



ALLEN
PRESS



Thermal Ecology of Five Sympatric Species of *Cnemidophorus* (Sauria: Teiidae)

Author(s): J. J. Schall

Source: *Herpetologica*, Sep., 1977, Vol. 33, No. 3 (Sep., 1977), pp. 261-272

Published by: Allen Press on behalf of the Herpetologists' League

Stable URL: <https://www.jstor.org/stable/3891937>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/3891937?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Allen Press and Herpetologists' League are collaborating with JSTOR to digitize, preserve and extend access to *Herpetologica*

JSTOR

HERPETOLOGICA

VOL. 33

SEPTEMBER 1977

NO. 3

THERMAL ECOLOGY OF FIVE SYMPATRIC SPECIES OF *CNEMIDOPHORUS* (SAURIA: TEIIDAE)

J. J. SCHALL

ABSTRACT: Thermal ecology of 2 parthenogenetic (*C. exsanguis* and *C. tessellatus*) and 3 bisexual (*C. inornatus*, *C. gularis*, and *C. tigris*) species of whiptail lizards, *Cnemidophorus*, was studied in southwestern Texas, USA. Randomly collected ambient temperatures vary among sites and environmental temperatures measured at time and point of collection of specimens vary between syntopic species. Among species, overall body temperatures (T_b) have similar means but heterogeneous variances. Means and variances of actively moving lizards are, however, similar among species. Lizards which were actively moving, basking, and immobile in shade had significantly different T_b distributions; basking animals had the lowest T_b whereas "shade" animals had the highest. Parthenogenetic and bisexual species show no differences in T_b distribution.

Body temperatures correlate with environmental temperature and (except for extreme substrate temperatures late in the day) are usually higher. Body temperature range, however, is small compared to that of environmental temperature. Whiptail T_b did not vary by collection site nor season and (except for *C. tigris*, in which ♀♀ had slightly higher T_b) did not differ between sexes. Gravid ♀♀ had slightly lower T_b than nongravid ♀♀ or ♂♂ in all species. Relative volume of food in the stomach and T_b are correlated. Mean T_b of lizards in thermal gradients are lower than field T_b ; T_b in gradients differed among behavior classes and sometimes days.

Cnemidophorus has an evolutionally conservative thermal tolerance (estimated by T_b). Despite radiation into various habitat niches, all species when actively moving have very similar T_b .

EARLY lizard thermoregulation studies (Cowles and Bogert, 1944; Mosauer, 1936) produced convincing evidence that many reptiles behaviorally maintain a preferred body temperature. The vast literature on this subject now clearly documents the complexity of lizard thermoregulation (Heath, 1965; Heatwole, 1970). Many thermoregulation studies have presented randomly gathered body temperatures with little or no consideration of the ecological or evolutionary factors shaping their distribution. Additionally, the activity of an animal prior to collection is often ignored, thus making such data suspect (Heath, 1964). A modern approach, though, stresses ecological considerations and attempts to correlate ecological variables with observed body

temperatures (see review in Huey and Slatkin, 1976).

In this paper I present the thermal ecology of 5 species of sympatric whiptail lizards (genus *Cnemidophorus*) from southwestern Texas. Two are parthenogenetic (*C. exsanguis* and *C. tessellatus*); the other 3 are bisexual (*C. tigris*, *C. gularis*, *C. inornatus*). This system is interesting because such density of sympatric congeners is unusual in North American lizard faunas. The 5 whiptail species vary in habitats utilized; unisexuals occupy a broader range of habitats than do the bisexual species (Schall, 1976). Thus, the parthenogenetic species could have a broader range of body temperatures or different thermoregulatory behaviors than the bisexuals.

HERPETOLOGICA 33:261-272. September 1977

Body temperature variation patterns are compared among the 5 species. Within species, variation is partitioned by behavior, site of collection, sex, reproductive condition, body size, and volume of food in the stomach. I attempt to correlate the thermal strategy of these lizards with ecological factors providing the basis for a synthetic view of *Cnemidophorus* ecology.

METHODS

During summers, 1973–1975, my assistants and I observed $\approx 2,500$ individual whiptails, and collected $>1,200$ of these at 45 locations in southwestern Texas in Brewster, Culberson, Jeff Davis, Pecos, Presidio, and Reeves counties. Location and other data on all sites are given in Schall (1976).

After sighting a lizard I would usually step back several meters and quietly observe its behavior for a few minutes. I then killed the lizard with .22 caliber dust shot and immediately measured cloacal temperature with Schultheis rapid reading thermometers using standard precautions. Data were excluded if there was a long delay or if a specimen was badly damaged. Time in hours since sunrise was recorded for most observed or collected lizards. I classified behavior of each collected animal as (1) actively moving: the animal was foraging, digging, eating, courting, etc.; (2) basking: animal was lying in sun with body pressed close to ground, often with toes curled upward; (3) shade: lying in shade; (4) unknown: animals fled at my approach and no observations were possible or behavior could not be easily classified.

Specimens were weighed very soon after collection. In the laboratory, sex, snout-vent length (SVL), and reproductive condition of females were determined. The volume of the stomach and its contents was approximated by water displacement in a graduated cylinder. Whenever field conditions permitted, 3 environmental temperatures were taken with a shaded thermometer at time of collection of specimens: air

temperature (T_a) 1 cm aboveground where animal was sighted (last location for moving animals), air temperature 1.5 m aboveground in general area where animal was collected (T_{an}) and substrate temperature 1 mm under substrate (T_s).

Ambient temperature diversity was measured 2 ways. Air temperatures 1 cm aboveground at 50 randomly spaced locations each in open between shrubs, at edge of vegetation, and inside vegetation were taken at 5 representative sites with a telethermometer having a shaded bead thermistor probe. All 150 temperatures at each location were taken within an hour after noon on sunny, cloud-free days. In the study region during midsummer, sunny days had similar daytime temperatures (sunny days in Alpine, Texas during July 1974: \bar{X} high temperature = 34.6°C , $SD = 1.44$), so day-to-day variation in temperature was not appreciable. Secondly, burrow temperatures were determined by gently lowering a bead thermistor probe down burrows and recording temperature every 3 cm.

Within hours of their capture, live individuals of each species were tied in open sun, and body temperatures recorded at first panting and at death when animal was unable to move when turned over.

During summer 1975, lizards were transported to Austin, Texas where they were kept in a large pen equipped with heat lamps and total spectrum Vitalights® on a timer set to approximate day length in the study region. A continuously recording thermometer revealed temperature range in the pen was similar to that recorded at the lizards' collection site. Within 2 weeks of capture these animals had 2-g thermosensitive radio transmitters (accurate to 0.1°C) implanted into the body cavity. Details of construction of this radio-demodulation system will be presented elsewhere. Lizards were placed in 1×2 m laboratory photothermal gradients equipped with three 250-W heat lamps 0.5 m over one end and Vitalights® hung overhead. Within a day lizards recovered from surgery and their behavior was indistinguish-

TABLE 1.—Random ambient temperatures ($^{\circ}\text{C}$) for 5 study areas in southwestern Texas. Fifty temperatures were taken 1 cm aboveground for each of 3 conditions: **open**, **edge** (of vegetation), and **interior** (of vegetation). Mean is followed by standard deviation in parentheses. Mean and SD also given for all 150 temperatures at each site. Species present at each site indicated by first two letters of specific name, and occur in order of their abundance.

Site	Species	Open	Edge	Interior	Overall
Red Pens Ranch (ecotone between higher grassy zone and lowland desert)	<i>ex</i> > <i>gu</i> > <i>te</i> > <i>in</i>	36.7 (1.4)	38.6 (2.8)	37.7 (2.8)	37.7 (2.5)
Balmorhea Flats (creosote desert)	<i>ti</i> > <i>te</i>	38.0 (1.0)	37.9 (1.4)	38.8 (2.7)	38.2 (1.9)
Blakemore Ranch (creosote desert-creo- sote/grass cline)	<i>in</i> > <i>te</i>	37.6 (1.9)	37.5 (1.8)	37.5 (2.2)	37.5 (2.0)
Thompson Ranch (higher elevation; grassy, shrubby)	<i>ex</i> > <i>gu</i>	35.2 (2.6)	35.5 (2.2)	35.1 (2.3)	35.3 (2.4)
Burnt House Canyon (riparian, highland woods-grassy)	<i>in</i> > <i>gu</i> > <i>ex</i>	35.8 (1.6)	35.9 (2.3)	35.7 (2.4)	35.8 (2.1)

able from control animals. To control for social interactions only 1 lizard was placed in each gradient.

Statistics used are described in Snedecor and Cochran, 1967; Siegel, 1956; and Sokal and Rohlf, 1969.

RESULTS

Microhabitat Temperatures.—Although sympatric, the 5 species differ in habitat associations. *Cnemidophorus tigris* has highest densities in sparsely vegetated, low-elevation flatland desert. *Cnemidophorus gularis* is found primarily in wetter, more vegetated zones, often with considerable grass cover. The smallest species, *C. inornatus*, is found in a variety of habitats, including flatland creosote desert where it may be syntopic with *C. tigris*, but is most common in shrubby, grassy areas. The 2 unisexual species have the greatest range of habitats; however, *C. exsanguis* is most similar to *C. gularis* whereas *C. tessellatus* often inhabits less vegetated zones typically used by *C. tigris* (Schall, 1976).

Table 1 presents random ambient temperature data for 5 study locations. Thermal

characteristics vary among sites for all 3 microhabitats (Kruskal-Wallis analysis of variance "*H*" tests, $P < .01$). For example, among sites, open and edge temperatures have significantly heterogeneous variances (Bartlett's χ^2 test, $P < .005$). Balmorhea, the creosote desert, has generally warmer and less variable random ambient temp within microhabitats than more heavily vegetated sites such as Thompson Ranch and Burnt House Canyon. Mean SD for Balmorhea random ambient temp is the lowest and mean overall random ambient temp at Balmorhea is the highest of the 5 localities. Generally, the 2 most similar sites, Balmorhea and Blakemore have similar thermal characteristics; both are flatland desert although Blakemore is more grassy. Thermal characteristics of various habitats utilized by the 5 whiptails differ.

Environmental temperatures taken at time lizards were collected are given in Table 2. Those temperatures in Table 2 comparable to those in Table 1 (T_a) are lower but more variable because they were collected during the entire activity time of the

TABLE 2.—Statistics on environmental temperatures (which were measured at time of collection of most whiptail specimens). Product-moment correlation coefficients for body temperature (T_b) with air temperature at 1 cm aboveground (T_a), 1.5 m aboveground (T_{ah}), and substrate (T_s) 1 mm below surface also given. Substrate temperature statistics must be viewed with caution because thermometer measured maximum temperature of 50°C and all temperatures >50° are combined. Significance levels: * = $P < .05$; ** = $P < .01$; *** = $P < .001$; **** = $P < .0001$. All temperatures expressed as °C.

Parameter	<i>C. tigris</i>	<i>C. tessellatus</i>	<i>C. exsanguis</i>	<i>C. inornatus</i>	<i>C. gularis</i>
Air temp at +1 cm (T_a)					
\bar{X}	31.9	31.5	30.9	30.8	32.3
SD	4.3	3.2	2.9	3.9	3.4
Range	25.0	16.0	14.4	23.8	19.7
N	268	142	159	299	146
T_b vs. T_a	$r = .46^{****}$	$.36^{****}$	$.28^{***}$	$.28^{***}$	$.38^{****}$
Air temp at +1.5 m (T_{ah})					
\bar{X}	30.8	28.8	27.7	28.8	29.9
SD	3.3	2.9	2.5	3.1	2.7
Range	15.2	13.6	12.8	16.1	13.5
N	105	99	144	167	89
T_b vs. T_{ah}	$r = .54^{****}$	$.42^{****}$	$.41^{***}$	$.39^{****}$	$.43^{***}$
Substrate temp at -1 mm (T_s)					
\bar{X}	38.6	36.6	36.1	37.1	37.7
SD	6.1	6.3	6.5	6.2	6.9
Range	26+	26+	26+	26+	26+
N	215	139	181	233	140
T_b vs. T_s	$r = .43^{****}$	$.25^{**}$	$.20^*$	$.30^{****}$	$.46^{****}$

lizards. Some species which are often syntopic have dissimilar environmental temperature statistics. For example, *C. gularis* has significantly higher mean T_{ah} and T_a than *C. exsanguis* although they are frequently syntopic and have about the same body size (t -tests, $P < .001$). Burnt House Canyon T_a values for *C. inornatus* and *C. gularis* differ, but not significantly (*C. inornatus* $\bar{X} = 31.2$, SD = 4.2, $N = 32$; *C. gularis* $\bar{X} = 33.3$, SD = 3.8, $N = 29$; t -tests, $.10 < P < .20$).

Body Temperature Distribution.—Field body temperature (T_b) statistics are presented in Table 3. When data for all behaviors are combined, mean T_b are very similar among the 5 species (H test, $P = .78$); however, variances are heterogeneous (F_{max} test, $P < .01$). When data within species are partitioned by lizard behavior a striking pattern emerges (Table 3 and

Fig. 1). The 3 behavior classes i.e., actively moving, basking, and immobile in shade, have different distributions (H tests, $P < .001$) with basking animals having the lowest T_b and those in the shade the highest. Mean T_b among species for each behavior class do not differ significantly (H tests, $P = .032-.612$). Body temperatures for actively moving animals have similar variances among species (F_{max} tests, $P > .05$) while basking and shade behavior classes have heterogeneous variances ($P < .05$ and $< .01$).

Summarizing, all species have similar mean T_b values for all behavior classes combined (grand mean, $\bar{X}_g = 40.2$) but differ in dispersion. Within species, basking animals had the lowest T_b ($\bar{X}_g = 38.6$) followed by actively moving animals ($\bar{X}_g = 40.5$) and shade animals ($\bar{X}_g = 41.5$). Actively moving animals had similar T_b variances but other behavior classes did not.

TABLE 3.—Body temperature ($^{\circ}\text{C}$) statistics (for 5 *Cnemidophorus* species collected in field) for 3 behaviors: basking, actively moving, and immobile in the shade. Data for all animals including those with unknown behavior prior to collection are combined into the “all” category. Values are $\bar{x} \pm \text{SD}$, with sample size in parentheses.

Species	All	Behaviors		
		Bask	Actively moving	Shade
<i>C. tigris</i>	40.4 \pm 1.5 (289)	38.8 \pm 1.7 (36)	40.5 \pm 1.2 (210)	41.7 \pm 1.3 (23)
<i>C. tessellatus</i>	40.1 \pm 1.6 (154)	38.1 \pm 2.7 (19)	40.3 \pm 1.1 (115)	41.1 \pm 1.1 (18)
<i>C. gularis</i>	40.2 \pm 2.0 (149)	38.3 \pm 2.1 (33)	40.7 \pm 1.1 (95)	42.0 \pm 1.1 (17)
<i>C. exsanguis</i>	39.9 \pm 2.3 (203)	38.5 \pm 2.9 (70)	40.6 \pm 1.3 (105)	40.9 \pm 2.3 (15)
<i>C. inornatus</i>	40.2 \pm 1.8 (318)	38.6 \pm 2.6 (58)	40.4 \pm 1.4 (217)	41.9 \pm .87 (17)

These results demonstrate differences among species in combined temperature variance is due to different shade and basking distributions and species with greater combined T_b variation have a greater proportion of this variation accounted for by basking and shade variance (Table 3).

Among species, overall T_b variance for all behaviors combined is negatively correlated with the proportion of animals of each species which were actively moving when collected (Spearman rank correlation, $r_s = .90$; $P < .05$). That is, in species with higher overall T_b variance (such as *C. exsanguis*) a smaller proportion of field collected individuals were actively moving. The origin of this relationship could simply be that some species are more difficult than others to collect when active. There is, however, no relationship between the ease of collection of actively moving animals for a species and the percent of encountered animals which were active. In fact, among the 5 species, the one most difficult to capture (*C. tigris*) was most frequently actively moving when collected and *C. exsanguis*, the most docile species, was least frequently active. A more likely explanation for the noted inverse relationship is there is a fundamental difference in behavior among the species. Some spend more time out of their burrows engaged in other than “actively moving” behavior.

Sources of T_b Variation.—Fig. 1 shows plots of T_b distribution for 3 behavior classes. These plots illustrate that some individual whiptails were basking at tempera-

tures well above modal T_b for actively moving and even shade-seeking behavior. Several individuals were actively moving precariously close to upper lethal temperatures (also plotted in Fig. 1). For example, a *C. tigris* lying in open sun while eating an insect had a T_b of 44.7°C , and a *C. inornatus* casually walking near the edge of vegetation for 10 m had a T_b of 43.6°C . A *C. exsanguis* digging in soft earth in open sun, stopped and basked and had a T_b of 43.4°C . Several courting *C. tigris* were collected in the open at very low T_b when escape response was probably suboptimal.

Although much of the combined T_b variation is accounted for by the behavior classes, the range in T_b values for active animals suggests that other factors are also involved. Here, effects of environmental temperature, time of day, collection site, season, body size, sex, reproductive condition, and stomach volume are considered.

Body temperature range is narrower than that of environmental temperature (Tables 2 and 3, Fig. 2). Correlations between T_b and environmental temperature are weak but significant (Table 2). Figure 2 shows plots of T_b by T_a , T_{ah} , and T_s for *C. inornatus*. Plots for other *Cnemidophorus* are similar. Body temperature is usually higher than T_a or T_{ah} but often is lower than T_s . Body temperatures are also correlated with time of day ($r = .22-.37$; $P < .01-.001$) and environmental temperatures also rise during the day (for T_a , $r = .25-.57$; for T_{ah} , $r = .30-.53$; and for T_s , $r = .39-.52$; all $P < .05-.0001$).

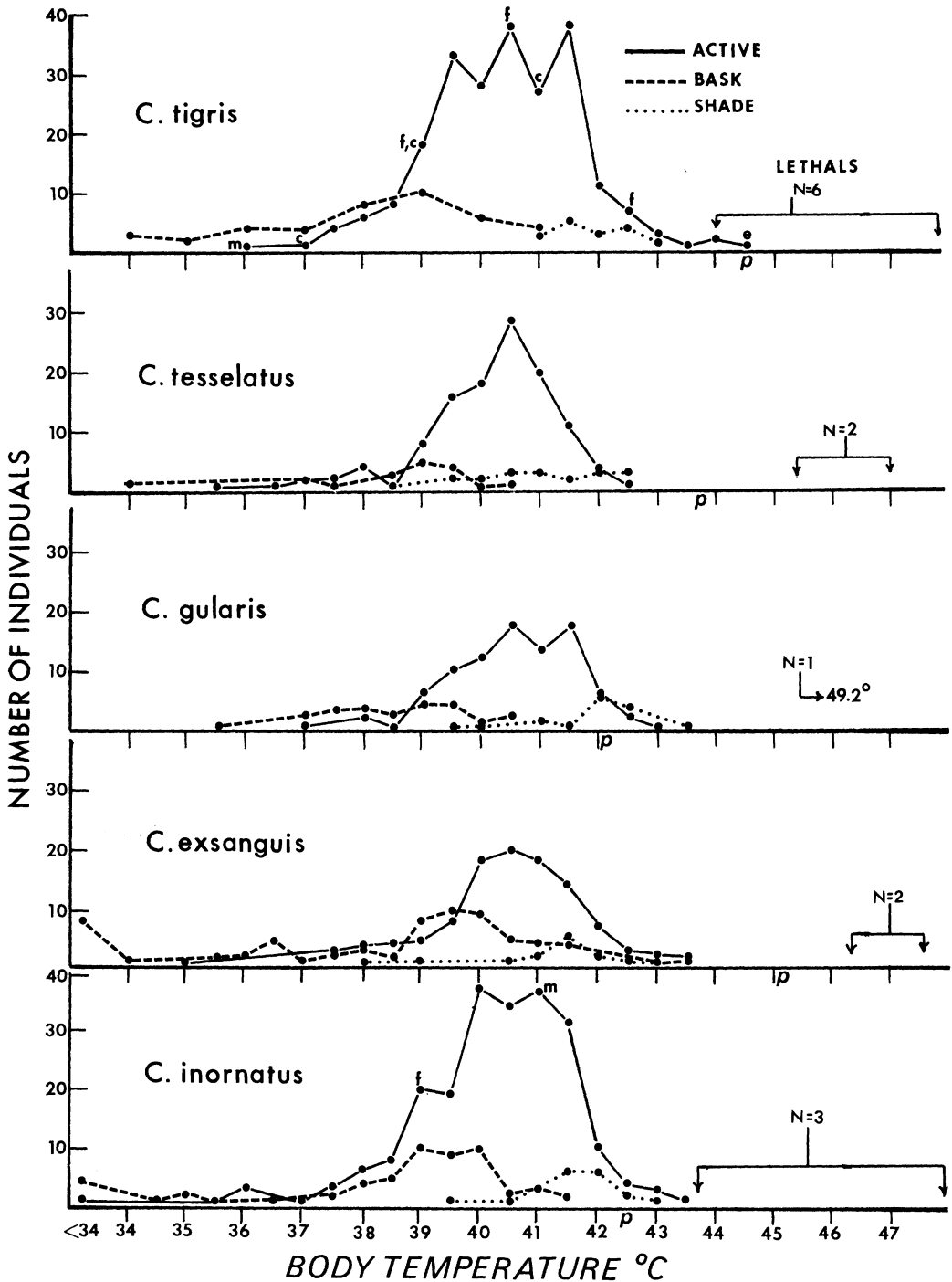


FIG. 1.—Distribution of field collected body temperatures (T_b) for 5 species of whiptail lizards (*Cnemidophorus*) for 3 behaviors: actively moving, basking, and immobile in the shade. Range of lethal temperatures and mean T_b at first panting behavior are indicated by arrows and a small p under lines, respectively. Individuals which were mating (m), courting (c), fighting (f), or eating (e) are also indicated.

There is a weak, though significant, negative correlation between body size (SVL and weight) and T_b for *C. tigris* and *C. tessellatus* ($r = -.16$ – $-.22$; $P < .05$ – $< .001$). No such significant correlation appeared for the other species. Only *C. tigris* had significantly different T_b for males ($\bar{X} = 40.2$) and females ($\bar{X} = 40.7$). Body temperatures did not vary by collection site (H test, $P > .05$). May and June are warmer in southwestern Texas than the rainy second half of the summer; yet, T_b , T_a , T_{ah} , and T_s did not vary seasonally (monthly periods, May to August). In all species, gravid females had lower mean T_b values than nongravid females or males, although these differences are not significant (H tests, $P > .05$).

Relative volume of food in stomach (stomach volume/SVL) is weakly, though significantly, correlated with T_b in all species ($r = .21$ – $.31$; $P < .001$ – $< .0001$). However, food volume increases with time ($r = .17$ – $.37$; $P < .05$ – $< .001$) presumably because lizards gradually fill their stomachs as they forage during the day. Since T_b and time are themselves correlated (see above) I computed partial correlations holding variation due to time constant. Body temperatures and food volume in stomach were then still significantly correlated in all species ($r_p = .14$ – $.26$; $P < .05$ – $< .001$). At best though, only about 7% of variation in T_b can be attributed to changes in stomach volume.

Thermoregulatory Behavior.—Basking is common during early morning although animals may bask at any time of day. During basking, lizards press their body close to the substrate and very often curl their toes. In extreme cases, toes of all 4 feet are curled upward and lizard rests on its wrists and ankles. I commonly observed toe curling in all species except *C. inornatus*. This behavior is similar to that of *Cnemidophorus deppei* and *Cnemidophorus guttatus* (Kennedy, 1968) and *Amphibolurus barbatus* (Brattstrom, 1971).

During windy periods lizards avoided

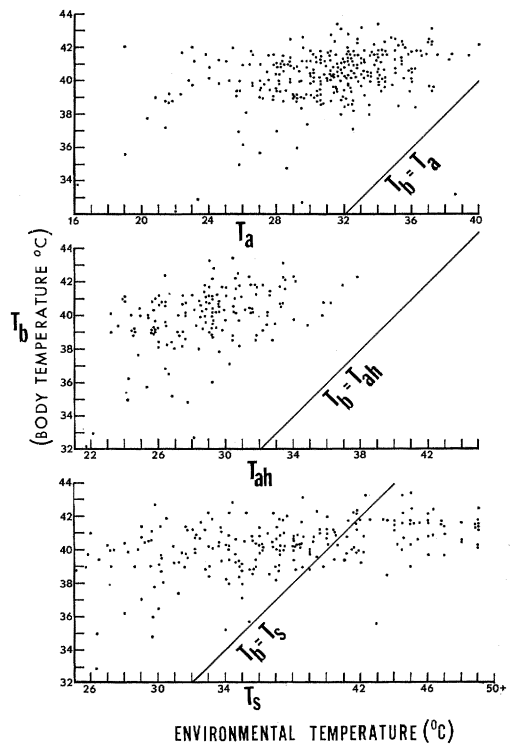


FIG. 2.—Body temperature of *C. inornatus* plotted against air temperature 1 cm aboveground (T_a), air temperature about 1.5 m aboveground (T_{ah}), and substrate 1 mm under surface (T_s). Line represents the $T_b =$ environmental temperature isocline. Other *Cnemidophorus* species had similar plots.

open areas and stayed on the leeward side of vegetation. On cool days, whiptails appear reluctant to move, remaining in small, protected depressions out of the wind. In the afternoon when ambient temperatures are high, lizards spend more time beneath vegetation. Of those *C. tigris* sighted at Balmorhea during 4 morning hours (over 2 summers) 87% were in open sun, whereas during 3 afternoon hours 64% were in the sun ($\chi^2 = 17.1$; $P < .005$). When moving during hot or windy periods, whiptails dart from shrub to shrub instead of walking slowly in the open. Whiptails occasionally perch off the ground in vegetation; several were observed lying on semi-horizontal

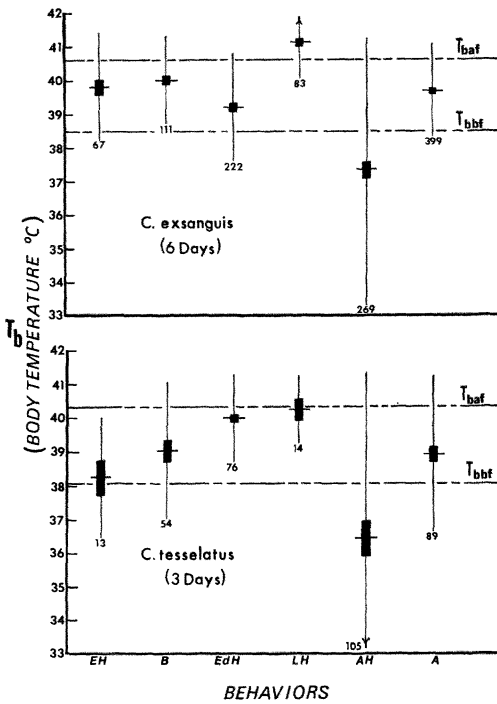


FIG. 3.—Whiptail body temperatures in 1 m × 2 m thermal gradient. Data for a *C. exsanguis* and a *C. tessellatus* partitioned by behavior. \bar{x} indicated by horizontal line, SE of \bar{x} by black bar, and SD by vertical line. Numbers are sample sizes. T_{baf} is mean T_b for field collected actively moving animals and T_{bbf} is mean for field basking T_b . Length of time animal was observed is in parentheses. Behaviors: EH = Enter heat spot cast by heat lamp; B = Basking in heat spot; EdH = Basking in cooler zone at edge of heat spot; LH = Leave heat; AH = Lying still away from hot end of gradient; A = Actively moving.

branches of ocotillo (*Fouquieria splendens*).

Burrows may play an important role in thermoregulation. Occasionally, active lizards collected during hot times of the day had T_b values very much below environmental temperature (for example, see isolated data point in $T_b \times T_a$ graph in Fig. 2). I suspect these were animals that had just emerged from a cool burrow. Air temperature within 7 deep burrows dropped 0.6 to 1.4°C per 3 cm of length ($r = -.77$ – $-.83$) and air temperature at burrow open-

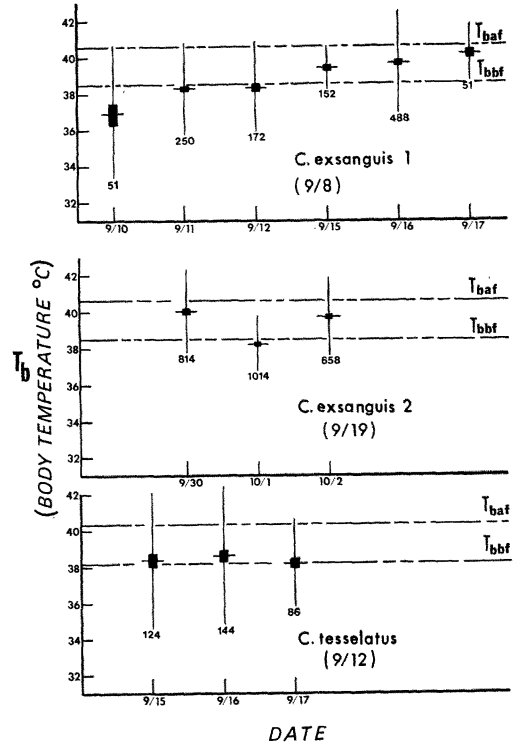


FIG. 4.—Gradient body temperatures for 3 individual whiptails over several days. Explanation of graphs as in Fig. 3. Date radio was implanted indicated in parentheses.

ings ($N = 17$) was 2.8 to 9.4°C higher than at a burrow's deepest point. One burrow, running parallel to the ground's surface had warmer temperatures within the burrow (0.9°C rise per 3 cm of length, $r = .85$). Burrow temperatures are complex and whiptails might thermoregulate within burrows as do *Dipsosaurus* (McGinnis and Dickson, 1967).

While basking, some lizards engorge the skin with blood, then shunt it to deep body tissues. This allows them to warm up faster than they cool and reduces basking time (Weathers, 1970; Weathers and Morgareidge, 1971). Cool whiptails I shot early in the morning very often bled profusely from tiny skin wounds, whereas lizards shot later in the day bled very little. These observations suggest that whiptails may also

shunt blood between peripheral and core tissues, depending on thermal conditions. *Gradient Studies*.—Data on 3 whiptails from the radiotelemetry gradient studies are presented in Figs. 3 and 4. In Fig. 3, T_b values are partitioned by lizard behavior. Lizards with low T_b entered a heat spot cast by one of the heat lamps and departed after T_b reached $40+^{\circ}\text{C}$. All 3 lizards spent time partially hidden by twigs or leaves in a warm part of the gradient away from heat spots (behavior class "AH") allowing their T_b to drop. Body temperatures of lizards in the gradient were generally lower than the field collected "actively moving" lizards. Actively moving lizards (those digging, feeding, walking about) in the gradient had mean T_b values which were $1-2^{\circ}\text{C}$ cooler than actively moving lizards in the field. Day to day mean T_b varied (Fig. 4) for combined *C. exsanguis* data.

DISCUSSION

A lizard's body temperatures are a reflection of its overall ecology including habitat use, foraging tactics, and times of activity. Therefore, knowledge of thermal relationships can aid in constructing an integrative overview of a lizard species' general ecology (Pianka and Parker, 1975).

Despite interspecific habitat differences and the broader range in habitats occupied by the unisexual species, mean T_b values of actively moving whiptails are very similar among species and compare closely with those described for other *Cnemidophorus* (see review in Schall, 1976). Assuming field collected T_b approximates optimal body temperature, the uniformity of mean T_b value suggests optimal T_b is an evolutionally conservative trait of whiptail ecology.

Whiptails have among the highest T_b values of any lizard genus (Brattstrom, 1965; Schall, 1976). All mainland *Cnemidophorus* are diurnal, widely foraging carnivores which hunt for small arthropods primarily

in open, hot areas between shrubs or along the edges of vegetation. Evolution of high optimal T_b is expected: first, to match generally high ambient temperatures and reduce costs of thermoregulation; and, second, to allow rapid physiological reactions which may be necessary for a constantly moving animal which relies on speed to elude predators. Because of their foraging behavior and high body temperatures, Regal (1977) opined that *Cnemidophorus* are among the most mammal-like of lizards.

A similar situation exists in certain species of the Australian skink genus *Ctenotus* which are approximate ecological analogues of *Cnemidophorus*. *Ctenotus* probably evolved from the "typical" skinks common in cool wet places in Australia. The widely foraging species of *Ctenotus* studied by Pianka (1969) had high mean T_b values, and one (*Ctenotus leonhardi*) had the highest of any skink known (38.0°C). Nonetheless, *Ctenotus* has lower average T_b than *Cnemidophorus* reflecting their phylogenetic origin from typical skinks.

The relative importance of phylogenetic and ecological factors on T_b distribution has stimulated considerable interest (Corn, 1971; Huey and Slatkin, 1976). In most lizard groups phylogenetically related forms have similar T_b even when utilizing different habitat types (Bogert, 1949a, b; Hillman, 1969). As a lizard group radiates into new habitats, thermoregulatory behavior evolves faster than does the physiological optimal T_b . The *Cnemidophorus* studied here exemplify these notions. They have evolved varied habitat niches, display subtle differences in thermal ecology, yet maintain very similar active T_b distributions.

Considering the array of thermal conditions whiptails must be exposed to as they forage, they maintain their body temperatures at a remarkably constant level. Ambient temperatures change throughout the summer yet whiptail T_b and the environmental temperatures they select do not vary seasonally. Whiptails must therefore adjust their thermoregulatory behavior to mediate seasonal changes in ambient tem-

peratures. This would include times of activity shifts and selection of differing foraging sites. Also, some species utilizing the same habitat select different environmental temperatures. Whiptail foraging strategy must not be independent of their thermoregulation and their movements through the desert anything but random. The complex assemblage of behaviors necessary for thermoregulation must have significant costs to the lizard. Whiptail T_b rises as ambient temperatures rise during the day, reflecting the subtle interaction of costs and benefits of thermoregulating in a temporally and spatially varying thermal environment (Huey and Slatkin, 1976).

The striking pattern of behavior-dependent differences in T_b demonstrates that behavior must be considered in any study of lizard body temperatures. Figure 1 illustrates that some individuals may voluntarily accept body temperatures much different from the mode for each behavior. Possibly there are several optimal T_b values for various activities and the distribution plotted in Fig. 1 is a summation of several distinct curves (Heatwole, 1976). These T_b values would be "optimal" in the sense that their maintenance would maximize lifetime fitness.

In the laboratory many herptiles seek different T_b levels depending on nutritional state (Gatten, 1974; Hadfield, 1966; Kitchell, 1969; Regal, 1966), lighting (Regal, 1967; Spellerberg, 1974), or social interactions (Regal, 1970). Body temperature and volume of food in stomach are weakly, though significantly, correlated in *Cnemidophorus*; animals with full stomachs have slightly higher T_b levels than those with empty stomachs. Likewise, optimal T_b could vary with reproductive condition of the animal. Garrick (1974) demonstrated that pregnant *Sceloporus cyanogenys* choose lower T_b than other females or males. Gravid female whiptails also have slightly lower mean T_b values than males or non-gravid females. Developing eggs may be more sensitive than adult soma to damage

by sudden temperature increases. This would result in strong selection for females to lower their body temperature and increase the safety margin against unavoidable thermal stresses.

Demonstrating differences in T_b by reproductive or nutritional state is difficult in field studies. Female whiptails are secretive when gravid (Schall, 1977) and may thermoregulate in burrows. After feeding, lizards may also enter burrows where they can find a diverse thermal structure. The ideal research strategy is to monitor an individual lizard over a variety of activities by telemetry.

The gradient studies reported here demonstrate some individuals vary in T_b distribution from day to day. In addition, "preferred body temperature" levels (Licht et al., 1966) in the gradient are consistently lower than field T_b levels. A discrepancy between gradient and field T_b has often been noted (Parker and Pianka, 1975; Pianka, 1971; Licht et al., 1966; Vance, 1973; Heatwole, 1970). These observations pose something of an evolutionary enigma; if environmental stresses are such that T_b cannot be maintained at preferred levels, natural selection should shift the preferred temperature. Even if lizard T_b distribution is not subject to rapid evolutionary change, it seems unlikely that so many species originated in habitats cooler than their present ones. The resolution of this problem may simply involve the artificial nature of gradients. For example, if lizards have several optimal T_b levels depending on activity, gradient T_b distribution may reflect fewer or different activity conditions faced by lizards in gradients as compared to field conditions.

Acknowledgments.—I was accompanied in the field by R. W. Schall who endured the often tedious data gathering process. Eric R. Pianka, G. Pool, and P. Levin also helped collect some specimens. Raymond Huey, E. R. Pianka, and L. Lawlor read the manuscript and offered many helpful suggestions. Landowners of the Big Bend Region allowed me access to their properties. Financial assistance came from the National Science Foundation (Grant GB-42239 to the author

and GB-43349X to E. R. Pianka), the American Museum of Natural History (Theodore Roosevelt Fund), The Society of the Sigma Xi, and the University of Texas.

LITERATURE CITED

- BOGERT, C. M. 1949a. Thermoregulation in reptiles, a factor in evolution. *Evolution* 3:195-211.
- . 1949b. Thermoregulation and ecritic body temperatures in Mexican lizards of the genus *Sceloporus*. *Ann. Inst. Biol. Mexico* 20: 415-426.
- BRATTSTROM, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73:376-422.
- . 1971. Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. *Copeia* 1971:484-497.
- CORN, M. J. 1971. Upper thermal limits and thermal preferences for three sympatric species of *Anolis*. *J. Herpetol.* 5:17-21.
- COWLES, R. B., AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* 83:261-296.
- GARRICK, L. D. 1974. Reproductive influences on behavioral thermoregulation in the lizard *Sceloporus cyanogenys*. *Physiol. Behav.* 12: 85-91.
- GATTEN, R. E., JR. 1974. Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. *Copeia* 1974:912-917.
- HADFIELD, S. 1966. Observations on body temperature and activity in the toad *Bufo woodhousei fowleri*. *Copeia* 1966:581-582.
- HEATH, J. E. 1964. Reptilian thermoregulation: evaluation of field studies. *Science* 146:784-785.
- . 1965. Temperature regulation and diurnal activity in horned lizards. *Univ. California Publ. Zool.* 64:97-136.
- HEATWOLE, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecol. Monogr.* 40:425-457.
- . 1976. *Reptile ecology*. Univ. Queensland Press, St. Lucia.
- HILLMAN, P. E. 1969. Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology* 50:476-481.
- HUEY, R. B., AND M. SLATKIN. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51:363-384.
- KENNEDY, J. P. 1968. Observations on the ecology and behavior *Cnemidophorus guttatus* and *Cnemidophorus deppei* (Sauria, Teiidae) in southern Veracruz. *J. Herpetol.* 2:87-96.
- KITCHELL, J. F. 1969. Thermophilic and thermophobic responses of snakes in a thermal gradient. *Copeia* 1969:189-191.
- LICHT, P., W. R. DAWSON, V. H. SHOEMAKER, AND A. R. MAIN. 1966. Observations on the thermal relations of western Australian lizards. *Copeia* 1966:97-110.
- MCGINNIS, S. M., AND L. L. DICKSON. 1967. Thermoregulation in the desert iguana *Dipsosaurus dorsalis*. *Science* 156:1757-1759.
- MOSAUER, W. 1936. The toleration of solar heat by desert reptiles. *Ecology* 17:56-66.
- PARKER, W. S., AND E. R. PIANKA. 1975. Ecological observations on the leopard lizard (*Crotaphytus wislizeni*) in different parts of its range. *Herpetologica* 32:95-114.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50: 1012-1030.
- . 1971. Comparative ecology of two lizards. *Copeia* 1971: 129-138.
- , AND W. S. PARKER. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975:141-162.
- REGAL, P. J. 1966. Thermophilic response following feeding in certain reptiles. *Copeia* 1966: 588-590.
- . 1967. Voluntary hypothermia in reptiles. *Science* 155:1551-1553.
- . 1970. Long term studies with operant conditioning techniques of temperature regulation patterns in reptiles. *J. Physiol.* 63:403-406.
- . 1977. Behavioral differences between reptiles and mammals: I. An evolutionary analysis. In P. McLean and N. Greenberg (Eds.) *The behavior and neurology of lizards: A colloquium*. *In press*.
- SCHALL, J. J. 1976. Comparative ecology of sympatric parthenogenetic and bisexual species of *Cnemidophorus*. Ph.D. thesis, Univ. Texas, Austin. 277 p.
- . 1978. Reproductive strategies in sympatric whiptail lizards (*Cnemidophorus*): two parthenogenetic and three bisexual species. *Copeia* 1978: *In press*.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Co., New York.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. *Statistical methods*. Iowa State Univ. Press, Ames.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman Co., San Francisco.
- SPELLERBERG, I. F. 1974. Influence of photoperiod and light intensity on lizard voluntary temperatures. *Brit. J. Herpetol.* 5:412-420.
- VANCE, V. J. 1973. Temperature preference and tolerance in the gecko, *Coleonyx variegatus*. *Copeia* 1973:615-617.
- WEATHERS, W. W. 1970. Physiological thermoregulation in the lizard *Dipsosaurus dorsalis*. *Copeia* 1970:549-557.
- , AND K. R. MORGAREIDGE. 1971. Cu-

taneous vascular responses to temperature changes in the spiny-tailed iguana, *Ctenosaura hemilopha*. *Copeia* 1971:548-551.

Received: 22 December 1975

Accepted: 9 May 1977

Department of Zoology, University of Texas, Austin, Texas 78712, USA (PRESENT ADDRESS: Department of Zoology, University of California, Berkeley, California 94720, USA)

PLASMA OSMOLARITY OF *RANA CATESBEIANA* AND *SCAPHIOPUS HAMMONDI* TADPOLES

ANNE FUNKHOUSER

THE body fluid osmolality of most anuran embryonic tissue ranges from 100 to 120 milliosmoles/litre (Rugh, 1962) and that of adults from 200 to 250 mosmol/l (Bentley, 1966), but little is known about when this osmolality increase occurs during larval development. Richmond (1968) showed that plasma proteins increase two-fold and plasma osmolality increases by 40% from early to late larvae in *Rana catesbeiana*. Unfortunately these animals were not staged, so the developmental sequence of increasing osmotic concentration is not clear. To determine the pattern of osmotic change during normal development, plasma osmolality was measured at selected developmental stages in two species of anuran larvae from different habitats.

Tadpoles of the bullfrog, *Rana catesbeiana*, and the western spadefoot, *Scaphiopus hammondi* were collected near Stockton, California. Tadpoles with forelimbs were sacrificed immediately or allowed to continue development to more advanced stages. Animals without forelimbs were sacrificed within 2 days of capture. Tadpoles were staged by the method of Gosner (1960). Animals were chilled on cracked ice, the heart exposed and blood collected in heparinized capillary tubes by direct cardiac puncture. The tubes were immediately centrifuged, red cells discarded and plasma from each animal transferred to a vial,

sealed and frozen. Osmolality of a 0.3 ml plasma sample of individual *R. catesbeiana* and an equal volume of pooled plasma from 2 *S. hammondi* larvae were measured on an Advanced Instruments® osmometer. *Scaphiopus hammondi* younger than stage 35 and *R. catesbeiana* younger than stage 30 were not used because more than two animals were required to provide an adequate plasma sample. Osmolality of standard Holtfreter's solution (isotonic with embryonic anuran tissues) and amphibian Ringer's solution (prepared without glucose according to Rugh, 1962), and of a 1:1 mixture of the 2 solutions was determined by the same method.

Plasma osmolalities of both species remained constant until the beginning of metamorphic climax (forelimb emergence at stage 41+), then increased abruptly (Fig. 1). During premetamorphic stages (35-40) *R. catesbeiana* plasma was 160 mosmol/l and reached 259 mosmol/l at the end of metamorphic climax (stage 46). At comparable stages the plasma osmolality of *S. hammondi* was consistently higher by 30 mosmol/l.

The osmolality of Holtfreter's solution was 100 mosmol/l, of Ringer's solution, 230 mosmol/l, and of a 1:1 mixture of the two solutions, 160 mosmol/l.

Alvarado and Moody (1970) report only a slight increase in plasma osmolality of *R. catesbeiana* from about 170 mosmol/l at