

THERMAL BIOLOGY OF *ANOLIS* LIZARDS IN A COMPLEX FAUNA: THE *CRISTATELLUS* GROUP ON PUERTO RICO¹

RAYMOND B. HUEY² AND T. PRESTON WEBSTER³

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 USA

Abstract. To describe the thermal biology of the three trunk-ground species of the *Anolis cristatellus* group on Puerto Rico, an island with 10 species of *Anolis*, we obtained samples of air and body temperatures of *A. gundlachi* (shady perches, montane forests), *A. cristatellus* (shady or sunny perches in open or closed forests, lowlands to mid-elevations), and *A. cooki* (sunny perches in open, xeric lowlands). Average body temperatures parallel altitudinal and habitat association (lowest for *A. gundlachi*, highest for *A. cooki*). Within a species, body temperatures are strongly correlated with air temperatures and thus vary with altitude, time of day, habitat, and weather. Observed differences between sympatric species in body temperatures and habitats probably reflect physiological requirements, but may be magnified by competition. Relative thermal niche breadth of individuals of these species is approximated and compared with data on species from simple anole faunas to evaluate hypotheses on the evolution of thermal niche breadth.

Extent of basking behavior is inversely related to associated costs for these species. In closed forests where costs of raising body temperatures are high, *A. gundlachi* and *A. cristatellus* rarely bask and seemingly are routinely passive to ambient conditions. In open habitats where costs are low, *A. cristatellus* and *A. cooki* frequently bask.

Key words: *Anolis*; competition; lizard; thermal evolution; thermoregulation; Puerto Rico.

INTRODUCTION

Some lizards behaviorally and physiologically regulate body temperatures (Templeton 1970), and the resultant control over metabolic processes is assumed to be adaptive (Cowles and Bogert 1944). Nonetheless, by reducing the amount of time available for certain activities, excessive thermoregulation can lower fitness (Soulé 1963, Heatwole 1966, DeWitt 1967). Furthermore, in habitats where other costs (e.g., energy expenditure in shuttling between sun and shade) inevitably associated with thermoregulation are excessive, careful thermoregulation may be uneconomical or risky (Pianka 1965, Pianka and Pianka 1970, Pianka and Parker 1975). Thus, the extent of thermoregulation may vary inversely with associated costs (Huey 1974a, b, Huey and Webster 1975, Huey and Slatkin 1976).

Here we examine the extent of thermoregulation relative to associated costs in three lizards of the *Anolis cristatellus* group on Puerto Rico, an island with a complex *Anolis* fauna (10 species). Additionally, we consider interspecific differences in thermal biology, the magnitude of intraspecific variation in body temperature, and the relative effect of environmental factors (e.g., altitude, habitat, competition) on that variation. We then compare the relative thermal niche breadth of individuals in this complex fauna with those of previously studied

anoles in simple faunas to evaluate certain hypotheses on the evolution of thermal niche breadth (Ruibal and Philibosian 1970, Huey and Webster 1975).

The three trunk-ground species of the *cristatellus* group are abundant and conspicuous. They are similar in size (Schoener 1970a), habitus (Williams 1972), and structural niche (Rand 1964, Schoener and Schoener 1971). They differ, however, in altitudinal and habitat associations [*A. gundlachi* occurs generally in shaded mountain forests; *A. cristatellus* is widely distributed from sea level to mid-elevation in forest or open habitats (or both) depending on altitude; and *A. cooki* is restricted to xeric lowlands of southwestern Puerto Rico: Williams 1972] and body temperatures (Rand 1964, Heatwole et al. 1969, Lister 1974). Differences in body temperatures and habitat associations between sympatric pairs mirror these overall species differences (Rand 1964, Turner and Gist 1970, Schoener and Schoener 1971, Williams 1972, Lister 1974). The abundance of these lizards and their occurrence in a wide variety of habitats makes them ideal subjects for studies of thermal biology and for comparisons with other anole species. The wealth of background information on these species is, of course, an added attraction.

MATERIALS AND METHODS

During early July 1972, we captured by hand or by noose, 248 *A. gundlachi* from six localities, 387 *A. cristatellus* from seven localities, and 306 *A. cooki* from five localities. For each lizard, we recorded body (cloacal) and air (shaded bulb, 1 cm above substrate) temperatures with a Schultheis thermom-

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² Present address: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.

³ Deceased 10 November 1975.

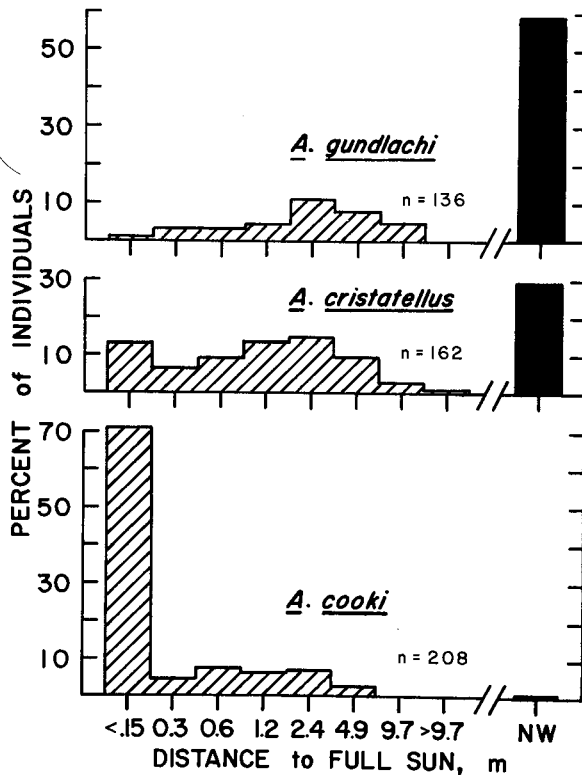


FIG. 1. Histograms of cost to raise body temperatures as indexed by distance from an anole perched in partial sun or shade to the nearest patch of full sun and by the frequency of individuals unable to reach full sun (NW). See Materials and Methods.

eter; sex; snout-to-vent length (SVL); time; perch height and diameter; whether the lizard was perched in full sun, partial sun, or shade (if sunny); and an index of the cost to thermoregulate (below). The locality and elevation of each sample are given in the Appendix. Additionally, we include data on 101 *A. cristatellus* and 65 *A. cooki* obtained between 21 and 25 July 1969 by T. P. Webster, A. Schoener, T. W. Schoener, and E. E. Williams at several localities east of Playa Caña Gorda (hereafter, 1969 data).

For a crude index of both the cost of raising body temperature (BT) by shuttling between sun and shade and the degree of shading in habitats, we measured the shortest transit distance from an anole to a patch of full sun on a contiguous perch and included a category "no way" (NW), indicating that the tree or shrub was completely shaded (Huey 1974b). Generally, this distance will be greater in more shaded habitats, and lizards would thus necessarily expend more time and energy in shuttling between sun and shade.

Anoles used in thermal gradient studies were acclimated for ≈ 24 h in an air-conditioned laboratory (20°C) with overhead fluorescent lighting (10L:14D). Then lizards were placed individually in

2×0.2 m thermal gradients with an electric radiant heater at one end. (Body temperatures of tethered lizards at the ends of the gradient ranged from about 21°C to well above lethal limits.) The following day thermistors were implanted into their intestines at 0800 h. After 30 min, preferred body temperatures (Licht et al. 1966) were recorded at 5-min intervals until samples of 50 temperatures were obtained for each lizard. The mean of each lizard was used to calculate the preferred body temperature (PBT) for a population.

Other lizards (acclimated to 20°C for ≈ 30 h) were used in determinations of experimental voluntary maximum (EVM) and critical thermal maximum (CTM) temperatures (see below). Anoles were placed in a 0.2 m diameter container and heated rapidly (1.5 to 2°C/min) with an overhead infrared bulb. The EVM was the body temperature (measured with the thermistor) at which the anole first jumped during heating (Ruibal 1961, Ballinger et al. 1970). The CTM was the temperature at loss of righting response (Brattstrom 1971). PBT were determined in the morning; EVM and CTM were measured in the late afternoon.

Unless noted, we used nonparametric Spearman rank (r_s) tests for correlations of means of variances, G -tests for $R \times C$ tests of independence (using STP analysis), t -tests for paired comparisons, and Student-Newman-Keul's tests for comparisons among means (Sokal and Rohlf 1969).

RESULTS

Overall species results

The three anoles of the *cristatellus* group differ significantly (Fig. 1) in the percentage of lizards unable to reach full sun without changing trees (NW, $p < .001$) and the distance to full sun for the remainder (Kolmogorov-Smirnov tests, $p < .01$). The predominantly closed-forest associations of *A. gundlachi* are reflected by the high percentage of NW and the considerable distances to full sun: the cost to raise BT is greatest for this species. At the other extreme, the scrub-forest associations of *A. cooki* are indicated by the low percentage of NW and the short distances to full sun: the cost is least for this species. *Anolis cristatellus* is intermediate because habitat associations vary with altitude (below).

These species differ significantly ($p < .001$) in relative occurrence on perches in full sun (Tables 1 to 3), a measure of basking incidence. *Anolis gundlachi* perched in full sun significantly less often than *A. cooki* or *A. cristatellus*, but the latter pair did not differ significantly.

Air temperatures (\overline{AT}) and mean body temperature (\overline{BT}) differ considerably among these anoles (Tables 1 to 3). \overline{AT} and \overline{BT} are lowest for *A.*

TABLE 1. Mean body temperatures (MBT), mean air temperatures (MAT), percent of lizards perched in full sun (anoles in partial sun counted as half in sun, half in shade), and percent "NW" (see Materials and Methods) of samples of *Anolis gundlachi*. See Appendix for exact localities. (cl = cloudy)

Locality (time of day)	N	MBT (°C) ± SE	MAT (°C) ± SE	MBT-MAT	% sun	% NW
Monte Guillarte						
1240-1418	12	25.5 ± 0.47	24.2 ± 0.33	+1.3	0	---
1445-1605	11	21.4 ± 0.18	21.1 ± 0.13	+0.3	cl	---
Toro Negro						
0923-1014	11	19.6 ± 0.15	19.4 ± 0.10	+0.2	cl	---
Km 37-7						
1058-1213	25	29.2 ± 0.17	28.9 ± 0.11	+0.3	2.5	---
El Verde						
0832-0939	25	24.6 ± 0.08	24.5 ± 0.07	+0.1	7.9	100.0
0557-0627	11	22.6 ± 0.06	22.3 ± 0.04	+0.3	0	91.9
0702-0729	11	22.8 ± 0.07	22.7 ± 0.06	+0.1	0	72.7
0809-0830	11	24.0 ± 0.09	23.6 ± 0.12	+0.4	0	40.0
0858-0920	11	24.7 ± 0.18	24.1 ± 0.09	+0.6	22.7	63.6
1027-1049	11	26.3 ± 0.09	26.0 ± 0.08	+0.3	9.1	63.6
1159-1227	11	26.9 ± 0.07	26.5 ± 0.08	+0.4	0.1	63.6
1335-1404	11	26.9 ± 0.18	26.5 ± 0.10	+0.4	4.5	63.6
1500-1520	11	26.6 ± 0.20	26.2 ± 0.11	+0.4	4.5	63.6
1628-1650	11	26.2 ± 0.10	26.0 ± 0.07	+0.2	7.7	45.5
1720-1752	12	25.7 ± 0.10	25.6 ± 0.05	+0.1	16.6	72.7
Maricao						
0934-1030	28	23.6 ± 0.21	23.0 ± 0.16	+0.6	12.5	50.0
1335-1351	10	23.2 ± 0.11	22.9 ± 0.09	+0.3	cl	---
Mt. Britten						
1031-1144	15	23.7 ± 0.49	22.0 ± 0.12	+1.7	28.6	---
Totals	248	24.8 ± 0.15	24.4 ± 0.15	+0.4	8.7	58.0

gundlachi, intermediate for *A. cristatellus*, and highest for *A. cooki*.

Sympatric associations

Anolis gundlachi and *A. cristatellus*. These species are broadly sympatric at moderate elevations in Puerto Rico. In our sympatric samples (Maricao, Toro Negro, El Verde), *A. cristatellus* occupied much more open habitats, basked more frequently (at Maricao, $p < .001$), and had much higher MBT than *A. gundlachi* (Tables 1 and 2).

Anolis cristatellus and *A. cooki*. Throughout much of its relatively small range, *A. cooki* is sympatric with *A. cristatellus*. East of Playa Caña Gorda, individuals of *A. cooki* occupy slightly more open habitats, perch on shorter shrubs (Kolmogorov-Smirnov test, $p < .001$), and have a higher BT ($p < .001$) than *A. cristatellus* (32.3°C vs. 31.0°C, respectively, 1969 data). Our 1972 data on habitat associations are similar. At Pta. Jagüey (tree sample), *A. cooki* perched on shorter shrubs and trees (Kolmogorov-Smirnov test, $p = .01$) and tended to perch more in the periphery of shrubs (62.5% [$N = 32$] and 23.7% [$N = 19$] of *A. cooki* and *A. cristatellus*, respectively, perched in periphery; $p < .001$). Where groves of well-shaded trees do occur (e.g., Guanica tree sample), *A. cristatellus* are numerically dominant.

However, we found only *A. cooki* in the shaded, but hot (Table 3) mangroves along the beach at Pta. Jagüey.

In contrast to the 1969 data (and Lister 1974), MBT and MAT of *A. cooki* and *A. cristatellus* did not differ significantly in our four sympatric samples. However, in all cases *A. cooki* had slightly higher BT, AT, and percentages of lizards in sun (Table 2 and 3). This pattern is consistent with previous data, and the lack of statistical significance in the 1972 data may reflect relatively small sample sizes.

Species niche breadth

Populations from a wide variety of thermal environments contribute to the overall species results, and lumping all data masks both the extent and determinants of intraspecific variation. The range of MAT among samples of each species (Tables 1 to 3), an index of the extent of environmental variation experienced (Ruibal and Philibosian 1970, Huey and Webster 1975), is 9.5°C for 19 samples of *A. gundlachi* and 8.8°C for 27 samples of *A. cristatellus*, but only 5.7°C for 19 samples of *A. cooki*. [During all censuses and in all habitats, individuals were observed feeding or interacting socially and hence are considered active. Nonetheless, because anoles were just commencing activity at sun-

TABLE 2. Temperature summarizations for *A. cristatellus*. Symbols as in Table 1

Locality (time of day)	N	MBT (°C) ± SE	MAT (°C) ± SE	MBT-MAT	% sun	% NW
Cabo Rojo Salt Plant						
Shrubs						
1105-1239	11	32.3 ± 0.33	30.8 ± 0.26	+1.5	4.5	---
Pta. Jagüey						
Trees						
0957-1132	17	32.3 ± 0.19	30.9 ± 0.16	+1.4	2.0	0
1440-1548	13	33.4 ± 0.26	31.4 ± 0.29	+2.0	3.8	0
Guanica						
Cliffs						
1231-1355	10	33.1 ± 0.30	31.7 ± 0.26	+1.4	0	---
Trees						
1114-1211	25	32.5 ± 0.14	31.2 ± 0.14	+1.3	6.0	---
Camto. Colberg						
Road edge						
1331-1434	15	31.0 ± 0.19	29.8 ± 0.14	+1.2	23.3	20.0
Forest						
1445-1511	11	29.5 ± 0.15	28.7 ± 0.05	+0.8	9.1	45.5
El Verde Open						
0632-0653	10	23.3 ± 0.10	22.9 ± 0.16	+0.4	15.0	100.0
Maricao Open						
0835-0931	24	30.3 ± 0.55	23.1 ± 0.11	+7.2	81.3	25.0
1152-1224	14	29.6 ± 0.51	25.1 ± 0.24	+4.5	40.9	22.2
1302-1332	13	26.2 ± 0.56	24.0 ± 0.31	+2.2	cl	---
Pta. Salinas						
Forest						
0608-0628	10	24.7 ± 0.10	24.8 ± 0.05	-0.1	cl	---
0703-0728	10	24.9 ± 0.11	24.9 ± 0.05	0.0	cl	---
0803-0824	10	26.1 ± 0.08	26.2 ± 0.07	-0.1	cl	---
0902-0921	10	25.8 ± 0.19	25.7 ± 0.05	+0.1	cl	---
1033-1052	10	28.2 ± 0.09	28.1 ± 0.10	+0.1	cl	---
1201-1223	10	26.8 ± 0.07	26.7 ± 0.07	+0.1	cl	---
1333-1348	10	28.0 ± 0.08	27.9 ± 0.12	+0.1	cl	---
1504-1524	10	28.6 ± 0.06	28.5 ± 0.05	+0.1	cl	---
1631-1658	10	28.4 ± 0.08	28.3 ± 0.08	+0.1	cl	---
1750-1816	10	27.9 ± 0.06	27.9 ± 0.05	0.0	cl	---
0615-0640	10	23.6 ± 0.08	23.5 ± 0.05	+0.1	cl	---
0725-0746	10	25.2 ± 0.09	24.9 ± 0.04	+0.3	5.0	90.0
0830-0858	11	26.3 ± 0.20	25.9 ± 0.08	+0.4	22.7	70.0
0935-0953	10	27.7 ± 0.20	27.6 ± 0.18	+0.1	15.0	---
Open Park						
0654-0721	10	29.8 ± 0.74	25.8 ± 0.18	+4.0	65.0	20.0
0803-1826	10	31.8 ± 0.50	27.8 ± 0.14	+4.0	65.0	0.0
0905-0932	10	31.6 ± 0.27	29.3 ± 0.19	+2.3	10.0	11.1
Totals	334	29.0 ± 0.16	27.4 ± 0.14	+1.6	25.0	29.0

rise, we have excluded sunrise census data from MAT and MBT ranges]. Similarly, the range of MBT, an index of the thermal niche breadth of a species (Ruibal and Philibosian 1970, Huey and Webster 1975), is larger for *A. gundlachi* and *A. cristatellus* (9.6°C and 9.8°C, respectively) than for *A. cooki* (4.8°C).

MBT vs. MAT

MBT is strongly correlated with MAT (Fig. 2) for *A. gundlachi* ($r_s = .971$, $p < .01$), *A. cristatellus* ($.797$, $p < .01$), and *A. cooki*, ($.951$, $p < .01$). Among

samples of each species, variance in BT is significantly correlated (all $p < .01$) with variance in AT ($r_s = .817$, $.766$, and $.781$, respectively). Similarly, MBT is strongly correlated with MAT in our all-day samples of each species (all $p < .01$, Fig. 3); and variance in BT is significantly correlated (all $p < .01$) with variance in AT for *A. cristatellus* ($r_s = .585$) and *A. gundlachi* ($.646$), but not *A. cooki* ($.508$), during these all-day samples. These correlations strongly suggest that those environmental factors which influence ambient conditions in turn influence BT of these anoles.

TABLE 3. Temperature summarization for *A. cooki*. Symbols as in Table 1

Locality (time of day)	N	MBT (°C) ± SE	MAT (°C) ± SE	MBT-MAT	% sun	% NW
Cabo Rojo Salt Plant						
Fence posts						
0915-1043	47	31.9 ± 0.12	29.7 ± 0.06	+2.2	6.3	0
1241-1308	11	32.8 ± 0.20	30.0 ± 0.24	+1.8	9.1	0
0600-0627	10	26.5 ± 0.10	26.2 ± 0.12	+0.3	cl	---
0704-0726	10	30.0 ± 0.41	27.3 ± 0.15	+2.7	66.7	0
0801-0821	11	30.6 ± 0.24	28.6 ± 0.07	+2.0	22.7	0
0903-0916	10	31.0 ± 0.19	29.4 ± 0.10	+1.6	0	0
1032-1047	11	32.2 ± 0.17	30.1 ± 0.11	+2.1	9.0	0
1207-1225	10	32.8 ± 0.18	31.0 ± 0.10	+1.8	0	0
1335-1348	7	29.3 ± 0.05	28.6 ± 0.06	+0.7	cl	---
1550-1520	10	32.9 ± 0.23	29.7 ± 0.20	+3.2	60.0	0
1633-1650	10	31.1 ± 0.30	29.0 ± 0.19	+2.1	20.0	0
Shrubs						
1105-1239	23	32.8 ± 0.19	31.2 ± 0.19	+1.6	8.7	---
1243-1319	10	31.2 ± 0.30	29.7 ± 0.29	+1.5	cl	---
Pta. Jagüey						
Trees						
0957-1132	13	32.8 ± 0.19	31.0 ± 0.23	+1.8	17.8	7.1
1440-1548	12	33.5 ± 0.36	31.8 ± 0.25	+1.7	4.2	0
Mangroves						
1139-1205	12	32.3 ± 0.25	30.3 ± 0.17	+2.0	12.5	---
1057-1149	22	33.8 ± 0.21	32.0 ± 0.20	+1.8	14.3	---
Guanica						
Shrubs						
0917-1045	15	33.6 ± 0.13	32.1 ± 0.12	+1.5	3.3	---
Cliffs						
1231-1343	15	33.5 ± 0.25	32.0 ± 0.27	+1.5	10.0	---
Ravine						
1424-1533	11	34.1 ± 0.30	33.0 ± 0.32	+1.1	0	---
Totals	280	32.0 ± 0.07	30.2 ± 0.10	+1.8	18.6	0.5

CTM, EVM, and PBT

The PBT, EVM, and CTM of *A. gundlachi* from El Verde are significantly lower than those of sympatric *A. cristatellus* (all $p < .001$) and of *A. cooki* from Guanica (all $p < .001$, Table 4). The PBT, EVM, and CTM of *A. cooki* and *A. cristatellus* from Guanica are not significantly different (all $p > .4$).

PBT and CTM do not differ significantly ($p > .9$ and $p > .1$, respectively) among populations of *A. cristatellus* from geographically and climatically dis-

tinct localities (Table 4), but the EVM of El Verde *A. cristatellus* is significantly lower ($p < .01$) than that of Guanica lizards.

DISCUSSION

We first focus on overall differences in distributions, habitats, behavior, and body temperatures of the three trunk-ground anoles of the *cristatellus* group on Puerto Rico. Then we consider the magnitude of intraspecific variation in body temperature, the relative effect of various environmental factors on

TABLE 4. Thermal parameters of anoles of the *cristatellus* group in Puerto Rico: experimental voluntary maximum temperature tolerated (EVM), critical thermal maximum (CTM) and preferred body temperature (PBT) (see Materials and Methods). N = number of individuals. Temperatures in °C

Species	Locality	EVM		CTM		PBT	
		\bar{x}	N	\bar{x}	N	\bar{x}	N
<i>A. gundlachi</i>	El Verde	26.4 ± .44	10	35.7 ± .46	10	25.1 ± .64	6
<i>A. cristatellus</i>	El Verde	29.7 ± .58	10	38.1 ± .42	10	29.0 ± .36	6
	Pta. Salinas	---	---	---	---	29.6 ± .59	6
	Guanica	33.2 ± .95	11	38.9 ± .30	11	29.6 ± .93	6
<i>A. cooki</i>	Guanica	34.0 ± .93	11	38.9 ± .32	11	30.6 ± .38	6

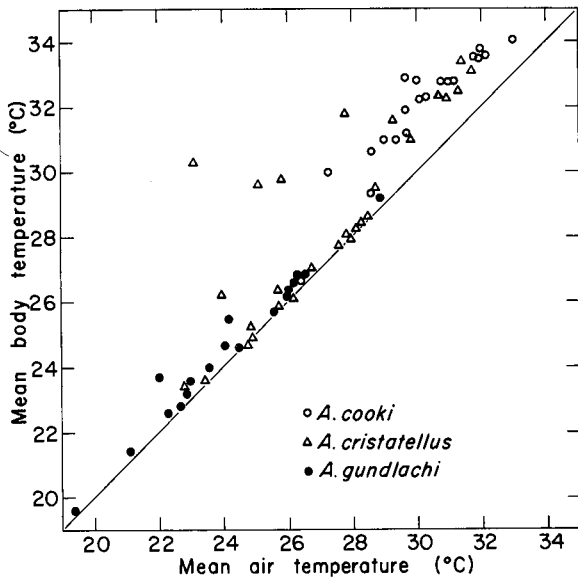


FIG. 2. Mean body temperature vs. mean air temperature of samples of lizards. Minimum sample size is 7. See Tables 1 to 3.

that variation, and the evolution of thermal niche breadths. Finally, we evaluate the extent of thermo-regulation in relation to associated costs.

Thermal biology of the cristatellus group

Anolis gundlachi are generally restricted to closed forests (Fig. 1, Rand 1964, Schoener and Schoener 1971) at moderate to high elevations, infrequently bask (Table 1, Rand 1964, Schoener and Schoener 1971), and are active at low MAT and MBT (Table 1, Rand 1964). *Anolis cristatellus* live in open or in closed forests at low elevations but exclusively in open habitats at moderate elevations (Table 2, Rand 1964), bask frequently (Table 2, Rand 1964, Schoener and Schoener 1971, Huey 1974b), and are active at intermediate MAT and MBT (Table 2, Rand 1964, Heatwole et al. 1969, Huey 1974b, Lister 1974). *Anolis cooki* are restricted to open habitats in xeric southwestern Puerto Rico (Fig. 1, Williams 1972), bask frequently (Table 3), and are active at high MAT and MBT (Table 3, 1969 data, Lister 1974).

Rand (1964) suggested that differences in distribution and BT of *A. cristatellus* and *A. gundlachi* have a physiological base (in 1964 *A. cooki* was not considered specifically distinct from *A. cristatellus*, Gorman et al. 1968). Heatwole et al. (1969), using lizards acclimated to 30°C for 1 wk, showed that *A. cristatellus* from near sea level were more heat tolerant (critical thermal maximum, CTM) than *A. gundlachi* from 350–650 m. Gorman and Hillman (1976) found that *A. cristatellus* from sea level were more intolerant of continuous low am-

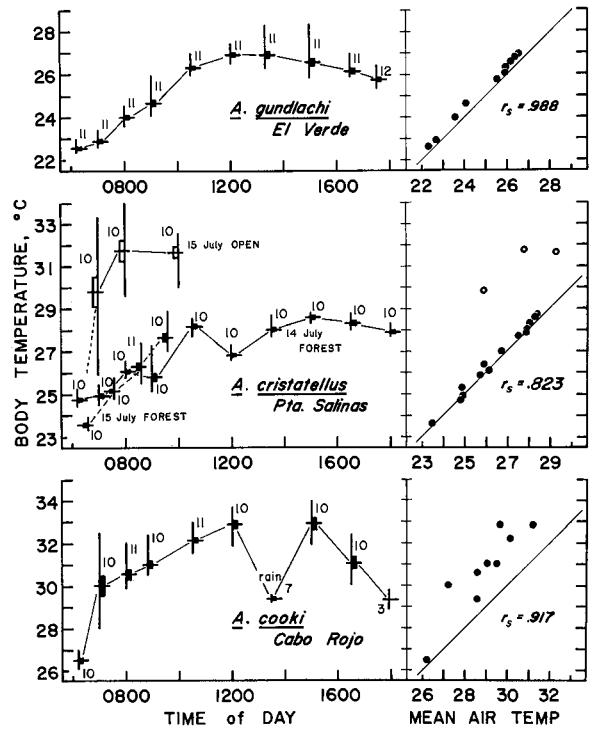


FIG. 3. Mean body temperatures as functions of time of day (left) and mean air temperature (right) for anoles during the day. Vertical lines represent ranges, horizontal lines represent means, boxes represent ± 1 SE and associated numbers represent sample sizes.

bient temperatures (16°C) than *A. gundlachi* from 650 m. Heatwole et al. (1969) and Gorman and Hillman (1976) suggest that these two anoles differ physiologically, but these conclusions would have been more substantive if sympatric populations had been compared. Our experiments with lizards acclimated to 20°C for 24 to 30 h (Table 4) indicate that *A. cristatellus* from El Verde preferred (PBT) and tolerated (CTM) significantly higher body temperatures than sympatric *A. gundlachi*. Further, *A. cooki* from Guanica preferred and tolerated higher temperatures than *A. gundlachi* from El Verde, but not significantly higher than *A. cristatellus* from Guanica. Because of the similarity in PBT and CTM of *A. cristatellus* and *A. cooki*, we suspect that the restriction of only *A. cooki* to the arid lowlands may in part be a function of its physiological intolerance to low temperatures, relative to both *A. cristatellus* and *A. gundlachi* (Spellerberg 1972a, b, c). [*Anolis cooki* apparently retreated during cool, overcast census periods (1350 and 1745) at the Cabo Rojo salt plant, supporting the suspicion that this species is intolerant to cool temperatures.]

Available laboratory data (Heatwole et al. 1969, Gorman and Hillman 1976, this report) support Rand's (1964) expectation that these anoles differ

physiologically and that present day differences in distributions and BT are an immediate consequence of these physiological differences (factors involved in the evolution of these differences are discussed below). [Further corroborative evidence comes from the recent findings (S. Hillman and G. C. Gorman, *personal communication*) that *A. gundlachi* are particularly sensitive to water loss and that *A. cristatellus* lose water faster than *A. cooki*.] In contrast to some other lizard groups (Bogert 1949), these species thus differ strikingly in overall thermal biology despite very close evolutionary relationships (Williams 1972).

Sympatric associations

Though primarily upland and lowland forms respectively, *A. gundlachi* and *A. cristatellus* overlap broadly at middle elevations in Puerto Rico (Williams 1972). Where sympatric, *A. gundlachi* occur in deep forest habitats while *A. cristatellus* live in open habitats (Rand 1964, Turner and Gist 1970, Schoener and Schoener 1971, Williams 1972, this report). However, Turner and Gist (1970) observed that *A. cristatellus* invaded an area of forest previously inhabited only by *A. gundlachi* after gamma irradiation caused significant leaf fall, indicating that some *A. cristatellus* occur normally or are transients within the forest. Also, Schoener (1970b) noted that, while *A. cristatellus* were numerous along an open road cut at Maricao during sunny censuses, *A. gundlachi* were more common in this same habitat under overcast skies. Thus habitat differences between these species, while very substantial, are not absolute. Nonetheless, BT reflect overall differences with *A. gundlachi* active at much lower BT than *A. cristatellus* in sympatry (Tables 1 and 2). Differences in habitat and BT in sympatry probably have a physiological basis (above).

Anolis cooki generally occupy slightly more open habitats (Williams 1972, Lister 1974, this report) and often (1969 data, Lister 1974), but not always (this report), have significantly higher body temperatures than *A. cristatellus* in sympatry. Nonetheless, these differences are far less pronounced than those between *A. gundlachi* and *A. cristatellus*. Moreover, differences in PBT and CTM of *A. cooki* and *A. cristatellus* are not significant (above); but rates of water loss are significantly different (S. Hillman and G. C. Gorman, *personal communication*). A more refined examination of possible physiological differences (particularly at low BT) between these two species would be of interest.

Even when differences in habitat and BT have a physiological basis, ongoing exploitation and interference competition (Park 1962) might reinforce these differences (Huey and Slatkin 1976). For *A. cristatellus* and *A. gundlachi*, spatial overlap is gen-

erally too low for competition to be influential, except perhaps along edges. However, for *A. cristatellus* and *A. cooki*, spatial overlap is relatively high, and competition could be important. G. C. Gorman (*personal communication*) observed a male *A. cristatellus* defeat a male *A. cooki*, and we found a juvenile *A. cooki* in the gut of an adult male *A. cristatellus* (*A. cristatellus* are slightly larger than *A. cooki*, Schoener 1970a). Interestingly, Lister (1974) found that *A. monensis* (a close relative of *A. cooki* which is solitary on Mona Island) occupy a broader range of habitats than *A. cooki* in sympatry and have a greater variance in BT than *A. cooki*. This evidence of ecological release of *A. monensis* is circumstantial but is consistent with an hypothesis that competition may influence habitat associations and BT of *A. cooki* and *A. cristatellus* in sympatry.

We have argued that present differences in habitat and BT among these anoles reflect primarily underlying physiological differences. However, these physiological differences in fact may have evolved because of competitive interactions among these species in the past (Williams 1972, Schoener 1974, Gorman and Hillman 1976).

Influences on MBT

The significant correlations between MBT and MAT and between variance in BT and variance in AT for the three anoles of the *cristatellus* group suggest that environmental factors influencing thermal level and thermal variability of a habitat in turn strongly affect the mean and variance in BT of lizards (Soulé 1963, Clark and Kroll 1974, Huey and Webster 1975). Below we examine the indirect effects of locality, habitat, time of day, and weather on the behavior and BT of these anoles.

Ambient temperatures generally decreased with altitude. Not surprisingly, *A. gundlachi* and *A. cristatellus* shift to more open habitats at higher elevations (Rand 1964, Huey 1974b, Tables 1 and 2) as do many other lizard species (Ruibal and Philibosian 1970, Burns 1970, Campbell 1971, Clark and Kroll 1974). *Anolis cristatellus* also bask more frequently at higher elevations ($p < .001$): on clear days in open habitats between 0900 and 1500 h, the percentage of lizards perched in full sun is 3.1% ($N = 163$) at sea level, 23.3% ($N = 15$) at 150 m, and 55.5% ($N = 27$) at 850 m. Though active from sunrise to sunset at low and moderate elevations, *A. cristatellus* may be active only when it is sunny at high elevation (Schoener and Schoener 1971, and on Toro Negro). Despite these behavioral shifts which will reduce the thermal effects of increasing altitude, MBT of *A. gundlachi* and of *A. cristatellus* is inversely correlated with altitude ($r_s = -.970$, $p < .01$; $r_s = -1.000$, $p = .05$, respectively). Altitude is seemingly the most important environmental influence

on MBT of *A. gundlachi*. Populations from 350 m (El Verde, Km 37-7) had midday MBT of 26°C to 29°C whereas populations from 650 m and 1,090 m have much lower MBT (23.7°C and 19.6°C, respectively, Table 1).

Thermal levels of sea-level localities influence BT of *A. cristatellus* even in open habitats. MBT of *A. cristatellus* between 1000 and 1300 h (sunny days in open habitats) are high (32.3°C to 33.1°C, Table 2) at hot, arid localities in southwestern Puerto Rico (Pta. Jagüez, Cabo Rojo, Playa Caña Gorda). At a cooler, more mesic locality on the north coast (Pta. Salinas), MBT are lower (28.9°C to 31.6°C, Huey 1974b).

Thermally distinct habitats within a given locality can influence the behavior and BT of anoles (Ruibal and Philibosian 1970, Lister 1974, Huey and Webster 1975). For *A. gundlachi* (Mt. Britten) and *A. cristatellus* (Campamiento Elisa Colberg and Pta. Salinas), lizards in the more open habitat basked more frequently (all $p < .05$) and had significantly higher MBT (all $p < .01$) (Tables 1 and 2, Huey 1974b). In contrast, *A. cooki* occupies localities where habitats are less thermally distinct. Not surprisingly, MBT of *A. cooki* in different habitats at single localities are very similar (Table 3).

Weather changes influence BT of these anoles as well. Overcast sprinkly skies during the 1335 census of *A. cooki* at Cabo Rojo resulted in a depression of the MBT by about 3.5°C (Fig. 3). Similarly, MBT of *A. cristatellus* in the open at Maricao during two sunny censuses (30.3°C and 29.6°C) were considerably higher than the MBT under cloudy skies (26.2°C, Table 2). In contrast, MBT of anoles in closed forests seem relatively independent of weather. The MBT of *A. gundlachi* in the forest at Maricao was only 0.4°C higher ($p < .01$) during a sunny census than during a cloudy census (0930 and 1335 censuses). Overcast had little effect on MBT of *A. cristatellus* in the forest at Pta. Salinas (Table 2). The relatively limited influence of weather conditions on forest populations of *A. gundlachi* and *A. cristatellus* undoubtedly reflects the buffered thermal environment of the forest interior (Geiger 1966).

Species niche breadth

MBT ranges are larger for *A. gundlachi* (9.6°C) and *A. cristatellus* (9.8°C) than for *A. cooki* (4.8°C). Since both *A. gundlachi* and *A. cristatellus* inhabit somewhat colder localities than any sampled here and since MBT is correlated with MAT for these lizards (Fig. 2), MBT ranges of these two species are probably minimal estimates. However, the niche breadth of *A. cooki* is probably a close approximation (at least for summer) since the retreat of most lizards during cool cloudy censuses suggests that these lizards are intolerant of BT < 29°C, except

when commencing activity at sunrise. Thus additional early morning censuses should increase the MBT range of *A. cooki* slightly. Overall, *A. gundlachi* and *A. cristatellus* seemingly have broader species thermal niches than *A. cooki*.

Eurythermy, stenothermy, and populational differentiation

The thermal niche breadth of a species can be due primarily to niche breadths of individuals or to populational differentiation. If the total range of MBT tolerated within populations is large relative to the total range of MBT for species with broad thermal niches, then individuals are eurythermal; and individual niche breadth, not populational differentiation makes the dominant contribution to the niche breadth of the species. Conversely, if that range is small, then individual lizards are stenothermal, but populational differentiation is important (Huey and Webster 1975). (However, in descriptive field studies like this, we cannot determine whether such populational differentiation is genetic or is the result of acclimatization.) For species with small thermal niche breadths (e.g., *A. cooki*), individuals are necessarily stenothermal.

The maximum range of MBT within populations as a percentage of the species MBT range is 43% for *A. gundlachi* (both Mt. Guillarte and El Verde, Table 1) and 70% for *A. cristatellus* (Pta. Salinas, Table 2), the two species with broad species thermal niches. (This value is 73% for *A. cooki* [Cabo Rojo Salt Plant, Table 3], the stenothermal species.) Individual *A. cristatellus* are therefore eurythermal (assuming no intrapopulational differentiation, see Huey and Webster 1975). Interestingly, the lack of significant differences in PBT and CTM (Table 4) among populations of *A. cristatellus* from thermally distinct localities (El Verde, Pta. Salinas, Guanica) support the inference that populational differentiation is small in *A. cristatellus*.

The relatively low percentage for *A. gundlachi* suggests that individuals are stenothermal and that populational differentiation makes the dominant contribution to its broad species niche. This is not necessarily the case: the buffered thermal environment of forests limits variation in BT within populations, and thus individuals would appear stenothermal even when they are eurythermal. Thus, we know only that the measured thermal niche breadth of individual *A. gundlachi* is small. In the absence of data from thermally heterogeneous localities, determination of the potential niche breadth cannot be made.

Large species MBT ranges have been reported for several solitary *Anolis*: 7.3°C for *A. oculatus* on Dominica (Ruibal and Philibosian 1970), 9.9°C for *A. marmoratus* on Guadeloupe (Huey and Webster

1975), and 7.5°C for *A. sagrei* on Abaco (Lister 1974). Within populations variation in MBT is apparently great in each of these species, and individuals are probably eurythermal.

Evolutionary aspects of eurythermy and stenothermy

Ruibal and Philibosian (1970) suggested that ecological release might be responsible for eurythermy in solitary anoles. However, because the extent of eurythermy in ancestral populations cannot be determined, present eurythermy of solitary anoles is not sufficient evidence of ecological release (Ruibal and Philibosian 1970, Huey and Webster 1975). Lister (1974) found that solitary populations of certain anoles have larger variances in BT than do sympatric populations, but whether this actually reflects a genetic expansion is unknown. Nonetheless, because *A. cristatellus* in the complex Puerto Rican fauna are eurythermal, it is clear that eurythermy can evolve for reasons other than ecological release.

Alternatively, eurythermy may be an adaptation to thermally variable habitats where conditions (e.g., frequent overcast or high costs of thermoregulation) prohibit careful thermoregulation (Huey 1974a, Huey and Webster 1975), particularly if environmental temperatures are often low relative to optimal temperatures of lizards (Huey and Slatkin 1976). *Anolis cristatellus* and *A. cooki* support this hypothesis. The former, inhabiting a wide variety of habitats, often with low environmental temperatures and high costs of thermoregulation, are relatively eurythermal. The latter, inhabiting a restricted variety of habitats with relatively high environmental temperatures, but with low thermoregulatory costs, are stenothermal. (We cannot evaluate *A. gundlachi* in terms of this hypothesis until the potential thermal niche breadth of this species is known.)

Extent of thermoregulation

While lizards may derive physiological benefits from thermoregulation, they simultaneously incur costs (e.g., energetic losses from shuttling between sun and shade). Thermoregulation to avoid hazardous extreme temperatures is almost always adaptive: within these limits, however, passivity may yield greater net benefits than thermoregulation if associated costs are relatively high (Pianka 1965, Pianka and Parker 1975, Hertz 1974, Huey 1974b, Huey and Webster 1975, Huey and Slatkin 1976). Here we demonstrate that anoles of the *cristatellus* group bask in habitats where an index of the costs of raising BT is low, but not where this index is high. (Other examples, including some possible exceptions, are discussed in Huey and Slatkin [1976].) We emphasize that our analysis is restricted to problems of raising body temperature. Avoidance of high body

temperature, the other aspect of thermoregulation, is a separate issue (Huey and Slatkin 1976).

Throughout most of its range, *A. gundlachi* lives in deeply shaded forests where distance to full sun is very large (Fig. 1), and thus the cost to raise BT should be high (see Materials and Methods section). Very few lizards were ever observed in full sun (Table 1), and we infer that the incidence of basking is very low. [Indeed, we observed conspicuous basking by *A. gundlachi* only at Mt. Britten where several individuals on the edge of the forest or in clearings (where costs are of course low) were basking.] Thus our data suggest that *A. gundlachi*, living in high-cost environments, are generally thermoconformers. (However, near the lower elevational limit of its range, *A. gundlachi* are probably avoiding sunny patches at midday.)

Costs of raising BT are low for *A. cooki*, a species generally living in open, xeric habitats where distances to full sun are short (Fig. 1). These lizards frequently bask early and late in the day (Table 3). *Anolis cooki*, living in low-cost habitats, are thermoregulators.

Costs of raising body temperature at Pta. Salinas are high in the forest but low in the open (Table 2). Indeed, *A. cristatellus* bask only in the open habitat (Table 2, Fig. 3). (In 1973, Huey [1974] returned to Pta. Salinas, extended these observations over a full day, and found a very similar pattern.) Thus, extent of thermoregulation varies in *A. cristatellus*: lizards in low-cost habitats behaviorally raise body temperatures while those in high-cost habitats do not.

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APPENDIX

Monte Guillarte, Hwy. 131 (\approx 950 m); *Toro Negro*, Km 18, Hwy. 143 (\approx 30 m below summit Cerro de Punta, 1120 m); *Km 37-7*, above Rio Toro Negro, Hwy. 149 between 144 and 157 (\approx 350 m); *El Verde Rain Forest*, Luquillo Forest AEC site (\approx 350 m); *Maricao Lookout*, Maricao Insular Forest (860-900 m); *Mt. Britten Trail base*, Luquillo Forest (\approx 650 m); *Cabo Rojo Salt Plant*, near Pta. Jagüey (sea level); *Pta. Jagüey* (near sea level), lighthouse; *Guanica Forest* (near sea level): cliff and tree samples 3.4 km E Playa Caña Gorda; shrub sample 6.2 km E Playa, and ravine sample \approx 9.5 km E Playa Caña Gorda; *Campamiento Elisa Colberg* (\approx 150 m), Hwy. 186 near town of El Verde; *Pta. Salinas* (Levittown), junction Hwy. 165 and Hwy. 868 (near sea level).