Winter Thermal Ecology of the Iguanid Lizard
Tropidurus peruvianus

RAYMOND B. HUEY

The iguanid lizard *Tropidurus peruvianus* was studied along an ocean cliff and beach in northern Peru during winter. *T. peruvianus* inhabit arid coastal areas of Peru providing refugia such as cliffs, rock outcrops and driftwood.

Lizards first appear at burrow entrances between 0730 and 0800 hrs, but may delay activity as much as four hours if conditions are unsuitable. The number of lizards active in a morning is strongly correlated with air temperature. Daily activity is unimodal. Mean body temperature of active field lizards is 36.3 ± 0.26 C; mean body temperature in a photo-thermal gradient is 35.6 ± 0.31 C.

Body temperatures and activity patterns of *T. peruvianus* in winter seem tightly regulated compared with *T. albemarlensis* in summer on the Galapagos Islands. Eurythermy of *T. albemarlensis* may relate to the higher cost of thermoregulation in an environment with frequent cloud cover and to seasonal influences. Strategies of thermoregulation are outlined.

DISTRIBUTED along the narrow arid coastline of South America from southern Ecuador to northern Chile, the lizard *Tropidurus peruvianus* offers potential for studies of ecological shifts along a broad latitudinal gradient. Here I describe various aspects of the daily activity and thermal biology of this small iguanid near the northern limit of its range during winter and make comparisons with similar data on *Tropidurus albemarlensis* from Santa Cruz, Galapagos Islands, during the late summer (Stebbins et al., 1967). In conclusion I suggest that the observed differences in daily activity and thermoregulation between these congeners represent not only seasonal adjustments, but also adaptive strategies tuned to differing climatic environments.

METHODS

The main study area consisted of 450 meters of beach front and adjacent cliffs (4–5 m high) at Tric Trac, 2 km NE of Bayovar, Departamento de Piura, Peru. I studied this population in July 1967 and again in late July and early August 1968. In 1967 I briefly sampled several other populations from northern and central regions of coastal Peru.

Body and adjacent air (bulb shaded and held 1 cm above substrate) temperatures were taken in the field with a Schultheis thermometer within a few seconds after noosing or darting. Preferred temperatures, also measured with a Schultheis, were obtained from lizards in a photo-thermal gradient measuring 1 × 0.5 × 0.3 m with a 100-watt light-heat source at one end above the sand-bottomed runway. Two or three newly captured lizards (maximum of one male) were placed simultaneously in the runway, and the temperatures were recorded between 20 and 48 hours after introduction.

From 28 July through 6 August 1968, I counted active *Tropidurus* by visually searching the cliffs and beach within the study area each day at 0800, 0930, 1230, 1530 and 1730 hours (Stebbins et al., 1967). Air and substrate temperatures were measured at a sandy location at the cliff base (above the high tide level to prevent the influence of evaporative cooling) immediately prior to each census. However, because microclimates vary with differences in exposure and substrate color, these measurements must be considered as approximations of general thermal conditions in the study area. I estimated relative cloud cover over the area on a scale of 1 to 11 (1 = completely overcast, 11 = completely clear) and wind velocity on a scale of 1 to 3 (1 = very mild breeze; 3 = strong, gusty winds). I defined emergence as the first appearance of a lizard at its burrow entrance and activity as complete exposure from its burrow.

Comparative studies should ideally be conducted using standardized procedures at similar seasons. Because my comparison is based on data of several workers at different seasons, evaluation of possible biases is necessary (for seasonal influences, see Discussion). First, differences in mechanics of taking body temperatures should be minimal as I learned these techniques personally from R. C. Stebbins. Second, because Stebbins et al. (1967) measured body temperatures of lizards above ground and not in retreats, we both sampled only active lizards (see above definition). Although the lower body temperatures of *T. albemarlensis* are due in part to my inability to capture the few *T. peruvianus* active at cool ambient temperatures (see Results), they are primarily due to the normal activity of *T. albemarlensis* (Stebbins et al., 1967) under conditions (cold, rainy, cloudy) too severe for *T. peruvianus*. Third, differences in design of photothermal gradients (gradient for *T. albemarlensis* had heat sources at both ends) should not invalidate comparisons: DeWitt (1967) and Pianka (1971a) found nearly identical preferred temperatures of *Dipsosaurus dorsalis* despite more extreme differences in gradients. Fourth, although our data do not strictly represent preferred temperatures (Regal, 1970) as Stebbins (pers. comm.) and I both placed several lizards in our runways, comparisons of our data are valid since we followed similar protocol. Fifth, Stebbins (pers. comm.) provided food during his experiments while I did not. The preferred temperatures of *T. peruvianus* should have been higher and more different had I also provided food (Regal, 1966). In summary, biases due to differences in technique certainly influence the results, but should not markedly influence the comparisons.

RESULTS

Study Area and Habitat Requirements.—The climate at Tric Trac is typical of arid coastal areas in northern Peru. Temperatures are mild and average daily maxima at 1200 hours range from 32 C in January to 24 C in August (S. Bertarelli, pers. comm.). Observations were made during the coolest season. Rains are very infrequent in northern Peru, and no measurable precipitation was was recorded during the study or in the four preceding years. Low, heavy cloud cover in the early morning occurs throughout the year; however, skies are usually clear by mid-morning.

T. peruvianus occupy a restricted habitat at Tric Trac bounded by the vertical cliffs and adjacent, narrow beach along the Golfo de Sechura. Other diurnal lizards (*T. occipitalis, Dicrodon guttulatum,* and *D. heterolepis*) are restricted to the sandy Sechura Desert inland from the cliffs. Cliffs are conglomeritic, fragmented, and striated with many ledges. Wave action undermines the base of the cliffs, and large sections regularly fall to the beach. *Tropidurus* frequent ledges and cliff talus, but less often the beach proper. Kelp was observed rarely along the beach and only two plants (small *Prosopis*) were recorded on the cliffs.

At the Estuario de Virrila (35 km SSE of Sechura), *T. peruvianus* are abundant on sandy soils along the edge of the estuary and on the adjacent conglomeritic outcrops. At an abandoned mining camp at Reventazon (several km from the ocean), these lizards occupy rock piles and brick walls but are absent from the surrounding sandy desert. I also collected *T. peruvianus* in driftwood accumulations on rocky beaches in central Peru.

In summary, the general habitat requirements for *T. peruvianus* in northern Peru are coastal localities providing refugia such as cliffs, rock outcrops, and driftwood. My observation that these lizards do not inhabit open, sandy desert regions corroborates observations of Mertens (1956).

Morning Emergence.—*T. peruvianus* first appear at burrow entrances (emergence) on the cliff face between 0730 and 0800 hours: 31 July (0747 hrs), 1 August (0755), 2 August (0745) and 5 August (0740). An emerged lizard exposes only its head and forequarters. On warm clear mornings lizards move away from burrow entrances and thus commence activity promptly, retreating to burrows only if disturbed. However, on cool cloudy mornings lizards do not leave their burrows and soon retreat (reappearing every few minutes), suggesting that first emergence and onset of activity can be distinct behavioral events (Evans, 1967). Moreover, since time of first emergence is relatively constant and may precede activity by several hours (compare above emergence data with activity data of Fig. 1), these data suggest
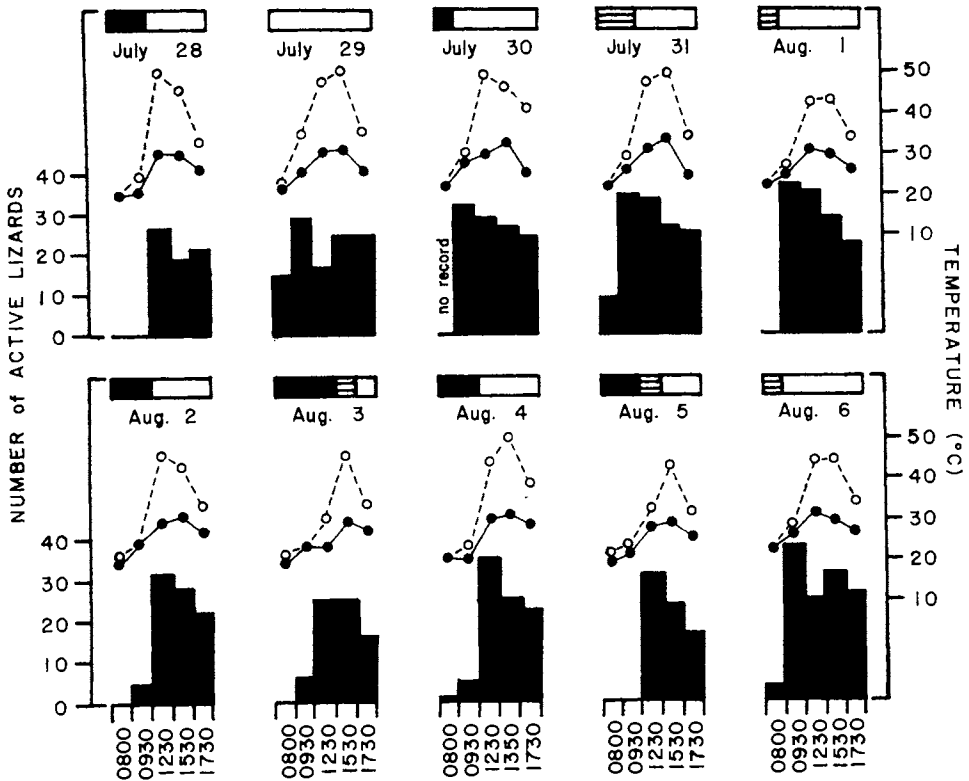
Fig. 1. Number of active *T. peruvianus* (vertical solid bars), air temperature (dots), substrate temperature (open circles), and cloud cover indices (solid horizontals = 1 to 3, hatched horizontals = 4 to 7, open horizontals = 8 to 11: see Methods) at 5 census periods on 10 days.

that emergence is under control of a circadian rhythm (Evans, 1967; Heath, 1962), while activity is not.

In the early morning lizards are especially wary, probably because of inadequate locomotion at low body temperatures (Rand, 1964). The few lizards which were active on cool, cloudy mornings had difficulty scaling the cliffs and repeatedly fell when trying to escape, whereas I never saw a lizard fall at midday.

Morning Activity.—There are daily differences in the times active lizards were first observed, in the number of lizards active at specific census times, and in the environmental conditions at those same times (Fig. 1). These concurrent variations suggest that the number of lizards active in a given morning could be causally related to environmental conditions. Three major factors might influence the morning thermal en-

vironment of lizards at Tric Trac: air temperature, substrate temperature, and cloud cover. Because the cliff faces northwest, few lizards are exposed to direct sunlight until 1000 hrs or later. Because strong winds were never recorded before the 1230 census (Table 1), differences in wind cannot explain variable lizard activity.

To analyze relations of variable lizard activities on different mornings to environmental conditions, I averaged the number of active lizards (Y_r, dependent variable, an index of lizard activity) and the environmental values (X_i, independent variables) for the 0800 and 0930 census on each of nine mornings. Because these values are averages, I used non-parametric Kendall Rank (τ) Correlation Tests (Siegel, 1956). These tests relate daily variation in lizard activity to variation in environmental conditions at specific times, but do not relate variation in lizard activity to environmental

TABLE 1. AVERAGE AND RANGE OF LIZARD ACTIVITY, AIR TEMPERATURE, SUBSTRATE TEMPERATURE, CLOUD COVER INDEX, AND WIND INDEX AT FIVE CENSUS TIMES FOR *T. peruvianus* AT TRIC TRAC. See Methods for explanation of clear sky and wind indices.

Time	Number of Active Lizards		Air Temperature		Substrate Temperature		Cloud Cover Index		Wind Index	
	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
0800	2.8	(0–15)	20.5	(19.4–22.0)	21.5	(20.4–23.0)	3.1	(1–11)	1.3	(1–2)
0930	18.7	(0–37)	23.8	(19.8–27.7)	26.8	(23.2–34.5)	4.7	(1–11)	1.2	(1–2)
1230	28.8	(17–35)	29.6	(24.5–31.8)	43.6	(30.7–50.0)	9.1	(1–11)	1.6	(1–3)
1530	25.8	(19–31)	30.7	(29.5–33.5)	46.3	(42.4–50.4)	10.1	(5–11)	1.6	(1–3)
1730	22.0	(16–25)	26.4	(24.5–28.5)	34.7	(32.0–39.0)	9.9	(5–11)	1.8	(1–3)

conditions at sequential times within any one morning.

All environmental variables are significantly correlated with the number of active lizards (Table 2), but air temperature has the highest correlation. Because all variables are significantly inter-correlated (Table 2), I use Kendall Partial Rank ($\tau_{xy\cdot z}$) Tests to compensate for statistical interactions among environmental variables (Siegel, 1956). These statistics also show that the average number of lizards active during a morning is most closely correlated with the average air temperature (Table 3).

Correlation does not imply cause and effect. Nonetheless, these correlations are consistent with the hypothesis that the extreme variability between mornings in lizard activity (Fig. 1) is causally related to environmental conditions. I infer that *T. peruvianus* at Tric Trac carefully regulate their morning activity to times of suitable environmental conditions (Heatwole et al., 1969).

Midday and Afternoon Activity.—T. peruvianus apparently have a unimodal pattern of activity with the number of lizards peaking at about 1230 hrs (Table 1, Fig. 1). Midday activity did decline on 29 July, 3 August and 6 August, but there was either heavy cloud cover or strong, gusty winds at 1230 on these days. The possibility of a midday decline between the 1230 and 1530 censuses cannot be discounted, although I never noticed a decline during casual observations.

Lizard activity declines throughout the afternoon (Table 1, Fig. 1), and no lizards were seen within one-half hour of sunset. No significant correlations were found between afternoon lizard activity and any environmental variable (air temperature, substrate temperature, cloud cover, or wind). This may result from the exposure of lizards during the afternoon to direct solar radiation, a factor which does not complicate the morning thermal environment because the cliffs are then shaded.

*Thermoregulation.—*Field body temperatures of active male and female *T. peruvianus* were not significantly different (median test, $P > .05$), and the overall mean body temperature (MBT) of 39 adults was 36.3 ± 0.26 C (range 32.3–39.0). Associated air temperatures were considerably lower and

TABLE 2. KENDALL RANK CORRELATION COEFFICIENTS (τ) FOR PAIRED COMPARISONS AMONG MEAN NUMBER OF ACTIVE LIZARDS IN THE MORNING (Y), MEAN AIR TEMPERATURE (X_1), MEAN SUBSTRATE TEMPERATURE (X_2), AND MEAN CLOUD COVER (X_3). Nine samples only (30 July not included as high tides prevented complete checks of study area during 0800 census).

Comparison	τ	P
$Y - X_1$	.754	.003
$Y - X_2$	.609	$.022 > P > .012$
$Y - X_3$	.626	.022
$X_1 - X_2$	.600	$.022 > P > .012$
$X_1 - X_3$	.669	.012
$X_2 - X_3$	.752	.006

TABLE 3. KENDALL PARTIAL RANK CORRELATION COEFFICIENTS ($\tau_{xy\cdot z}$). Symbols as Table 2. ($YX_1 \cdot X_2 = Y$ vs. X_1, X_2 held constant).

Comparison	$\tau_{xy\cdot z}$
$YX_1 \cdot X_2$	.613
$YX_2 \cdot X_1$	.298
$YX_3 \cdot X_1$	.250

averaged 27.8 ± 0.37 C (range 22.0–32.9). Body temperatures were not significantly correlated with air temperatures (r = +.251, P > .05). Photo-thermal gradient measurements (n = 17) of preferred body temperature (PBT) averaged 35.6 ± 0.31 C, not significantly different from the MBT (median test, P > .05).

DISCUSSION

Not all lizards, even diurnal desert species, maintain body temperatures within narrow limits (Brattstrom, 1965; Heatwole, 1970; Mayhew, 1968; Ruibal and Philibosian, 1970). I present comparative data to show tentatively that *T. peruvianus* at Tric Trac is more stenothermal than *T. albemarlensis* in the Galapagos and propose an explanation of the adaptive significance of their different thermoregulatory strategies.

Regulation of activity to times of suitable conditions is one method of behavioral thermoregulation (Heatwole et al., 1969). For example, *T. peruvianus* in winter appear to regulate activity times carefully, as evidenced by strong correlations between lizard activity and environmental conditions. Additionally, *T. peruvianus* postpone activity until 1 to 4 hrs after sunrise, do not have a midday retreat, and cease activity before sunset: total activity time must therefore be short. In contrast, *T. albemarlensis* in late summer are active from sunrise to sunset except at midday (Stebbins et al., 1967). *T. albemarlensis* appear to regulate activity times less carefully, as evidenced by their greater total activity time and by their activity at sunrise even during hard rains. Seasonal influences undoubtedly account in part for these differences. Indeed, activity of adult *T. albemarlensis* is apparently reduced during winter (pers. comm. of Mrs. Nelson, cited in Stebbins et al., 1967). It is therefore impossible to argue conclusively that *T. peruvianus* regulate activity times more carefully than *T. albemarlensis*. However, the available information, supplemented by data on differences in regulation of body temperature (see below and Heatwole et al., 1969), is consistent with this hypothesis.

Body temperatures of active *T. albemarlensis* in the field were distinctly bimodal in distribution (modes at about 25 and 35 C), with the lower mode representing lizards active (Stebbins et al., 1967:846) ". . . in the morning, late afternoon, or on overcast days when it was impossible for the animals to reach the higher levels." *T. peruvianus* were active at significantly higher (MBT = 36.3 ± 0.26 C) temperatures (median test, P < .001) and over a narrower range (32–39 vs. 22–39). Because one would expect the MBT of *T. peruvianus* to be even higher in summer and that of *T. albemarlensis* to be lower in winter (Pianka, 1971b), a study on these species at the same season should magnify differences, not eliminate them.

Preferred temperatures of *T. albemarlensis* in a photothermal gradient (mean = 34.4 ± 0.39 C, data courtesy R. C. Stebbins) were significantly lower (median test, P < .05) than those of *T. peruvianus* (mean 35.6 ± 0.31 C). Preferred temperatures of *T. albemarlensis* had a suggestively greater variance (F-test, .10 > P > .05). Because one would expect the MPT of *T. peruvianus* to be higher in summer and that of *T. albemarlensis* to be lower in winter (Ballinger et al., 1967), repetition of these studies at the same season might again magnify differences.

Overall, *T. peruvianus* appear to be active at higher temperatures and over narrower ranges of temperatures than *T. albemarlensis*. Heatwole et al. (1969) argued that stenothermal lizards regulate times of activity carefully. Therefore, the observed more careful regulation of activity by *T. peruvianus* may be real, even though certainly influenced by seasons. Despite biases due to seasons and to differences in technique (see Methods), available data are consistent with the hypothesis that *T. peruvianus* are more stenothermal than *T. albemarlensis*.

Why is *T. albemarlensis* eurythermal compared with *T. peruvianus*? The concept of ecological release, suggested by Ruibal and Philibosian (1970) to explain the eurythermy of *Anolis oculatus* of Dominica, is inapplicable here as neither species has syntopic diurnal lizard competitors.

Average climatic differences between Tric Trac and Santa Cruz might be influential. Cloud cover at Tric Trac usually burns off by midmorning during winter (Fig. 1), even earlier during summer, and afternoon cloud cover is rare throughout the year (S. Bertarelli, pers. comm.): in contrast, there may be only 1 to 2 hrs of sunshine daily on

Santa Cruz during winter (Stebbins et al., 1967), and both morning and afternoon cloud cover is persistent during summer months. Although these weather data are limited, the apparent heavier cloud cover of the Galapagos implies limited solar insolation for *T. albemarlensis*.

If sunshine is less available to *T. albemarlensis* (an analogous situation would be for a "trunk-ground" lizard in a closed forest compared to an open-forest lizard), selection will broaden and lower ranges of acceptable body temperatures. Otherwise these lizards will expend too much time and energy attempting to elevate and maintain uniform, high body temperatures at the sacrifice of time and energy for feeding and social interaction. By similar reasoning one would predict that *T. peruvianus* from coastal areas of southern Peru and northern Chile should be more eurythermal than lizards from Tric Trac, because of the more persistent cloud cover of these areas.

To generalize these hypotheses, I suggest that the mean and variance of a lizard's thermal niche are indirect functions of maximizing its fitness through shifts, expansions, or compactions of its temporal activity in a given environment. The primary factor governing an increase in the variance will be the balance between possible gains from increased activity time and possible costs from decreased metabolic efficiency (in part Soulé, 1963; McGinnis, 1970; Heatwole et al., 1969), decreased competitive ability, and increased susceptibility to predators. The direction of this inequality will change in different environments and through adaptations. For example, in areas where the environmental temperature array is spatially heterogeneous (e.g., deserts and open forests), lizards should be stenothermal for the cost of thermoregulating is low. In areas where environmental temperatures are spatially homogeneous (e.g., closed forests), lizards should be eurythermal for the cost of thermoregulating is greater than the benefits.

Acknowledgments

Literature Cited

BALLINGER, R. E., J. HAWKER AND O. J. SEXTON. 1969. The effect of photoperiod acclimation on the thermoregulation of the lizard, *Sceloporus undulatus*. J. Exp. Zool. 171:43–48.

BRATTSTROM, B. H. 1965. Body temperatures of reptiles. Amer. Midland Natur. 73:376–422.

CARPENTER, C. C. 1970. Miscellaneous notes on Galapagos lava lizards (*Tropidurus*—Iguanidae). Herpetologica 26:377–386.

DEWITT, C. B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. Physiol. Zool. 40:49–66.

EVANS, K. J. 1967. Observations on the daily emergence of *Coleonyx variegatus* and *Uta stansburiana*. Herpetologica 23:217–222.

HEATH, J. E. 1962. Temperature-independent morning emergence in lizards of the genus *Phrynosoma*. Science 138:891–892.

HEATWOLE, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. Ecol. Monogr. 40:425–457.

———, T. LIN, E. VILLALÓN, A. MUÑIZ AND A. MATTA. 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. J. Herpetol. 3:65–77.

MAYHEW, W. W. 1968. Biology of desert amphibians and reptiles. p. 196–356. *In*: Desert Biology, Vol. 1. G. W. Brown, Jr., ed. Academic Press, New York.

McGINNIS, S. M. 1970. Flexibility of thermoregulatory behavior in the western fence lizard *Sceloporus occidentalis*. Herpetologica 26:70–76.

MERTENS, R. 1956. Zur Kenntnis der Iguaniden-Gattung, *Tropidurus* in Peru. Senck. Biol. 37:101–136.

PIANKA, E. R. 1971a. Comparative ecology of two lizards. Copeia 1971:129–138.

———. 1971b. Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. Copeia 1971:527–536.

RAND, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45:863–864.

REGAL, P. J. 1966. Thermophilic response following feeding in certain reptiles. Copeia 1966:588–590.

———. 1970. Long term studies with operant conditioning techniques of temperature regulation patterns in reptiles. Journal de Physiologie 63:403–406.

RUIBAL, R., AND R. PHILIBOSIAN. 1970. Eurythermy and niche expansion in lizards. Copeia 1970:645-653.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

SOULÉ, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. Copeia 1963:107-115.

STEBBINS, R. C., J. M. LOWENSTEIN AND N. W. COHEN. 1967. A field study of the lava lizard (*Tropidurus albemarlensis*) in the Galapagos Islands. Ecology 48:839-851.

DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF TEXAS AT AUSTIN, AUSTIN, TEXAS 78712. PRESENT ADDRESS: MUSEUM OF COMPARATIVE ZOOLOGY, HARVARD UNIVERSITY, CAMBRIDGE, MASSACHUSETTS 02138.

Oxygen Consumption and Evaporative Water Loss in Four Species of *Acanthodactylus* (Lacertidae)[1]

I. DUVDEVANI AND A. BORUT

Oxygen consumption (OC) and total evaporative water loss (EWL) were measured simultaneously in males of four species of fringed-toed lizards, *Acanthodactylus* (Lacertidae), at ambient temperatures of 25 C to 45 C during the summer. In Israel these four species occupy habitats of different aridity. Lizards of the genus *Acanthodactylus* are not exceptional in their low OC or EWL when compared to other xeric lizards discussed in the present paper. However, a correlation was found in the four species between the aridity of the habitat and the OC, EWL and the Q_{10} values of OC and EWL at the lizards' range of activity temperatures. These findings support the concept that lowering of OC, EWL and their Q_{10} values are important in the adaptation of a lizard for life in the desert, even within a single genus.

OUR study of the physiological adaptations of desert lizards focused on oxygen consumption (OC) and evaporative water loss (EWL). Low weight-specific OC at high ambient temperatures was suggested as an important factor in the thermophilic lizards' adaptation for life in the desert (Schmidt-Nielsen and Dawson 1964; Dawson 1967). Low values for the temperature coefficient (Q_{10} value) of OC may also be important. Decreasing values of Q_{10} with the elevation of ambient temperature thus express a tolerance to higher temperatures in a lesser oxygen demand and less temperature dependent metabolic reactions (Schmidt-Nielsen, 1964). In his review Dawson (1967) did not succeed in demonstrating any correlation between Q_{10} values and thermophily (daily active desert lizards are thermophilic, that is, have a mean activity temperature above 36 C—see Dawson, 1967). This is ascribed to differences in techniques and data analyses presented in the literature. Dawson (1967) suggested collection of additional information on lizard species before renewed attempts to correlate metabolism and Q_{10} values with habitat are made.

Intensive study of water loss in reptiles has established a correlation between rate of evaporation and aridity of habitats (Bogert and Cowles, 1947; Bentley and Schmidt-Nielsen, 1966; Schmidt-Nielsen and Bentley, 1966; Dawson et al., 1966; Claussen, 1967; Ernst, 1968; Munsey, 1972). The correlation is better demonstrated in closely related groups of reptiles. Gans et al. (1968), Krakauer et al. (1968) and Prange and Schmidt-Nielsen (1969) studied amphisbaenids and different snake families. They found that in species that inhabit wet biotopes the EWL is high and similar to that of amphibians, while in related species from arid zones this loss is a hundred times lower. It is consequently of interest to study interspecific differences in EWL of species within a single genus.

In the present study oxygen consumption, total evaporative water loss and their Q_{10}

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[1] This paper is dedicated to the memory of Benny Silber, chief technician in our laboratory, who was killed in action 8 October 1973 in the Sinai.