

EFFECTS OF LATITUDE, SEASON, ELEVATION, AND MICROHABITAT ON FIELD BODY TEMPERATURES OF NEOTROPICAL AND TEMPERATE ZONE SALAMANDERS¹

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Abstract. We analyzed field body temperatures of neotropical salamanders (Feder et al. 1982b) to examine existing generalizations about salamander thermal ecology, which have been based almost entirely upon data for temperate zone species. Our findings can be summarized as follows:

1) *Behavioral thermoregulation* in the field is evidently uncommon among the vast majority of tropical and temperate salamander species. Body temperatures of tropical salamanders closely parallel seasonal and altitudinal changes in the thermal environment.

2) *Body temperatures* of salamanders show a complex relationship with latitude. Temperate zone species experience lower minimum temperatures than neotropical salamanders, but there are no consistent latitudinal trends in maximum body temperatures. Tropical plethodontids and ambystomatids show similar rates of decline in mean body temperature with increasing elevation, but ambystomatid temperatures are significantly warmer than plethodontid temperatures at the same elevation.

3) *Variation in body temperature* is greater seasonally for temperate salamanders than tropical salamanders. At a given time or locality, however, variation in field body temperature among members of a population is similar for tropical and temperate salamanders.

4) *Interspecific thermal differences* are not evident in sympatric species of tropical salamanders, and therefore may not serve as a means of niche segregation in tropical salamander communities.

These latitudinal and phylogenetic differences in thermal ecology correspond to aspects of the morphology, life history, energetics, and physiological capacities of salamanders.

Key words: Ambystomatidae; ectothermy; Plethodontidae; Temperate Zone; temperature; thermoregulation; tropical; variability.

INTRODUCTION

In the Neotropical Region, salamanders exploit diverse habitats from lowland rain forest to montane paramo (Wake and Lynch 1976). The neotropical salamanders include two families: the Plethodontidae, which lack lungs, and the Ambystomatidae. The tropical plethodontids are widely distributed and are terrestrial or arboreal; the tropical ambystomatids have restricted distributions in northern and central Mexico and are primarily aquatic. The neotropical salamanders are expected to differ from their temperate zone counterparts in many aspects of their biology, particularly in thermal relationships. Here we analyze field body temperatures of tropical salamanders to test the validity of previous generalizations about salamander thermal ecology. The latter have been based almost entirely upon observations of temperate-zone species.

The first of these generalizations is that salamanders in the field exert little behavioral control of their body temperatures, i.e., that salamanders are classical 'poikilotherms' (Bogert 1952, Brattstrom 1963, 1970a). One of several potential causes for such poikilothermy in terrestrial salamanders from the temperate zone is that microhabitats that might otherwise be selected to regulate body temperature are prohibitively dry (Feder and Pough 1975, Tracy 1976, Brattstrom 1979). If lack of suitably moist microhabitats indeed limits behavioral thermoregulation of temperate zone salamanders, then such thermoregulation might be expected to occur more frequently in the humid tropics.

A second generalization is that salamanders, particularly plethodontids, are physiologically restricted to relatively cool temperatures. Abundant field data for temperate zone salamanders (Brattstrom 1963, Feder et al. 1982b) support this contention. Some investigators have suggested that the generally cool body temperatures of temperate zone plethodontids reflect

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physiological limitations, and that such limitations have constrained the geographic distribution, local abundance, behavior, reproductive tactics, and morphological diversification of salamanders (Whitford and Hutchison 1965, 1967, Bachman 1969, Beckenbach 1975). Maximum field body temperatures of tropical salamanders, especially plethodontids, are of special interest in this regard (Wake 1970, Feder 1976).

A third generalization concerns thermal variability. Because tropical climates typically exhibit much lower seasonal and daily thermal variability than temperate climates (Janzen 1967), the thermal regime of tropical salamanders should be relatively stable. Latitudinal differences in climatic stability are thought to underlie both the finely partitioned altitudinal segregation of tropical species (Schmidt 1936, Wake and Lynch 1976, Huey 1978) and latitudinal variation in the physiological responses of amphibians to thermal variation (Snyder and Weathers 1975, Feder 1978, 1982a). However, latitudinal differences in annual variation of body temperature in individual species have not been documented previously, and are examined here.

Temperature is a potentially important niche dimension along which species may segregate to lessen competitive overlap (Magnuson et al. 1979). However, temperature appears to play little or no role in the local structuring of temperate zone salamander communities, despite the restriction of some species to certain elevational or vegetational zones. At a given location, sympatric salamander species have similar body temperatures (Bogert 1952, Spotila 1972, Lynch 1974). Differences in water relations and competition for space seem to be the major determinants of interspecific segregation for terrestrial salamanders in the Temperate Zone (e.g., Dumas 1956, Jaeger 1971a, 1971b, Spotila 1972, Hairston 1980). In the present study we consider thermal differences as one potential means of niche segregation in tropical salamander communities. Up to 15 salamander species occur on a single tropical mountainside, and as many as 6 of these may be locally sympatric (Wake and Lynch 1976).

In summary, this report contrasts tropical and temperate zone salamanders with respect to: (1) behavioral thermoregulation, (2) maximum and minimum field body temperatures, (3) spatial and temporal variability in field body temperatures, and (4) interspecific differences in body temperature within local communities.

MATERIALS AND METHODS

We gathered body temperatures of tropical plethodontids by measuring the temperature of the substrate immediately beneath resting salamanders with either a YSI Telethermometer (Yellow Springs Instrument Company, Antioch, Ohio) or a Schultheis quick-reading mercury thermometer. Bogert (1952) has shown that this method yields accurate approximations of salamander body temperatures. We shaded the temperature sensor and carefully avoided changing the substrate temperature inadvertently during measurements.

Our data for tropical ambystomatids all refer to aquatic forms. Water temperatures were taken 15 cm deep at arm's length from the water's edge, the general area where most salamanders were captured. Voucher specimens have been deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, California. A complete listing of the primary data, including localities, habitat information, and collection dates, is available from the Herpetological Information Service, Smithsonian Institution, Washington, D.C., (Feder et al. 1982b).

We also reviewed the literature for records of body temperatures for temperate zone salamanders; a listing of these data is likewise available (Feder et al. 1982b). We have omitted unreliable records (e.g., measurements of air temperature at collection sites) from this compilation.

To analyze the effects of season, latitude, and elevation on body temperatures of tropical salamanders, we performed stepwise multiple linear regression on the mean temperature for each sample of a tropical species taken at a given place and date. We omitted means for tropical plethodontids that represented records for fewer than three conspecific individuals. This protocol avoided undue weighting of large numbers of temperature records for a given species at one particular time and location; at the same time it eliminated possibly misleading isolated temperature records for single individuals. Records for tropical species were pooled into two seasonal categories (Winter = November–March; Summer = April–October), and two latitudinal zones (Northern tropical = Mexico north of Chiapas; Mid-tropical = Chiapas and Middle America). Season, latitude, and family (plethodontid or ambystomatid) were entered into the regression equation as dummy variables (Draper and Smith 1966), with values either 0 or 1.

Tests of between-sample differences in central tendency or variability used nonparametric statistical procedures as described by Siegel (1956).

RESULTS

Body temperatures

Elevation, season, and family each significantly influence mean body temperatures of neotropical salamanders (Table 1, Fig. 1). For tropical plethodontids, a simple regression of mean body temperature against elevation explains nearly two-thirds of the variance in mean body temperature [$r^2 = \text{Coefficient of Determination} = .63$]. Addition of season to the regression equation (step 2) increases r^2 to .75, but the inclusion of latitude (step 3) has no significant effect. The regression equation for tropical plethodontids is thus:

$$\begin{aligned} \text{Mean body} \\ \text{temperature (}^\circ\text{C)} &= 27.3 - 5.1 \text{ Elevation (km)} \\ &\quad - 3.2 \text{ Season} \end{aligned} \quad (1)$$

where season is coded 1 for winter and 0 for summer.

TABLE 1. Summary of analysis of covariance for mean body temperatures of tropical salamanders.

| Source of variation | df | Mean square | F | P |
|-----------------------------|-----|-------------|---------|-------|
| Constant | 1 | 30102.48 | 3798.60 | <.001 |
| Elevation | 1 | 1217.84 | 153.68 | <.001 |
| Season | 1 | 279.88 | 35.32 | <.001 |
| Family | 1 | 509.41 | 64.28 | <.001 |
| Elevation × season | 1 | 3.85 | 0.49 | .487 |
| Elevation × family | 1 | 0.13 | 0.02 | .900 |
| Season × family | 1 | 27.60 | 3.48 | .065 |
| Elevation × season × family | 1 | 4.91 | 0.62 | .433 |
| Within + residual | 110 | 7.92 | | |

The relationship between mean temperature and elevation is similar for tropical ambystomatids:

Mean body temperature (°C) = 32.0 - 5.0 Elevation (km) - 5.0 Season (2)

However, temperatures for tropical ambystomatids and tropical plethodontids differ in several ways. At comparable seasons and elevations, mean temperatures for ambystomatids are greater, possibly more seasonal ($P = .065$, Table 1), and less well correlated with elevation and season (r^2 for Eq. 2 = .47) than are equivalent values for plethodontids.

For most tropical species, samples are too few or elevational ranges too narrow to allow a meaningful test for elevation-body temperature correlations within species. However, for 12 tropical populations of the ambystomatid *Ambystoma tigrinum*, the body temperature, elevation, and season are related as follows:

Mean body temperature (°C) = 29.7 - 3.7 Elevation (km) - 5.4 Season (3)

Elevation accounts for 33% of the variance in body temperature, and season accounts for an additional 28%. Of the three species of tropical plethodontids (*Bolitoglossa franklini*, *Chiropterotriton chiropterus*, and *Pseudoeurycea leprosa*) for which at least four samples are available throughout a substantial elevational span, only *P. leprosa* ($n = 4$ samples) showed a significant correlation between mean body temperature and elevation (Spearman's $r = -1.0$; $P < .05$). However, values of r_s for the remaining two species have the predicted negative sign, and we suspect that larger samples would reveal significant altitudinal trends within all tropical salamander species that have significant elevational distributions.

Fig. 2 depicts maximum and minimum temperatures for both tropical and temperate salamander species. In species with records for only one season, winter temperatures were omitted from analysis of maximum temperature and summer temperatures were omitted from analysis of minimum temperature.

Maximum body temperatures are greater for non-

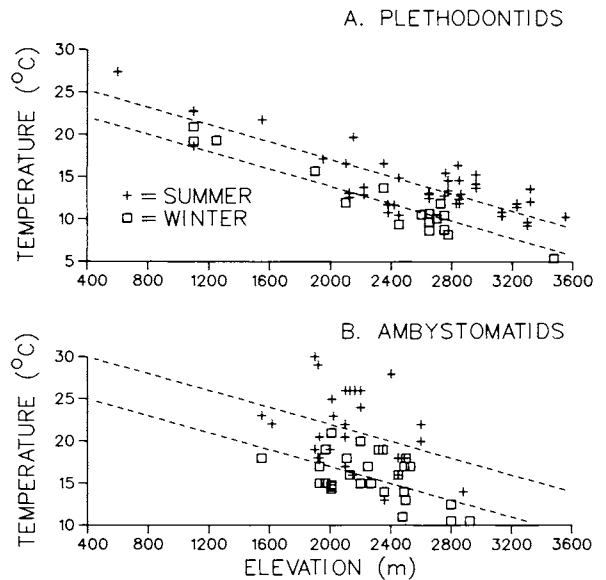


FIG. 1. Effect of elevation and season on body temperatures of tropical plethodontid (above) and ambystomatid (below) salamanders. Regression lines for winter and summer are plotted in each figure.

plethodontids than for plethodontids, both at tropical and temperate latitudes (Table 2). Most instances in which maximum temperatures for nonplethodontids exceed 25° involve either aquatic larvae (e.g., *Ambystoma* spp., *Taricha rivularis*) or adults of species that inhabit still water (e.g., *Siren* spp.). The only comparably high value for a temperate plethodontid involves *Eurycea [Manculus] quadridigitatus* (maximum temperature = 26.3°), a swamp-dwelling form (Feder et al. 1982b).

Temperate species experience lower minimum temperatures than tropical species (Table 2). In addition, tropical plethodontids have lower minima than tropical ambystomatids.

Variation in body temperature

Each sample of body temperatures (all records for a given species taken at a single locality on the same day) reflects thermal variation experienced by a population under prevailing climatic conditions. We quantified this variation by calculating the range and standard deviation for each sample. Few previous reports have included both of these statistics, so we have analyzed them separately.

Both range (Fig. 3) and standard deviation of temperatures within a sample show the same pattern. No differences in within-sample variability are evident between tropical and temperate plethodontids or between temperate plethodontids and nonplethodontids ($P > .05$; Kruskal-Wallis test for difference in central tendency and Kolmogorov-Smirnov test for shape of distributions).

For tropical plethodontids, the standard deviation

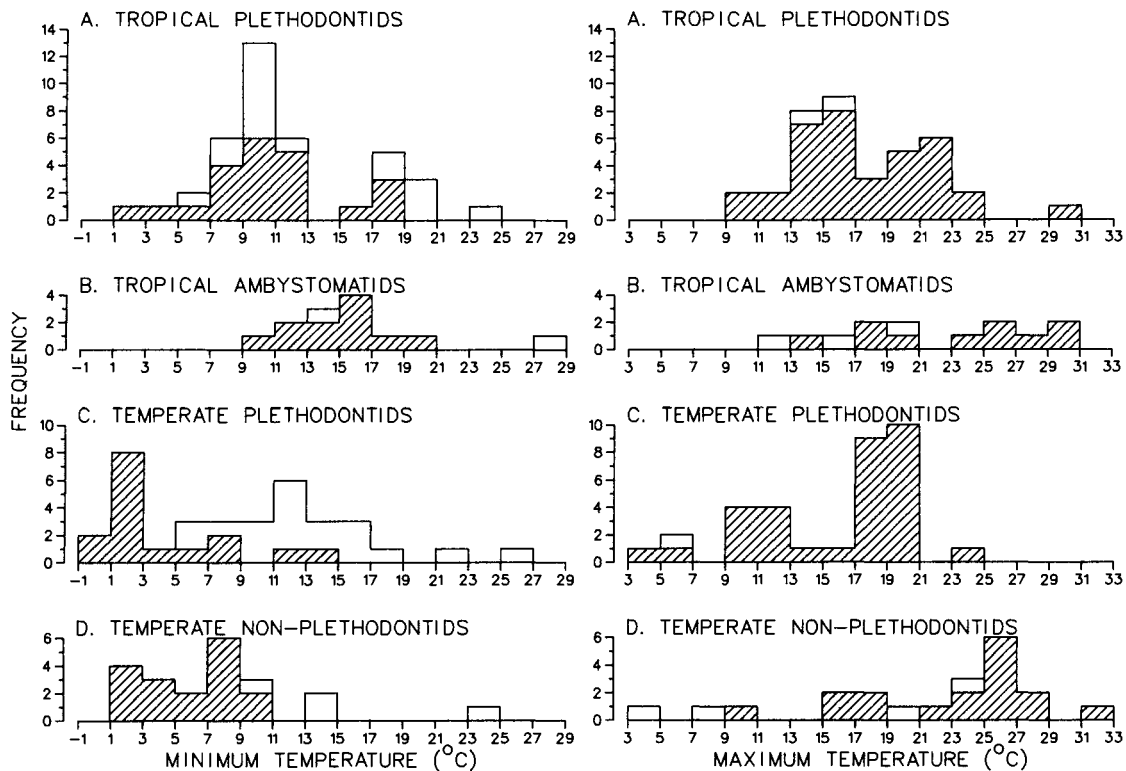


FIG. 2. Minimum and maximum body temperatures of salamanders. Unshaded bars represent species for which only summer records were available for minimum temperature or species for which only winter records were available for maximum temperature.

of series temperatures is unrelated either to elevation or to the number of temperature records in a series ($P > .05$; Kendall's tau). However, the range of temperatures is proportional to the number of temperature records in a series; the partial correlation coefficient between range and sample size (with elevation held constant) is $.52$ ($P < .001$).

Detailed seasonal records of temperatures are lacking for most species, but sufficient data are available for 48 populations (Feder et al. 1982b) to allow some generalizations. Tropical and temperate salamanders differ markedly in seasonal variability in temperature. With values for plethodontids and nonplethodontids pooled, annual variation is $16.8 \pm 1.1^\circ$ (mean \pm standard error) for temperate species ($n = 28$) but only $7.6 \pm 0.7^\circ$ for tropical species ($n = 20$). These differences in variation are highly significant (Table 2). Thus, temperate salamanders experience more than twice the annual thermal variation of their tropical counterparts. Indeed, the figures presented here undoubtedly understate the true latitudinal differential, as many temperate species must experience near-freezing temperatures in their winter retreats, where they are inaccessible to collectors. Except for a few high montane forms, tropical salamanders are rarely or never subjected to temperatures this low.

The above generalizations fail to encompass some temperate and tropical species. Notable exceptions (Feder et al. 1982b) include temperate species that live in forested, thermally equable streams (e.g., *Dicamptodon*, *Rhyacotriton*), caves, or cave outflows (e.g., *Eurycea multiplicata*). These taxa resemble tropical species in encountering only modest seasonal temperature fluctuations.

Species differences

Body temperatures are available for 11 pairs of neotropical salamander species collected in sympatry (Feder et al. 1982b). None of the members of these species pairs differs significantly in temperature, and the largest measured temperature difference between any two species at a given site is only 1.1° . Thus, thermal segregation seems uncommon as a mechanism for subdividing habitat space among locally sympatric neotropical plethodontids.

DISCUSSION

It is important to recognize the implicit assumptions in using single measurements from different individuals to estimate the range of thermal conditions encountered by a salamander population as a whole. Many terrestrial salamanders alternate between sur-

TABLE 2. Mean temperature records and mean annual variation for tropical and temperate salamanders. We performed all possible pairwise Mann-Whitney *U* tests among groups within columns. Superscript letters indicate results of tests with Bonferroni's inequality. Groups are considered significantly different when *P* of *U* < (.05/number of pairwise tests). Means with common superscript letters do not differ significantly.

| Group | Body temperature | | |
|----------------------------|------------------|-------------------|-------------------|
| | Minimum | Maximum | Annual range |
| Tropical nonplethodontids | 14.6 | 23.2 ^d | 7.9 ^a |
| Tropical plethodontids | 9.7 | 17.4 ^e | 7.3 ^a |
| Temperate nonplethodontids | 5.6 ^b | 21.8 ^d | 17.5 ^c |
| Temperate plethodontids | 3.3 ^b | 17.9 ^e | 16.1 ^c |

face and subterranean microhabitats, and 90–100% of a given population may be underground at any given time, even when surface activity is feasible (Anderson 1960, Heatwole 1962, Burton and Likens 1975, V. Maiorana, personal communication). Because deep soil temperatures are stable and moderate (Geiger 1965), measurement of surface temperature alone is likely to overestimate the thermal variability of the population as a whole. In addition, salamanders often are highly sedentary, with home ranges of only a few square metres (Maiorana 1974). Hence no individual animal may encounter the full range of temperatures measured from a series of salamanders at a given locality. In the extreme case, one individual may experience consistently warm temperatures throughout the activity season, while another individual in a shady spot a few metres away might experience cooler but equally stable temperatures. Yet a series of single temperature readings representing many individuals might suggest that individual salamanders are subjected to a variable thermal environment. Continuous records of individual salamanders or appropriate microhabitats may be necessary to resolve such ambiguities, but repeated disturbance of cover objects is likely to disrupt both the animals themselves and their microclimate. Pending the availability of data from highly miniaturized thermal telemeters, the admittedly imperfect data we present here are as realistic as can be obtained in the field.

A surprising outcome of our tropical-temperate comparison is that tropical plethodontids do not experience maximum temperatures greater than those of temperate salamanders. This result may in part reflect our unintentional bias in favor of montane tropical species; only 11% of our 97 temperature series are from populations living below 1500 m elevation. This underrepresents the tropical lowland plethodontids, which constitute 20% (30 species) of all tropical plethodontids (Wake and Lynch 1976, Feder et al. 1982a). Body temperatures of lowland tropical plethodontids occasionally are as warm or warmer than those of their

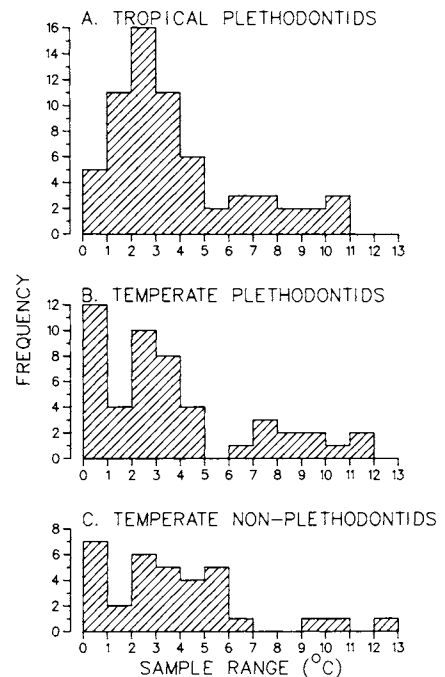


FIG. 3. Range of body temperatures for salamanders. Each range is for a sample of conspecific salamanders taken at the same site on a given day. Only samples for which *n* > 3 are included.

temperate zone counterparts (Maximum = 30°C; Fig. 2). Nevertheless, the overall lack of latitudinal differences in maximum temperature is not entirely unexpected, for maximum warm-season temperatures are similar in many temperate and tropical areas (Mac Arthur 1972).

In general, tropical plethodontids experience the same moderate maximum body temperatures as their temperate zone counterparts. We speculate that a major factor underlying this similarity is the interaction between lunglessness and the temperature of suitable microhabitats. Except in the moist tropical lowlands, warm terrestrial microhabitats tend to be too dry to be suitable retreats for salamanders (Feder and Pough 1975). Because they lack lungs, plethodontids may have difficulty in exploiting warm but oxygen-deficient aquatic microhabitats (Ultsch 1976a, Feder 1977). Oxygen exchange in submerged plethodontids is highly susceptible to hypoxic limitation (Beckenbach 1975, Ultsch 1976b), and plethodontids cannot compensate for aquatic hypoxia by inspiring air at the surface, a common practice in many aquatic vertebrates (Randall et al. 1981). The fact that most records of body temperatures $\geq 25^\circ$ involve aquatic nonplethodontid salamanders, both in the tropics and the temperate zone, supports this speculation.

Our data provide no evidence for behavioral thermoregulation in either temperate or tropical salamanders.

ders. The mean decrease in salamander body temperature with increasing elevation (5.1°/km) is similar to the adiabatic lapse rate for moist air, 6.5°/km (Miller and Thompson 1975). Tropical salamanders act as essentially passive indicators of the prevailing surface temperature, and show little tendency to depart from 'average' conditions expected for a given site. The few known instances of thermoregulation in the field by tropical plethodontids (Feder 1982b) are clearly exceptional. These involve extremely diminutive salamanders (*Thorius*) that seek out warm temperatures in the space beneath loose bark on logs exposed to the sun. The larger size of most other tropical salamanders denies them access to this moist thermal gradient.

The data (Feder 1982b, Feder et al. 1982b, and references cited therein) suggest only that thermoregulation is infrequent among salamanders, and not that temperature is unimportant to salamanders. Temperature has profound effects on the energetics, growth, and reproduction of salamanders (see below). Our data also do not rule out the possibility that salamanders engage in activities such as courtship and foraging only within limited temperature ranges, and thereby effectively 'maintain' stable body temperatures during activity. Both energetic costs and the potential vapor pressure gradient are proportional to temperature; salamanders may be restricted to nocturnal foraging within a narrow range of temperatures even though the temperature per se does not limit foraging (Spotila 1972). No conclusive data are available to substantiate these possibilities; however, circumstantial evidence suggests that foraging activity in terrestrial salamanders is primarily a function of their water relations and not of temperature per se (Rosenthal 1957, Spotila 1972, Jaeger 1978), and that tropical plethodontids court and oviposit without regard to seasonal thermal variation (Houck 1977).

The apparent rarity of behavioral thermoregulation in tropical salamanders may be due in part to the low thermal heterogeneity in moist tropical forests, particularly in the cloud forest inhabited by many species (Wake and Lynch 1976). Records for contiguous moist microsites within individual bromeliads (*Tillandsia* spp.) and banana plants (*Musa* sp.) yield temperature ranges of 2.0° and 3.7°, respectively (Feder 1982b). Given this modest thermal gradient, salamanders can exert little behavioral control of their body temperatures, and clearcut interspecific differentiation cannot occur within a local habitat. Moreover, we are unable to document any consistent thermal differences associated with particular microhabitats, other than their elevation. Thus, little distinguishes the thermal environment of terrestrial vs. arboreal sites, or leaf litter vs. rocks or logs as cover objects.

Many studies that have contrasted thermal specializations of temperate and tropical organisms (e.g., Brattstrom 1968, 1970b, Levins 1969, Snyder and Weathers 1975, Feder 1978, 1982a) have been predi-

cated on the well-established difference in thermal variability between tropical- and temperate-zone climates (Janzen 1967). However, none of these studies has measured thermal variation experienced by individual organisms; instead, gross climatic characteristics have been used as an index of probable variation in animal body temperature. This approach can lead to erroneous results for at least two reasons. First, microclimate often differs markedly from the macroclimate measured by weather stations (Swan 1952, Bartholomew 1958, Geiger 1965). In addition, a thermoregulating animal may experience a thermal environment that is very different from the 'climatic' temperature, however the latter is measured (Pearson 1954). Thus, our field data are significant in that they are the first documentation of major latitudinal differences in variability of body temperatures of related animals.

Possible ecological consequences of the observed latitudinal differences in thermal ecology include differences in feeding and assimilation rates (Merchant 1970, Bobka et al. 1981), reproductive periodicity (Houck 1977), growth and differentiation (Houck 1977, Hanken 1979), and other fundamental aspects of life history (Hanken et al. 1980). Tropical plethodontids have lower temperature-specific rates of oxygen consumption than temperate salamanders (Feder 1976, 1977). Also, tropical plethodontids are less able than temperate species to undergo thermal acclimation of oxygen consumption (Feder 1978). These differences may reflect an historical loss of ancestral physiological capacities by neotropical plethodontids, perhaps in response to the reduced thermal variability of their environments.

Physiological ecology has advanced considerably beyond the classical dichotomous characterization of organisms as 'poikilotherms' and 'homeotherms.' Recent research has documented the diverse means by which organisms exert behavioral and physiological control of their thermal environment (Brattstrom 1979, Regal and Gans 1980). Accordingly, it is somewhat ironic to conclude from our field studies that most salamanders, particularly plethodontids, functionally embody the classical definition of poikilothermy. However, this is less than surprising given that thermoregulatory strategies evolve only within the constraints of the physical environment (Spotila 1980).

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