

COMPENSATION FOR ALTITUDINAL CHANGES IN THE THERMAL ENVIRONMENT BY SOME *ANOLIS* LIZARDS ON HISPANIOLA¹

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Abstract. Populations of the *Anolis cybotes* species group on Hispaniola behaviorally compensate for changes in the thermal environment associated with altitude. Lizards occupy more open habitats, increase basking frequency, and restrict times of activity at high elevation: a result is that the change in mean cloacal temperature with elevation is very small relative to that known for other anoles. In contrast to this large behavioral variation among populations, physiological differences appear to be minor. In this regard, the *cybotes* group has several parallels with the well-studied *crisatellus* group of *Anolis* on Puerto Rico. However, the *cybotes* group has no equivalent to *Anolis gundlachi*, which employs physiological adaptations to compensate for different thermal environments.

Key words: altitudinal variation; *Anolis* lizards; basking; behavioral thermoregulation; body temperature; critical thermal maximum; habitat shift; Hispaniola.

INTRODUCTION

Thermal environments change dramatically with altitude (McCullough and Porter 1971). Lizards can compensate for such changes in several ways: long- and short-term shifts in regulatory behaviors (habitat selection, basking frequency, restriction of time of activity), physiological acclimatization, and genetic differentiation among populations (see Slobodkin and Rapoport 1974). Behavioral shifts are believed to be the primary compensatory mechanism in most lizards (Bogert 1949, Huey and Slatkin 1976), but few studies have examined the magnitude of the other responses (Spellerberg 1972a, b, c, Hertz 1977, 1980b, Hertz et al. 1979).

Many West Indian lizards of the iguanid genus *Anolis* are abundant over a broad elevational range. Thus they are well suited for a study of responses to altitudinal changes in the thermal environment. Moreover, independently derived species groups occur on each of the Greater Antilles (Williams 1976). Therefore, one can identify general patterns of both altitudinal distributions and associated responses.

Here we consider the thermal biology of several populations of the *Anolis cybotes* species group along a 2200-m altitudinal transect in Hispaniola. We examine changes in apparent thermoregulatory behaviors and in physiology and find that behavior rather than physiology appears to be the primary compensatory mechanism. (The extent of genetic differentiation, as estimated by morphological and electropho-

retic studies, will be treated separately.) We also compare present results with similar data on other anoles—in particular, the related *A. cristatellus* species group on Puerto Rico (Wyles and Gorman 1980)—to determine the general applicability of our findings for this lizard genus.

Anoles of the *cybotes* species group are small lizards (maximum snout-to-vent length \approx 65 mm) that perch on the lower parts of tree trunks and sometimes on rocks or on the ground. Most species have restricted distributions (e.g., *A. longitibialis* in lowland desert scrub and *A. shrevei* in high mountain grasslands), but one, *A. cybotes*, occurs in diverse habitats and from sea level to 1200 m elevation (Schwartz and Thomas 1975).

MATERIALS AND METHODS

During visits to the Dominican Republic in the summers of 1974 and 1976 (total work time = 10 observer wk), we collected data on 278 *cybotes* from three primary localities: a relatively closed-canopy, xeric coastal forest (near Playa Saladilla, 2 km south of Barahona, Barahona Province, 5 m elevation); a lush, middle-elevation woodland (0.2 km northeast of Sabana Larga, Peravia Province, 550 m elevation); and a highly developed agricultural habitat (Palera, Valle Constanza, La Vega Province, 1150 m elevation); and on 42 *shrevei* from a mountaintop pine savanna (Valle Nuevo, Peravia Province, 2200 m elevation). We collected smaller secondary samples on *cybotes* from three disturbed habitats (near Jarabacoa, La Vega Province, 520 m elevation; the Hotel Montaña, La Vega Province, 660 m elevation; near Polo, Barahona Province, 700 m elevation) as well as a sample of *longitibialis* from desert scrub (near Cabo Rojo, Pedernales Province, 5 m elevation).

To describe the diurnal thermal biology of the lizards in our primary samples, we captured active sub-

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adult and adult lizards by hand or with a noose, using standard precautions, and recorded the following data: body (cloacal, = T_b) and air (shaded bulb, 1 cm above perch, = T_a) temperatures with a quick-reading Schultheis thermometer (calibrated to a United States Bureau of Standards-calibrated mercury thermometer), time, snout-to-vent length, sex, use of a basking site (i.e., perched in full sun, sun filtered by vegetation, or shade), weather (sunny or overcast), and an index of the potential cost of basking (below). Unlike some *Sceloporus*, in which individuals within a population may have variable activity periods (Simon and Middendorf 1976), individual cybotoid anoles appear to be active whenever weather conditions permit. Thus, the conclusions drawn from our population studies probably apply to individuals.

For a crude index both of the potential cost of raising T_b by basking and of the extent of shading in habitats during sunny weather, we measured the transit distance from a shaded or partially shaded anole to the nearest patch of full sun on a contiguous perch; we also included a category "no way" (NW), indicating that the tree or shrub was completely shaded. Long transit distances increase the time and energy expended during basking, may increase the risk of predation, and might interfere with feeding and social activities (Huey 1974, Huey and Webster 1976). Transit distance and frequency of NW generally will be greater in more shaded habitats. (Note, however, that because transit distance is in part a function of perches selected by lizards, the unqualified use of this index of shadiness could be misleading in the absence of corroborative field impressions.)

Discussions of the "precision" of temperature regulation are surprisingly confused in the literature. A major reason is that some workers examine only the behavioral or physiological processes that are used in regulating temperature, whereas others examine only the results of those processes (a regulated T_b). Because temperature regulation (Cabanac 1979) consists of both processes and results, at least two complementary indices must be used to describe temperature regulation (Huey 1981). To quantify the behavioral component, we use the percentage of lizards sitting in full sun, which is a measure of basking frequency (e.g., Huey and Webster 1976). Other behaviors (posture, orientation, shift in perch height; Heath 1965, Muth 1977) could also be studied. To quantify the result of such behaviors, we use the slope of the linear regression of T_b on T_a , which is an estimate of the extent to which T_b varies with T_a (see below). A slope near 0 implies independence of T_b from T_a and, thus, perfect thermoregulation, whereas a slope approximating 1 implies thermoconformity (Huey and Slatkin 1976). These measures evaluate both the frequency and the effectiveness (see Results) of basking behavior, a conspicuous component of temperature regulation in these lizards.

These indices, however, have several potential deficiencies. First, they estimate the extent of regulation only *within* a specified time period; nevertheless, a lizard that does not bask while active might still achieve body temperatures near preferred levels by carefully restricting its time of activity or habitat. Second, T_a is a convenient but incomplete estimate of ambient heat loads on small animals (e.g., *Anolis*) in shade. Operative environmental temperatures (Bakken 1976) or biophysical models (Porter et al. 1973) provide better estimates of the thermal environment particularly for large lizards, which are coupled more to the radiant than to the convective thermal environment (Muth 1977). Third, because of diurnal changes in the relative availability of sun and shade on tree trunks in open habitats (Huey et al. 1977), even a thermoconforming lizard (i.e., one moving randomly with respect to sun and shade) could have a slope approaching 0. Given these potential problems, we use caution in estimating the frequency and effectiveness of temperature regulation.

To investigate the extent of physiological differentiation among populations, we collected adult lizards on the mornings after the all-day censuses and determined sensitivity to high temperatures later each day. (Thus these lizards were acclimatized to natural thermal conditions, see Results). Responses were measured between 1400 and 1800 to reduce bias from possible diel fluctuations in heat sensitivity (Kosh and Hutchison 1968). Animals were heated continuously with an overhead infrared lamp, and we recorded the T_b (with a calibrated Yellow Springs Instrument Model 46 telethermometer) at which three sequential indicators occurred (Hertz et al. 1979). Experimental voluntary maximum (EVM) was the T_b at which an anole first jumped during heating (Ruibal 1961). Panting threshold (PT) was scored when an animal gaped and breathed deeply (Heatwole et al. 1973). Critical thermal maximum (CTM) was scored at the loss of righting response (Brattstrom 1971).

Unless stated otherwise in the text, we used *t* tests for the comparison of two means, one-way analysis of variance and Student-Neuman-Keuls tests to evaluate differences among groups of means, *G*-tests for $R \times C$ tests of independence (using a Simultaneous Test Procedure [STP] analysis), and Spearman rank correlations to evaluate altitudinal variation in environmental parameters and lizard responses (Sokal and Rohlf 1969). A probability of 0.05 is the standard criterion of statistical significance. Because no aspect of the data varied significantly with the size or sex of the lizards in any sample, all results are based upon combined samples.

RESULTS

The effectiveness of basking (i.e., the rate of change of T_b of a lizard perched in sun) is a complex biophysical function of organismal (body size and shape,

TABLE 1. Frequency of individuals sampled during sunny weather, transit distance (m) to nearest basking site ($\bar{x} \pm SE$), and frequency of lizards with no basking site available (NW). Common superscript letters indicate values that are not significantly different. These data are based upon several days of sampling at each locality.

Population	N	Sunny weather	Transit distance	NW
<i>cybotes</i> (5 m)	116	1.00	1.3 \pm 0.13	0.23
<i>cybotes</i> (550 m)	60	0.92 ^a	0.3 \pm 0.08 ^b	0.09 ^c
<i>cybotes</i> (1150 m)	102	0.80 ^a	0.3 \pm 0.09 ^b	0.09 ^c
<i>shrevei</i> (2200 m)	42	0.53	undefined	0.00

coloration, physiology, behavior) and environmental (convection, conduction, radiation) factors (Porter et al. 1973). The quantitative results of this interaction necessarily vary with altitude because of changes in the thermal environment: air temperature and diffuse radiation decrease, but direct solar radiation increases slightly (McCullough and Porter 1971). (Actual direct solar radiation in the mountains of Hispaniola is, however, reduced by frequent cloud cover [Table 1]).

A consequence of such environmental changes is that equilibrium T_b —at least of small lizards—should decline with altitude (R. D. Stevenson, *personal communication*). However, by behaviorally adjusting their exposure to solar radiation, or through morphological changes (Spellerberg 1972b), lizards may minimize the impact of altitude on T_b .

Use of compensatory behaviors

The habitat associations of these lizards are not fixed, but change as a function of altitude. In the desert lowlands at one extreme of the climatic/altitudinal transect on Hispaniola, *longitibialis* are commonly associated with the shadiest available habitats (on large trees, in cave entrances). In less arid and hot lowlands, *cybotes* occur chiefly in well-shaded forests, as indicated by transit distance and frequency of NW (see Materials and Methods, Table 1) and sometimes on large shade trees, but not in open areas. In contrast, montane *cybotes* are found in relatively open habitats (Table 1) and are notably absent from nearby shaded forests. In the cold mountains at the top of the tran-

sect, *shrevei* occur in very open grasslands, but not in adjacent forests.

Although *Anolis* lizards are typically active from sunrise to sunset (Heatwole et al. 1969), anoles living in very hot or very cold environments may restrict activity to times of moderate temperatures (Ruibal and Philibosian 1970, Huey and Webster 1976, Hertz 1977). Although we found no evidence of activity restriction by *cybotes*, we noted that *shrevei* conspicuously regulated activity by postponing emergence and by retreating under rocks or logs during prolonged cloudy periods. Conversely, *longitibialis* were most conspicuous when skies were overcast (see Irwin 1965). Thus, changes in times of activity are marked only at the extremes of the altitudinal transect.

The proportion of lizards perched in full sun indexes basking frequency (but see Huey et al. 1977:1072). Despite the increased frequency of cloud cover at high elevation (Table 1), the proportion of *cybotes* perched in full sun increased with altitude (Table 2, complete samples) because montane lizards basked much more frequently during sunny weather than did lowland lizards (Table 2, sunny weather samples). Similarly, lowland *longitibialis* were rarely perched in full sun, whereas *shrevei* invariably bask during sunny weather (Table 2).

Overall air and body temperatures

\bar{T}_b and \bar{T}_a (Table 3) were inversely correlated with altitude for *cybotes* ($r_s = -.829$ and $-.886$, respectively; $P < .05$) and for all populations of the *cybotes* group ($r_s = -.899$, $-.935$; $P < .01$). The difference between \bar{T}_b and \bar{T}_a increased markedly with altitude (Table 3, $r_s = .943$ for *cybotes*, $.988$ for all populations of the *cybotes* group; $P < .01$), reflecting the described shifts in habitat and in basking frequency and perhaps the slightly higher intensity of solar radiation in the mountains (McCullough and Porter 1971).

Interpopulational differences in \bar{T}_b of *cybotes* are small relative to those of other broadly distributed West Indian anoles. This can be demonstrated by estimating the change in \bar{T}_b per 100 m change in elevation from the slope of the linear regression of \bar{T}_b on altitude: *cybotes* exhibits a small change relative to other anoles (Table 4).

TABLE 2. Frequencies of lizards perched in full sun, filtered sun, and shade in complete samples (all weather) and in sunny weather samples. For sunny weather samples, lizards without available basking sites (=NW) excluded. Common superscript letters indicate populations of *cybotes* that do not differ significantly in frequency of individuals in full sun.

Population	Complete samples (all weather)					Sunny weather samples			
	N	Full sun	Filtered sun	Shade	Overcast	N	Full sun	Filtered sun	Shade
<i>cybotes</i> (5 m)	116	0.09	0.20	0.71	0.00	89	0.11 ^b	0.25	0.64
<i>cybotes</i> (550 m)	60	0.23 ^a	0.23	0.46	0.08	50	0.28 ^b	0.22	0.50
<i>cybotes</i> (1150 m)	102	0.38 ^a	0.19	0.23	0.20	75	0.52	0.19	0.29
<i>shrevei</i> (2200 m)	42	0.57	0.00	0.00	0.43	24	1.00	0.00	0.00

TABLE 3. Body and air temperature (°C) statistics for species of the *cybotes* group.

Population	N	Body temperatures		Air temperatures	
		$\bar{x} \pm SE$	Range	$\bar{x} \pm SE$	Range
<i>longitibialis</i> (5 m)	11	32.2 ± 0.46	30.2–34.3	31.1 ± 0.58	29.2–33.8
<i>cybotes</i> (5 m)	116	31.4 ± 0.19	26.0–34.6	30.0 ± 0.16	25.8–32.6
<i>cybotes</i> (520 m)	20	31.6 ± 0.38	28.4–33.5	29.8 ± 0.42	26.4–32.0
<i>cybotes</i> (550 m)	60	30.2 ± 0.32	23.2–33.0	27.4 ± 0.32	22.3–31.0
<i>cybotes</i> (660 m)	12	30.5 ± 0.39	29.0–33.0	28.4 ± 0.25	27.0–29.6
<i>cybotes</i> (700 m)	13	29.6 ± 0.34	27.0–31.9	26.5 ± 0.38	24.5–28.4
<i>cybotes</i> (1150 m)	102	29.9 ± 0.16	23.2–33.0	26.8 ± 0.17	20.8–30.0
<i>shrevei</i> (2200 m)	42	29.2 ± 0.38	23.6–32.4	22.1 ± 0.25	19.0–25.2

*Diurnal shifts in body temperatures,
extent of thermoregulation*

Body temperatures of active cybotoid anoles at various times of day are plotted in Fig. 1. The mean hourly \bar{T}_b shows a greater change during the day in lowland populations. The apparently greater thermoconformity of lowland *cybotes* can be examined in more detail by comparing slopes of regression lines for T_b on T_a (Materials and Methods). For the anoles in our primary samples (sunny weather only), slope is inversely related to altitude (Fig. 2); and among all populations of the *cybotes* group (Fig. 3), slope is also inversely correlated with altitude ($r_s = -.744$, $P < .05$). These patterns suggest that the changes in behaviors detailed above can influence the statistical dependence of T_b on T_a .

Responses to high temperatures

Anoles in the primary samples differ slightly in sensitivity to heat stress (Table 5), but none of the measures of heat stress is significantly correlated with altitude. (Similarly, *Anolis marcanoi*, a cybotoid sampled near the 500-m *cybotes* locality (Hertz 1980a) is as tolerant of high temperatures (CTM = 40.5 ± 0.18°C) as the arid lowland sample of *cybotes*.) The estimated change in CTM per 100 m change in elevation for *cybotes* is small relative to values for other anoles (Table 4).

DISCUSSION

Behavioral, physiological, and genetic responses by lizards can collectively compensate for altitudinal changes in thermal regimes. We initially evaluate field evidence of behavioral adjustments and indirect laboratory evidence bearing on physiological and genetic responses. We then discuss comparable data on anoles from an independently derived anoline radiation, the *crisatellus* group on Puerto Rico.

Compensation for altitude

Anoles of the *cybotes* group use both long-term (habitat choice) and short-term (basking frequency, activity restriction) behavioral responses to changes in their thermal environment. Lowland populations (at <100 m) occupy relatively shaded habitats and infrequently bask—we suspect that they actually avoid sunny perches. These behaviors reduce body temperatures in hot environments. In contrast, high montane populations (at 1150 m and 2200 m) occupy relatively open habitats, bask frequently (especially *shrevei*, Table 2), and cease activity during inclement weather. Occupation of only open habitats at high elevation increases the proportion of perches that are exposed to full sun, which elevates body temperatures and also decreases potential risks and energetic costs of basking (Huey and Slatkin 1976). Thus, apparent thermoregulatory behaviors are conspicuous at the

TABLE 4. Decline in mean T_b and CTM (°C) per 100 m increase in elevation for various anoles. Rate of change estimated from linear regression equations. N = number of populations sampled.

Species	Island	N	Mean body temperature		Critical thermal maximum (CTM)		References	
			Δ Elevation (m)	$\Delta \bar{T}_b / 100 \text{ m}$	Δ Elevation (m)	Δ CTM / 100 m		
<i>crisatellus</i>	Puerto Rico	7	875	0.19	2	345	0.23	Huey and Webster 1976, Hertz 1977
<i>cybotes</i>	Hispaniola	6	1145	0.15	3	1145	0.10	This report
<i>gundlachi</i>	Puerto Rico	11	850	0.70	5	580	0.55	Huey and Webster 1976, Hertz 1977
<i>krugi</i>	Puerto Rico	4	450	0.24	Hertz 1979
<i>occulatus</i>	Dominica	4	845	0.41	Ruibal and Philibosian 1970
<i>roquet</i>	Martinique	3	620	0.67	5	630	0.12	Hertz 1977
<i>semilineatus</i>	Hispaniola	3	1185	0.21	Hertz 1979

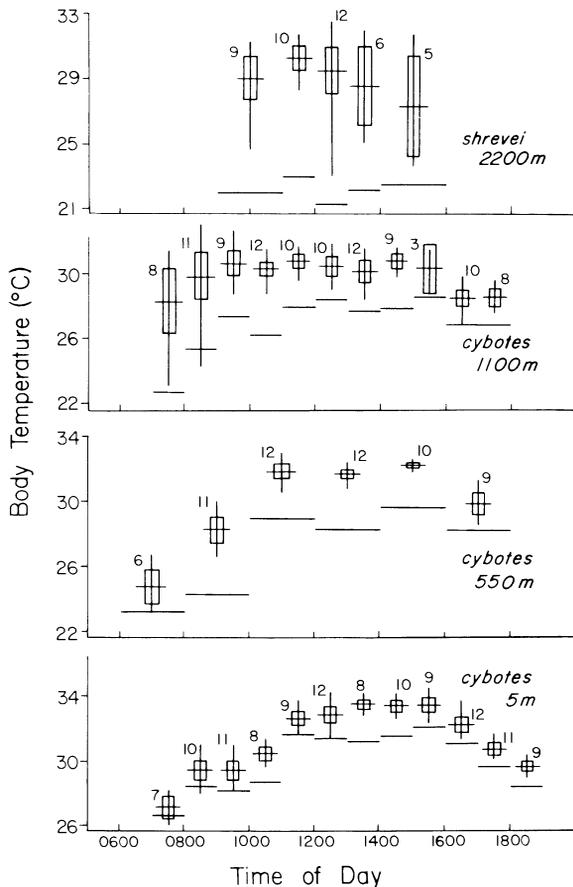


FIG. 1. Body temperatures of anoles of the *cybotes* group on Hispaniola at various times of day. Upper horizontal line = mean T_b ; box encloses 95% confidence limits of mean T_b ; vertical line = range of T_b . Lower horizontal line = mean T_a . Sample size indicated.

extremes of the altitudinal gradient. Similar behavioral shifts are described and sometimes quantified for other anoles (Rand 1964, Ruibal and Philibosian 1970, Clark and Kroll 1974, Huey and Webster 1975 and 1976, Hertz 1977) and for some other lizards (Burns 1970, Spellerberg 1972c). Morphological changes (e.g., body size, solar reflectivity), which we have not examined here, might augment these behavioral shifts (Spellerberg 1972b).

Slopes of the regressions of T_b on T_a support the argument that the behaviors exhibited by anoles at high altitude effectively elevate body temperatures (Figs. 2 and 3). However, there are two possible interpretations of the slopes (near 1) for lowland populations (Huey and Slatkin 1976: 379–380). These lizards may be sufficiently warm in relatively shaded habitats and thus would not need to bask. Alternatively, they may actively seek the coolest available microenvironments because they would be heat stressed elsewhere. Regression equations alone cannot discriminate between these two interpretations, but

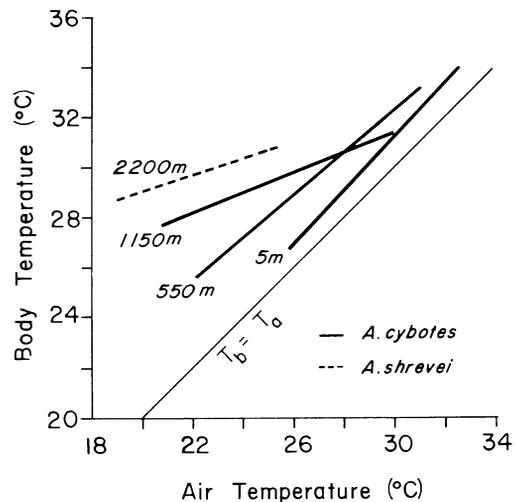


FIG. 2. Regression lines for T_b vs. T_a for primary populations of *cybotes* group on Hispaniola (sunny weather only). Altitude of each population indicated.

the conspicuous absence of these lizards in open lowland habitats argues in favor of the latter interpretation.

Altitudinal shifts in the nature of behavioral temperature regulation allow these populations to maintain relatively similar T_b . The maximum difference in \bar{T}_b among populations separated by 2200 m is only 3.0°C (Table 2). The rate of change in \bar{T}_b per 100 m elevation for *cybotes* is small relative to values for other anoles (Table 4).

We emphasize that both we and prior researchers have implicitly assumed that concomitant shifts in habitat and basking represent overt thermoregulatory shifts by lizards. Alternatively, if the lizards select habitat at random, the absence of lizards either in shaded montane forests or in some open lowland habitats could merely reflect the inability of lizards to survive in thermally extreme habitats (Gorman and Hillman 1977). Moreover, the apparent increase in basking at high elevations might in part be an artifact of the greater proportion of perches that are sunny in open habitats (see Huey et al. 1977). Our present data, which are descriptive, are insufficient to discount satisfactorily these alternative hypotheses (Heath 1964, Huey et al. 1977).

In contrast to the large changes in behavior, the extent of physiological compensation, either by acclimatization or by genetic differentiation, appears very minor in these anoles. The maximum difference in Critical Thermal Maxima among populations (Table 5) is small (1.7°)—less even than has been induced by laboratory acclimation (2.0°) in some anoles from Florida (Corn 1971). Similarly, the rate of change of CTM with elevation is relatively small (Table 4). The effectiveness of behavioral compensation for altitude, as reflected in small changes in T_b , may have precluded

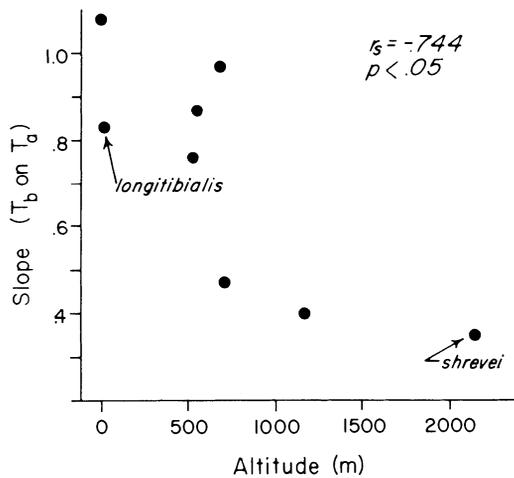


FIG. 3. Slope of regression of T_b on T_a vs. altitude for all populations of the *Anolis cybotes* group on Hispaniola (see Table 3). A slope of 0 suggests perfect temperature regulation, whereas a slope of 1 suggests thermoconformity. See Materials and Methods. Unlabeled dots are *A. cybotes* populations.

the necessity of local physiological and genetic adaptations (Bogert 1949, Hertz 1977, 1978, 1980b) in these species.

Convergence on Hispaniola and Puerto Rico

Our data on the thermal biology of the *cybotes* group on Hispaniola invite a direct comparison with similar information on the three trunk-ground anoles of the *crisatellus* group on Puerto Rico (Rand 1964, Heatwole et al. 1969, Williams 1972, Huey and Webster 1976, Lister 1976, Gorman and Hillman 1977, Hertz 1977, Hertz et al. 1979): members of these two species groups are similar in habitus and occupy comparable perch sites. Specifically, we show that these independent anoline radiations (Williams 1976) have only partially converged in biogeographical distributions and in compensatory responses to altitude.

Several species in both radiations can be arranged as obvious counterparts in altitudinal series. In lowland deserts *A. longitibialis* and *A. whitemani* are the Hispaniolan equivalents of *A. cooki* on Puerto Rico. From less arid lowlands to moderate elevations, the Hispaniolan *cybotes* and possibly the recently described *A. strami* (Schwartz 1979) are roughly equiv-

alent to *A. cristatellus* on Puerto Rico. However, *cybotes* presently occurs at much higher altitudes than does *crisatellus*.

Differences in the faunas exist, however, and can be attributed to Hispaniola's much greater size and topographic complexity (Williams 1965). For example, the *cybotes* radiation includes at least seven tree-trunk and ground-dwelling species compared with only three such species on Puerto Rico. The lack of high elevation savannah on Puerto Rico certainly accounts for the absence of a *shrevei*-like anole on this less mountainous island. However, the absence of a nonbasking, deep-forest anole (i.e., a *gundlachi*-equivalent) in the *cybotes* group is problematical, but may reflect both historical and biological phenomena. Species from older radiations in the *Anolis*-rich Hispaniolan fauna (e.g., *A. christophei*) may have pre-empted the montane forest habitat prior to the radiation of the *cybotes* group (Rand and Williams 1969).

Anolis cristatellus behaviorally compensates for altitude by changing habitat, basking intensity, and activity times (Huey and Webster 1976), a pattern that is consistent with our observations on the *cybotes* group and with those on other lizards (Bogert 1949, Spellerberg 1972c, Huey and Slatkin 1976). *Anolis gundlachi*, however, stands out as an exception. This cool forest anole rarely shifts to more open habitats and very rarely basks even at high elevation (Huey and Webster 1976, Hertz 1977). The consequently large variation in T_b among populations of *gundlachi* (Table 4) is accompanied by large interpopulational variation in CTM (Table 4). Compensation for altitude by *gundlachi* thus appears to be largely physiological and possibly genetic rather than behavioral (Hertz et al. 1979).

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TABLE 5. Body temperatures ($\bar{x} \pm SE$, °C) at which lizards exhibited responses to high temperatures: EVM = experimental voluntary maximum; PT = panting threshold; CTM = critical thermal maximum (see Materials and Methods). Common superscript letters indicate values that are not significantly different.

Population	N	EVM	PT	CTM
<i>cybotes</i> (5 m)	10	34.9 ± 0.10	37.9 ± 0.10	40.1 ± 0.15 ^b
<i>cybotes</i> (550 m)	12	34.3 ± 0.07 ^a	36.8 ± 0.13	38.4 ± 0.13
<i>cybotes</i> (1150 m)	12	33.9 ± 0.13 ^a	36.2 ± 0.09	39.0 ± 0.21
<i>shrevei</i> (2200 m)	10	34.1 ± 0.18 ^a	38.7 ± 0.18	40.1 ± 0.12 ^b

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