

Comparative field responses to diel and annual thermal regimens among Sceloporine lizards, with specific reference to *Sceloporus malachiticus*

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Abstract: *Sceloporus malachiticus* is a diurnal iguanid lizard occupying upland and montane areas through much of Mexico and Central America. In Costa Rica, where field observations were made, this species utilizes various habitats between elevations from about 600 to more than 3,000 meters. In response to the diel march of temperature, activity usually demonstrated a unimodal peak in the late morning hours, prior to the onset of cloud cover. Body temperatures generally exceed those of both ambient air and substratum; active animals exhibit a greater differential than inactive ones. Body temperatures range from 8.4 °C to 34.4 °C, of which the voluntary activity range is 22.0 to 34.4 °C (±28.6 °C). No significant differences were found among different size or sex groupings. Basking behavior is common throughout the range of activity in all groups. Neither hibernation nor acclimation is exhibited in montane *S. malachiticus*.

In comparing these thermal responses with other sceloporines, the most conspicuous feature of this population of *S. malachiticus* is its low thermal preferendum. Among the collective voluntary activity ranges and preferenda reported for other members of the genus there is an obvious contrast with the results obtained. Further evidence acquired during this study indicates that thermal preferenda among sceloporines are more characteristic of their autecology than their phylogeny.

The iguanid lizard species, *Sceloporus malachiticus* ranges in distribution from the Chiapas and Veracruz regions of Mexico through Central America to Panamá (Peters and Donoso-Barros, 1970). In Costa Rica, where data for this report were obtained, this lizard inhabits the upland and montane elevations from about 2,000 to over 12,000 feet (610 to 3,658 m).

Thermal responses and activity among lizard species have been extensively studied in both field and laboratory (valuable reviews have been published by Brattstrom, 1965; Cloudsley-Thompson, 1971; Dawson, 1967; and Templeton, 1970). In his report on thermal characteristics of Mexican sceloporines Bogert (1949) included information on a Honduran population referred to *Sceloporus formosus malachiticus* Wettstein, a race synonymized with *S. m. malachiticus* Cope, by Taylor (1956). My objective in this study has been to determine certain thermal requirements of montane Costa Rican populations of *S. malachiticus* for comparison with congeneric populations at different elevations and latitudes.

MATERIAL AND METHODS

Field studies relating to this report were conducted in the Cordillera de Talamanca in Costa Rica over an altitudinal range of approximately 1 400 m (from 2 130 to 3 510 m). The lizards were either noosed alive or taken by .22 caliber dust shot. Temperatures were recorded with a Schultheis rapid reading small animal thermometer, previously standardized with laboratory instruments. Body (core) temperatures were taken within 15 seconds of capture or shooting. Immediately following, substratum readings were made at point of sighting with the shaded instrument bulb pressed horizontal to the surface. Air temperatures, also shaded, were recorded at 2 cm above the substratum.

In making comparison of defined thermal responses, I am translating various uses of the terminology to the context of Brattstrom (1965).

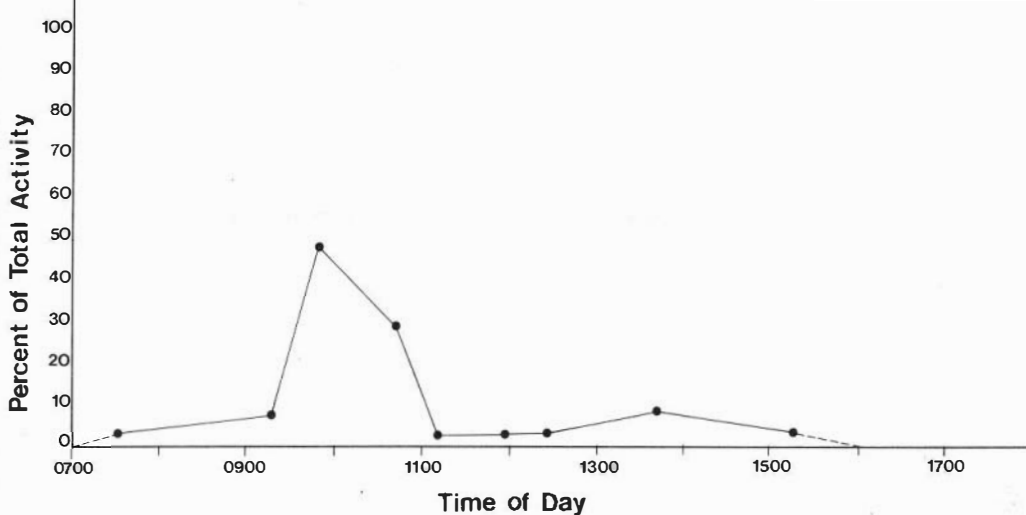


Fig. 1. Diel periodicity of activity for *S. malachiticus* plotted as percentage of total observations for time of day (hours are GMT-6).

RESULTS

General behavior: *Sceloporus malachiticus* occurs in diverse habitats in Costa Rica including urban, rural, and remote settings. It is considerably opportunistic and facile in occupying rock fences or outcroppings, comparatively open sites of cultivated gardens or crops, low brush, or sparse timber (being to some degree arboreal). Such habitats commonly provide the direct light exposure required for a functional heliotherm, which is thus precluded from utilizing much of the well developed forest environments. Inactive lizards are typically found beneath rocks or hidden under vegetation and debris in crevices or depressions. The emergence pattern is one of slow exposure, requiring several minutes at least, in which the head is first protruded from the shelter followed gradually by more of the body (similar to that described by Fitch, 1956, for *Crotaphytus*). It is not uncommon for an animal to remain stationary for some time at the entrance to its retreat prior to beginning active forays.

Periodicity: *Sceloporus malachiticus* is invariably diurnal in its activity regime. Over a period of several years and seasons during which records were obtained, I never observed any

crepuscular or nocturnal activity. Although light is certainly the primary cue, temperature modulates the daily regime of activity on montane Costa Rica as shown in Figure 1, in which I have plotted accumulated frequencies of sightings of active lizards, as percentages, against time of day (GMT-6 hrs). Between 9 and 10 °N, the latitude of my field work, there is less than one hour variation in annual photoperiod. Sightings of active *Sceloporus malachiticus* rarely occurred before 0730 or after 1520 hours. By far the greatest percent of activity occurs during the middle to late morning, between 0900 and 1100; a definite unimodal pattern. Physical factors contributing to this pattern I have described extensively (Vial, 1968); summarily, it follows the typical march of daily temperature in the area.

In Costa Rica, these lizards can be found active throughout all seasons in every habitat where they occur. While occasional shifts in daily activity cycles were seen, corresponding to local climatic changes, these were but ephemeral variations of the illustrated sequence.

Ambient temperatures: My field records include 80 observations in which correlative ambient air, substratum and body temperatures are reliably accurate. Air temperatures (at 2 cm) ranged from 8.4 °C (in May) to 28.4 °C

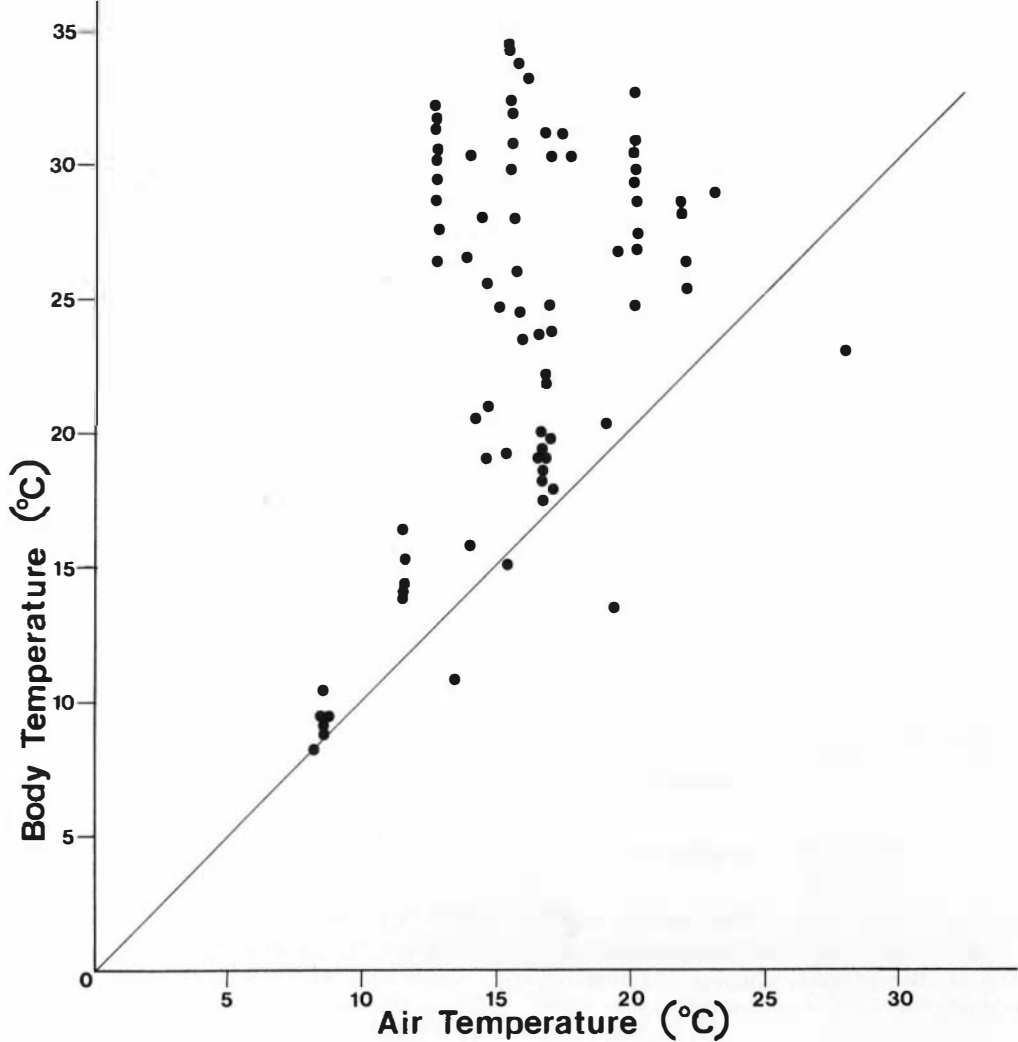


Fig. 2. Concurrent ambient air and body temperatures obtained for *S. malachiticus*.

(late February), \bar{x} of 15.6 °C. The extremes of substratum temperatures were 9.0 °C and 44.2 °C (\bar{x} 21.1 °C).

Thermal related behavior: Habitats occupied by *S. malachiticus* invariably provide a sun-shade mosaic, which includes basking sites and retreats enabling the animal to adjust behaviorly within ambient thermal extremes. Air and substratum temperatures recorded nearly simultaneously with body temperatures are shown graphically in Figures 2 and 3, respectively. Body temperature extremes,

including inactive animals, were 8.4 °C and 34.4 °C (\bar{x} 23.8 °C).

In only five of eighty records did air temperatures exceed body temperatures: in all but one case these were associated with inactive animals. Active animals generally exhibit a higher differential above air temperature than those found inactive. In no instance did air temperatures equal or exceed the high extreme of the voluntary activity range.

Substratum temperatures more nearly approach the isotherm with body temperature (Fig. 3), although there is still considerable

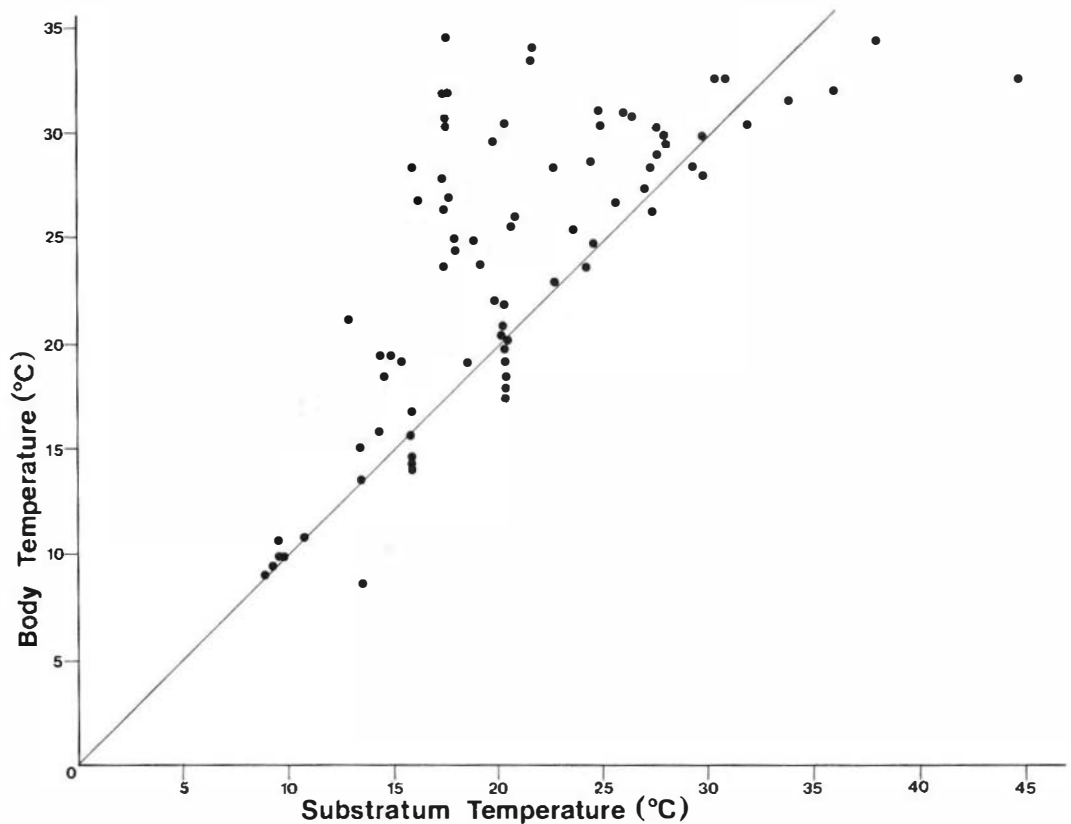


Fig. 3. Concurrent substratum and body temperatures obtained for *S. malachiticus*.

scattering of the points. Nine records show higher substratum than body temperatures—all among inactive animals, whereas 21 inactive individuals had body temperatures lower than the substratum. Only two substratum temperatures are in excess of the voluntary maximum of 34.4 °C body temperature, a strong indication of the extent of behavioral thermoregulation present.

All lizards with body temperatures of less than 22.0 °C were inactive when discovered. The range of temperatures obtained for inactive animals (N = 30) was from 8.4 °C to 21.8 °C (\bar{x} 15.9 °C). In contrast, the voluntary thermal range of active lizards (N = 50) was from 22.0 °C to 34.4 °C (\bar{x} 28.6 °C).

Of the 80 records, 66 individuals were identified as to maturity and sex. Among these 21 adult males had body temperatures of from 10.6 °C to 33.2 °C (\bar{x} 25.4 °C); active males (N=15) ranged from 23.6 °C to 33.2 °C (\bar{x} 28.7 °C); inactive (N=6) from 10.6 °C to 21.8 °C (\bar{x}

16.7 °C). Among 32 females the range was from 8.4 °C to 34.4 °C (\bar{x} 24.6 °C); active females (N=24) from 22.0 °C to 34.4 °C (\bar{x} 28.1 °C); inactive females (N=8) from 8.4 °C to 20.6 °C (\bar{x} 13.9 °C). Juveniles (N=5) exhibited a range of from 9.6 °C to 32.4 °C (\bar{x} 23.1 °C); active (N=15) from 22.0 °C to 32.4 °C (\bar{x} 28.1 °C); inactive (N=10) from 9.6 °C to 20.6 °C (\bar{x} 16.9 °C). A summary of these data is given in Table 1. Chi square analyses do not indicate differences within the active and inactive groupings, nor in comparison of all males, females, and juveniles.

TABLE 1
Summary of body temperature (°C) ranges and means for male, female, and juvenile *S. malachiticus*, both active and inactive.

	Male	Female	Juvenile
Active	23.6-33.2 (\bar{x} 28.7)	22.0-34.4 (\bar{x} 28.1)	22.0-32.4 (\bar{x} 28.1)
Inactive	10.6-21.8 (\bar{x} 16.7)	8.4-20.6 (\bar{x} 13.9)	9.6-20.6 (\bar{x} 16.9)
All	10.6-33.2 (\bar{x} 25.4)	8.4-34.4 (\bar{x} 24.6)	9.6-32.4 (\bar{x} 23.1)

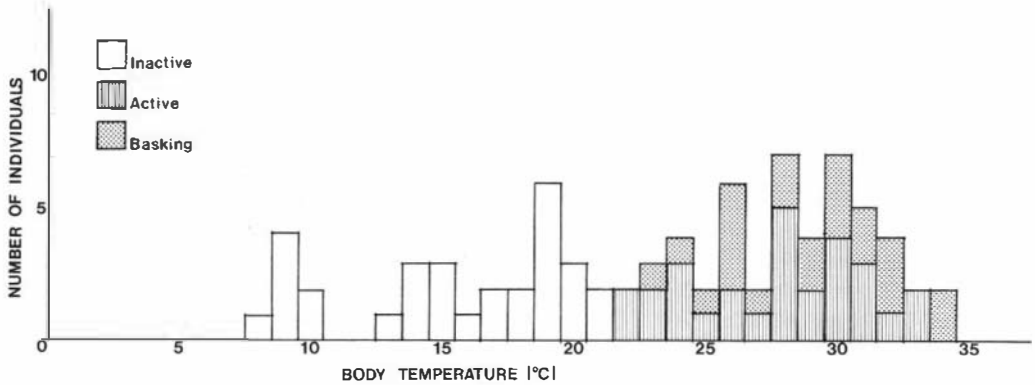


Fig. 4. Range and frequency of body temperatures obtained for inactive, active and basking *S. malachiticus* (N = 80)

Basking behavior: By definition, all heliotherms exhibit basking behavior which enables them to attain relatively rapid absorption of solar radiation. It is typical of many sceloporines including *S. malachiticus* (Bogert, 1949; Brattstrom, 1956; Templeton, 1970). A histogram showing the range of body temperatures over which basking behavior was observed is shown in Figure 4. These records demonstrate that basking behavior in *S. malachiticus* not only occurs shortly after the lizard becomes active, but is also common throughout the voluntary activity range. It is probable that some of the higher body temperatures obtained were the result of basking behavior just prior to the time of observation. Mayhew (1963) has noted several of the possible factors contributing to variable body temperature measurements obtained in the field.

Acclimation: Among the populations of *Sceloporus malachiticus* I studied, there was no evidence of statistical significance in the thermal measurements that would indicate an acclimation to either seasons or elevations.

DISCUSSION AND CONCLUSIONS

As with other tropical sceloporines, *S. malachiticus* does not demonstrate the seasonal hibernation so typical of extratropical species (Burns, 1970; Mayhew, 1963; Mueller, 1969; Vitt, 1974).

The restriction to diurnal activity is a characteristic of the genus and only rare exceptions have been noted among individuals (not

species). Mayhew (1963) observed a specimen of *S. orcutti* to remain exposed throughout the night, although it apparently did not change its location or position. My own records on this species show that it is emergent between dawn and dusk.

Bogert (1949) described the distinctive patterns of diel activity cycles between those *Sceloporus* populations inhabiting hot, arid regions and those occupying cooler, moist habitats: basically the contrast is between bimodal and unimodal peaks related to ambient thermal conditions. In the cloud forest of Honduras he observed *S. malachiticus* to have a late afternoon activity peak that followed the dissipation of cloud cover and fog. In montane Costa Rica the orogenic climatic effect is such that cloud cover typically develops during late morning and early afternoon, often producing a dramatic reduction in ambient temperatures. As one example of note, during a late morning in March, rapidly forming ground level clouds resulted in lowering the substratum temperature from 44.2 °C (the highest recorded—see Figure 3) to 36.2 °C within 2.5 minutes.

Most investigators who conduct field studies on thermal criteria of herptiles include measurements of air and substrata in their observations. With some notable exceptions (e.g. the difficulty of obtaining accurate readings on irregular rock surfaces) it is generally accepted that the former records are less informative than the latter (Cole, 1943). Mayhew (1963) in particular notes the discrepancies encountered with air temperature measurements. My own readings obtained during this study show considerable

scattering in both air and substratum temperatures; however, a line placed by inspection would also indicate that the substratum temperatures are somewhat more indicative of thermal related activity than that of air (compare Figures 2 and 3).

In montane Costa Rican populations, *S. malachiticus* exhibits a voluntary activity range of 12.4 °C (from 22.0 to 34.4 °C), greater than twice that reported for the Honduras sample of Bogert (1949); *i.e.* 5.8 °C (30.0 °C to 35.8 °C). He limited his description of the "normal" activity range to that "thermal range... extending from resumption of ordinary routine (after the animal has ceased basking) ... terminating at a point just below the level at which high temperatures drive the animal to shelter", as originally defined in 1944 by Cowles and Bogert. Apparently he excluded body temperatures in the "basking range" for calculating the voluntary temperature range, which otherwise would have amplified the ranges and lowered the means. It thus remains questionable that his values can be accurately compared with subsequent studies.

This question was also raised by Mayhew (1963) in considering the disparity of his results and may also contribute to the differences I find between the Costa Rican and Honduran populations. That Bogert (1949) presents a histogram of body temperatures including the "basking range" of *S. variabilis olloporus* only tantalizes the issue. My records, shown in Figure 4, discern basking only among exposed, active animals that were obviously orienting to the sun. Basking was exhibited over most of the activity range for *S. orcutti* (Mayhew, 1963), *S. graciosus* (Mueller, 1969), and *S. occidentalis* (Vitt, 1974). As evidence from thermal studies accumulates, it is apparent that the larger ranges are more typical. The above authors have reported voluntary activity ranges for, in sequence: *S. orcutti* 20.0 °C - 37.4 °C; *S. graciosus* 21.7 °C - 36.8 °C; *S. occidentalis* 21.0 °C - 35.3 °C. Burns (1970) studied *S. jarrovi* in Arizona mountains. While he does not specifically mention basking behavior, I interpret from his description that it is included in his given activity range of 19.0 °C - 37.0 °C. He also described what he termed "stacking" behavior in rock crevices as a response to cooler temperatures, of which I found no incident in *S. malachiticus*. Vitt (1974) observed basking in *S. occidentalis*

primarily in the cooler levels of activity. The broad thermal range over which basking behavior occurs in *S. malachiticus* is probably related to the fact that air and substratum temperatures on the Cordillera rarely exceed the voluntary maximum.

To compare more easily the nature of these differences I have arranged in graphic form the voluntary activity ranges and means for each of 14 species and subspecies of *Sceloporus* (Fig. 5). The upper ten are taken from Bogert (1949) and were used by Brattstrom (1965) in his review, while others are from sources cited above and those I obtained from this study. The questioned extension for *S. v. olloporus* includes the "basking range" Bogert (1949) considered as distinct and apart from the voluntary activity range. There is a striking difference in his measurements of ranges and those defined by other investigators. The one exception could be that of *S. v. olloporus*: if the basking range of this lizard is included, the voluntary activity range enlarges to 24. °C - 38.8 °C (with mean of 34.3 °C). As there has been an approximate consistency of technique and instrumentation among the studies I have referred to, it would appear that Brattstrom's (1965) caveat regarding artifacts in the collection of data has been of less importance than in their definition and useage.

Of further interest is the comparison of mean voluntary temperatures (*i.e.* eccentric or preferred). Bogert's (1949) calculation of 32.9 °C for Honduran *S. malachiticus* was the lowest reported in Brattstrom's (1965) review for any *Sceloporus*, although Mayhew (1963) reported 32.6 °C for *S. orcutti*. Subsequently, Burns (1970) noted a mean of 31.4 °C in *S. jarrovi*; Mueller (1969), 30.8 °C in *S. graciosus* and Vitt (1974), 31.4 °C in *S. o. occidentalis*. In contrast, montane Costa Rican *Sceloporus malachiticus* exhibit a mean of 28.6 °C, the lowest yet observed for any member of the genus.

Burns (1970) and Mueller (1969), reported significant seasonal differences in mean voluntary temperatures, probably the result of acclimation, which cannot be detected among my data. However, considering that the annual range of mean air temperatures at 3 000 m in the Cordillera de Talamanca is less than 2.0 °C (Coen, 1953), an absence of seasonal acclimation in *S. malachiticus* is not surprising.

Brattstrom (1965) graphically summarized

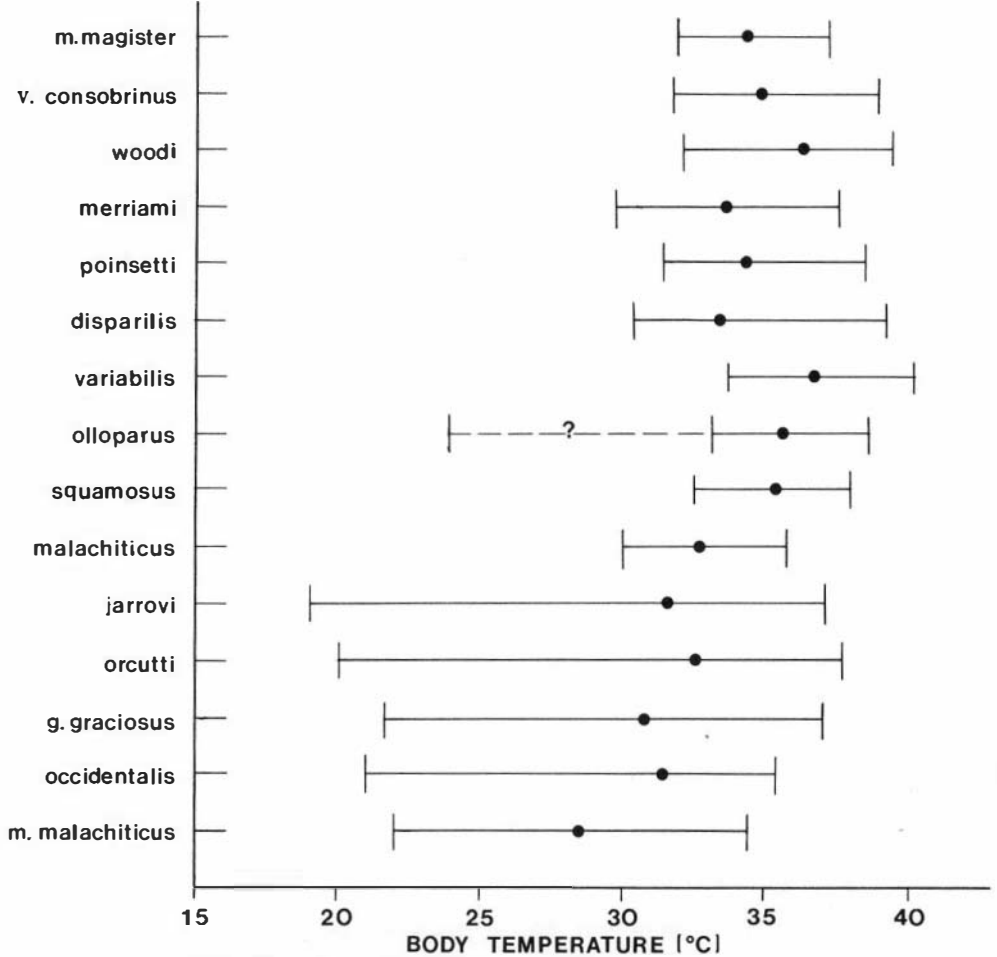


Fig. 5. Voluntary temperature ranges and means (preferenda) for 14 species and subspecies of *Sceloporus*. Topmost ten are those reported by Bogert (1949). The questioned extension for *S. variabilis olloparus* is based on inclusion of the basking range.

the data presented by Bogert (1949) and concluded, contrary to the latter's analysis, that there is a definite relationship between eccentric body temperature and elevation among the *Sceloporus* species. Others (notably Burns, 1970; Mueller, 1969; and Vitt, 1974) have commented on this correlation in their reports, although the latter does not list any elevations. In Figure 6 I have amplified Brattstrom's (1965) graph in order to include this information. Bogert (1949) calculated an eccentric temperature of 32.9 °C for *S. malachiticus*, between 1 500 to 2 000 m, that Brattstrom (1965) averaged to 1 850 m for his graph. My

records at an average elevation of about 2 850 m (range 2 130 to 3 510 m) compute to 28.6 °C. The data for *S. jarrovi*, *S. graciosus*, and my own *S. malachiticus*, thus show a continued trend in the mean voluntary temperature-elevation slope. But while the correlation between mean body temperatures and elevations does appear, there are some particular features worth examining. Mueller (1969) found *S. graciosus* at 2 300 m in Yellowstone Park to occupy only locations in the vicinity of geothermal activity, a situation that should only incidentally conform to elevation. If I have correctly identified the location of

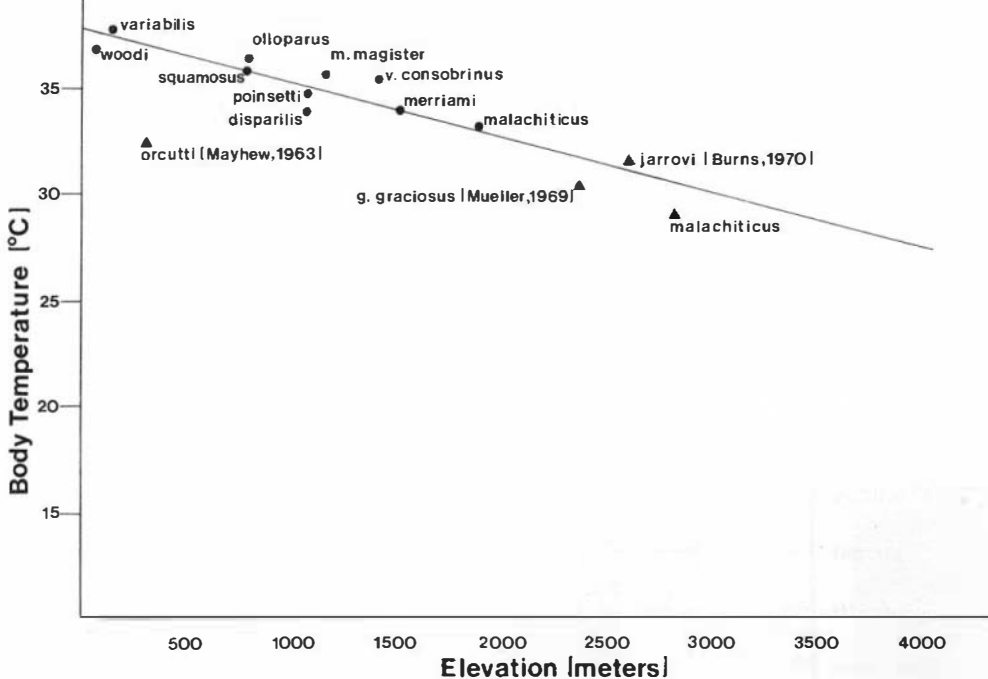


Fig. 6. Means of voluntary activity ranges plotted against average elevation for sampled populations of *Sceloporus*. Modified from Brattstrom (1965). Triangle for *S. malachiticus* represents field data of present report.

Mayhew's (1963) study (*i.e.* "...on or near the Riverside Campus of the University of California"), an elevation of 300 m is fairly accurate and shows the greatest deviation from this trend. Vitt's (1974) report of 31.4 °C as the thermal preferendum for *S. o. occidentalis* (the same as that for *S. jarrovi*) would have made an interesting inclusion had elevations been available.

Although the picture presented is fairly neat overall and does exhibit a relationship between thermal acclimation and elevation, other factors cannot be excluded. In his studies on coloration and reflectivity in reptiles, Norris (1967) stated that there is nothing unusual in uptake of solar radiation in high altitude lizards. He proposed that such invasions may be related to body size, behavioral traits or low temperature activity thresholds. At present there is not enough evidence available to examine adequately these aspects of the problem. My preliminary efforts in comparing elevations with maximum

snout-vent lengths and minimum activity temperatures of the 14 different *Sceloporus* have been thus far unproductive. However, the very lack of significant differences among individual *S. malachiticus* of diverse body size *i.e.* juveniles and adults, does indicate that within this species there is some degree of regulatory control about a common thermal preferendum.

In the Cordillera de Talamanca I have found only one other lizard, *Gerrhonotus monticolus*, to be common in the habitats of *S. malachiticus*. It, however, has a total thermal range of 18.2 °C (8.6 °C to 27.2 °C, \bar{x} 17.5) and a voluntary activity range of 7.1 °C (20.1 °C to 27.2 °C, \bar{x} 23.0 °C). It therefore shares only the lower part of the thermal range I have described for *S. malachiticus*. In contrast also, is a more significant relationship between substratum and body temperatures than shown in *S. malachiticus* (Vial, 1975).

Dawson (1967) generalized about such a comparison as I am making here by stating

that "congeneric lizards occupying dissimilar environments tend to have similar thermal preferenda, whereas sympatric representatives of different genera may have quite different ones". Yet, in final consideration, the range of thermal preferenda among the several allopatric species and subspecies of *Sceloporus* examined in this report (from 28.6 °C to 36.9 °C, a difference of 8.3 °C) is greater than that I obtained (5.6 °C) between sympatric *S. malachiticus* and *G. monticolus*. It would thus appear that, at least among sceloporine lizards, thermal preferenda may be more indicative of their autecology than phylogeny.

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