditions (Heatwole et al. 1969), the behaviors associated with eurythermy are of interest. *Anolis marmoratus*, *A. oculatus*, and *A. acutus* infrequently thermoregulate. At least *A. marmoratus* and *A. acutus* (Ruibal and Philibosian 1974) are active from sunrise to sunset and therefore do not limit activity times. Additionally, since all three species normally occur on fully shaded perches, they do not shuttle or use postural adjustments. Ruibal and Philibosian (1970) observed basking of *A. oculatus* only at their coldest study area. We observed basking on only three occasions: at Locality 4 in the mountains, at Locality 8 late in the afternoon, and at Locality 3 early in the morning. In general, however, all three solitary anoles are passive to a broad range of ambient conditions.

Evolutionary aspects of eurythermy

Ruibal and Philibosian (1970) suggested that ecological release in the absence of congeneric competition might be responsible for eurythermy in solitary species. However, information on the source population is required to document ecological release (Grant 1972). The extent of eurythermy in ancestral populations cannot be determined. Hence, as noted by Ruibal and Philibosian (1970), the present eurythermy of these solitary species is not evidence for ecological release.

A. S. Rand (*unpubl. data*) argued that social factors might influence the development of eurythermy. At Rosalie on Dominica (Ruibal and Philibosian 1970 give thermal data at this locality), Rand found significantly larger males (*t*-test, $P < .05$) in the deeply shaded and cool windbreak ($N = 15$, $\bar{X} = 75.7 \pm 1.16$ mm) than in the warmer and more open coconut groves ($N = 12$, $\bar{X} = 71.7 \pm 1.59$ mm). However, sex ratio does not differ between habitats

($P > .30$). Rand argued that habitat discrimination at Rosalie is expressed by social dominance. Since an anole may inhabit several thermal environments during its life, a broad thermal niche will be adaptive. Habitat spread can help explain the occurrence of eurythermy in these anoles.

For an alternative but nonexclusive hypothesis to ecological release and habitat spread, we suggest that eurythermy is a general characteristic of *Anolis* related to its origin in moist tropical forests (Williams 1969). For a lizard living below a closed-forest canopy, passivity to ambient conditions (= thermoconformity) is the optimal strategy; active thermoregulation is impractical because lizards would, for example, expend too much time and energy attempting to reach distant basking sites (Huey 1974b). Eurythermal lizards with low thermal optima will have greater average energy gains than stenothermal individuals with high thermal optima (Huey 1974a, Huey and Slatkin, 1975). Anoles may have therefore coevolved passivity (Ruibal 1961, Rand and Humphrey 1968, Hertz 1974), low activity temperatures (Ruibal 1961, Brooks 1968, Fitch 1972, Clark and Kroll 1974; also Brattstrom 1965), and eurythermy (Ballinger et al. 1970, Jenssen 1970, Ruibal and Philibosian 1970) as a strategy appropriate to life in tropical forests. We suspect that active thermoregulation, relatively high thermal optima, and stenothermy are derived conditions in *Anolis*, advantageous only for those species that inhabit arid, open-forest, or canopy habitats. Those anoles that routinely thermoregulate and have high body temperatures live in such habitats (Ruibal 1961, Rand 1964, Heatwole et al. 1969, Ballinger et al. 1970, Jenssen 1970, Clark and Kroll 1974, Huey 1974b).

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LITERATURE CITED

- Ballinger, R. E., K. R. Marion, and O. J. Sexton. 1970. Thermal ecology of the lizard, *Anolis limifrons*, with comparative notes on three additional Panamanian anoles. *Ecology* 51:246-254.
- Beard, J. S. 1949. The natural vegetation of the windward and leeward islands. Oxford, Clarendon Press. 192 p.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73:376-422.
- Brooks, G. R. 1968. Body temperatures of three lizards from Dominica, West Indies. *Herpetologica* 24:209-214.

- Brown, J. H., and C. R. Feldmeth. 1971. Evolution in constant and fluctuating environments: Thermal tolerances of desert pupfish (*Cyprinodon*). *Evolution* **25**:390-398.
- Clark, D. R., Jr., and J. C. Kroll. 1974. Thermal ecology of anoline lizards: Temperate versus tropical strategies. *Southwest. Nat.* **19**:9-19.
- Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**:261-296.
- Fitch, H. S. 1972. Ecology of *Anolis tropidolepis* in Costa Rican cloud forest. *Herpetologica* **28**:10-21.
- Grant, P. R. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* **4**:39-68.
- Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. *Univ. Calif. Publ. Zool.* **64**:97-136.
- Heatwole, H., T.-H. Lín, E. Villalón, A. Muñiz, and A. Matta. 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. *J. Herpetol.* **3**:65-77.
- Hertz, P. E. 1974. Thermal passivity of a tropical forest lizard, *Anolis polylepsis*. *J. Herpetol.* **8**:323-327.
- Huey, R. B. 1974a. Winter thermal ecology of the iguanid lizard *Tropidurus peruvianus*. *Copeia* 1974: 149-155.
- . 1974b. Behavioral thermoregulation in lizards: Importance of associated costs. *Science* **184**:1001-1003.
- Huey, R. B., and M. Slatkin. 1975. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* (*in press*).
- Jenssen, T. A. 1970. The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). *J. Herpetol.* **4**:1-38.
- Lazell, J. D., Jr. 1964. The anoles (Sauria: Iguanidae) of the Guadeloupean archipelago. *Bull. Mus. Comp. Zool.* **131**:359-401.
- . 1972. The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull. Mus. Comp. Zool.* **143**:1-115.
- McManus, J. J., and D. W. Nellis. 1973. Temperature and metabolism of a tropical lizard, *Anolis acutus*. *Comp. Biochem. Physiol.* **45A**:403-410.
- Pianka, E. R., and H. D. Pianka. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. *Copeia* 1970:90-103.
- Porter, W. P., and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**:227-244.
- Rand, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* **45**:745-752.
- . 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proc. U.S. Nat. Mus.* **122**:1-79.
- Rand, A. S., and S. S. Humphrey. 1968. Interspecific competition in the tropical rain forest: Ecological distribution among lizards at Belém, Pará. *Proc. U.S. Nat. Mus.* **125**:1-17.
- Ruibal, R. 1961. Thermal relations of five species of tropical lizards. *Evolution* **15**:98-111.
- Ruibal, R., and R. Philibosian. 1970. Eurythermy and niche expansion in lizards. *Copeia* 1970:645-653.
- Ruibal, R., and R. Philibosian. 1974. The population ecology of the lizard *Anolis acutus*. *Ecology* **55**:525-537.
- Soulé, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. *Copeia* 1963: 107-115.
- Stamps, J. A. 1973. Display and social organization in female *Anolis aeneus*. *Copeia* 1973:264-272.
- Stebbins, R. C. 1961. Body temperature studies in South African lizards. *Koedoe* **4**:54-67.
- Stehle, H. 1936. Flore de la Guadeloupe et dépendances, I: Essai d'écologie et de géographie botanique. Basse Terre, Government Printer. xiv + 286 p.
- Templeton, J. R. 1970. Reptiles, p. 167-221. *In* G. C. Whitton [ed.] *Comparative physiology of thermoregulation*, Vol. 1. Academic Press, New York.
- Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* **44**:345-389.

APPENDIX

Locality 1.—*A. marmoratus* (*marmoratus* × *alliaceus* × *girafus* intergrades). 2 km E Dole, on south coast Basse Terre, Guadeloupe. A banana plantation, with lizards taken on bananas, coconuts, and shade trees. 22 July 1971.

Locality 2.—*A. marmoratus girafus*. Baillif (1 km W town of Basse Terre), Basse Terre, Guadeloupe. Lizards on grounds of restaurant fronting the shore and on immediately adjacent trees. 22 July 1971.

Locality 3.—*A. marmoratus marmoratus*. 3.6 km SW Capesterre, Basse Terre, Guadeloupe. A large banana plantation with rows of young coconut palms lining the road, a few clumps of large shade trees (mangoes and *Tabebuia*), and extensive bananas. These three vegetation types represent three habitat samples. 26 and 31 July 1971.

Locality 4.—*A. marmoratus* near *alliaceus*. Midway between St. Claude and La Soufriere (elev. ca. 750 m), Basse Terre, Guadeloupe. Lizards collected along road edge and in forest. Forest is mix of primary montane rain forest and secondary forest. Very large trees (*Sloanea* and *Dacryodes*) provide deep shade. There is a deep shrub layer beneath the canopy. 26 July and 1 August 1971.

Locality 5.—*A. marmoratus girafus*. North edge village of Malendure, west coast Basse Terre, Guadeloupe. Lizards collected from coconuts, shade trees, sea grape, and other vegetation adjacent to beach. 27 July 1971.

Locality 6.—*A. marmoratus setosus*. Plage de Amandiers, W. of St. Rose along beach, Basse Terre, Guadeloupe. Lizards taken from palms, coconuts, and shade trees adjacent to beach. 28 July 1971.

Locality 7.—*A. marmoratus speciosus* × *setosus* intergrades, ?). Bis, W of La Boucan (off route N 2), Basse Terre, Guadeloupe. Vegetation included bananas, cocoa, and coffee with some large shade trees. 28 July 1971.

Locality 8.—*A. marmoratus speciosus*. Baie Mahault, Basse Terre, Guadeloupe. Scattered large shade trees, coconuts, and logs with little understory. An open lot. 28 July 1971.

Locality 9.—*A. marmoratus girafus*. Plage de Rocroy, E of Vieux Habitants, Basse Terre, Guadeloupe. Lizards taken from *Acacia* trees, palms, and rocks. An open habitat. 29 July 1971.