

THERMAL DEPENDENCE OF LOCOMOTION AND AGGRESSION IN A XANTUSIID LIZARD

WILLIAM J. MAUTZ¹, CHRISTOPHER B. DANIELS^{2,3},
AND ALBERT F. BENNETT²

¹*Department of Community and Environmental Medicine
and*

²*Department of Ecology and Evolutionary Biology,
University of California at Irvine, Irvine, CA 92717, USA*

ABSTRACT: The thermal dependence of sprint speed, exertion distance and time, and aggressive response was examined in the island night lizard, *Xantusia riversiana*, over a body temperature range of 10–35 C. Critical thermal limits were 6.6 and 39.0 C. Thermal optima for sprint speed and distance approximated preferred body temperature (28.3 C) and declined at higher or lower body temperatures. Exertion time was largely independent of body temperature, and lizards ran for about 70–90 s. Speed during exertion sprinting declined exponentially with increasing time and distance covered. Maximum oxygen consumption at 30 C ($\dot{V}_{O_{2max}}$) occurred immediately following burst sprinting and was greater than values recorded for other species of lizards of similar body mass; factorial aerobic scope relative to standard \dot{V}_{O_2} was 29. Maximal aggressive responses occurred at low body temperatures which are suboptimal for sprinting, but aggressive behavior was always preceded by a sprint to exhaustion. Temperature and exercise state appear to be interacting factors influencing aggressive responses.

Xantusia riversiana is a diurnal but reclusive lizard with relatively low preferred body temperature and low temperature optimum for sprinting. In the dense vegetative scrub and rocks that the lizards inhabit, sprint escape from predators is the initial response at all activity body temperatures. Sprint performance also represents capacity for struggle against restraint, and the increased aggressive response of exhausted lizards at low body temperatures may be a defensive response compensating diminished capacity for struggle at low body temperatures.

Key words: Aggression; Lizard; Oxygen consumption; Speed; Sprint performance; Temperature; *Xantusia riversiana*

ALTHOUGH active defenses of ectotherms against predation are influenced by body temperature, maximum performance of defensive actions may not be realized at or near mean preferred body temperatures (T_p) (Bauwens and Thoen, 1981; Bennett, 1980; Daniels, 1984; Hertz et al., 1982). For example, lizards at cold body temperatures have reduced locomotor capacity for escape, but they may display more aggressive defensive behavior, such as open mouth threats and biting (Crowley and Pietruszka, 1983; Greene, 1988; Hertz et al., 1982), or take flight at greater predator approach distances (Rand, 1964). Tail autotomy is another important anti-predator defense in lizards, and tail autotomy frequency is greater at body temperatures both above and below T_p

(Bustard, 1968; Daniels, 1984, 1985). The thermal dependence of individual defensive tactics thus varies such that optimal thermal conditions for one mechanism do not necessarily overlap those for another, and the complete repertoire of defenses provides effective responses to attack over a broad range of body temperatures.

The purpose of this study was to examine the effect of body temperature on maximum sprint speed, exertion capacity (distance and time run to exhaustion under pursuit), and aggression in the xantusiid lizard *Xantusia riversiana*. Xantusiid lizards are secretive and confine activities to dense shelter. They are generally active by day (Lee, 1974; Mautz, 1979a; Mautz and Case, 1974), sprint ably when exposed in their retreats, and bite furiously when grasped (Greene, 1988). Compared to other species of lizards that are active abroad in open habitats, xantusiids have relatively low $T_p = 26\text{--}33$ C in thermal gradients

³ PRESENT ADDRESS: Department of Physiology, School of Medicine, Flinders University of South Australia, Bedford Park, S.A. 5042, Australia.

(Brattstrom, 1965; Kaufmann and Bennett, 1989; Mautz, 1979b; Mautz and Case, 1974; Regal, 1968). The thermal dependence of sprint speed in xantusiids might therefore be expected to facilitate performance at lower body temperatures. Furthermore, xantusiids have standard rates of oxygen consumption (\dot{V}_{O_2}) which are only one-half to one-third those of lizards of other families (Mautz, 1979a). We measured \dot{V}_{O_2} during activity to examine whether maximum \dot{V}_{O_2} was also reduced and possibly limiting locomotor performance.

Xantusia riversiana inhabits three of the Channel Islands off southern California. Although these lizards are not readily observed abroad in the field, they move among thickets of low scrub vegetation with peak activity centered at midday (Fellers and Drost, 1991). They actively seek sources of heat (Regal, 1967, 1968), have a T_p of 28.3 C in a thermal gradient, and in the field on sunny days they have body temperatures ranging from 15–32 C that are elevated an average of 5.7 C over retreat site air temperatures (Mautz, 1979b). *Xantusia riversiana* ranges up to 109 mm body length and 37 g (Goldberg and Bezy, 1974), and on Clemente Island, individuals fall prey to native kestrels and shrikes. Feral cats and pigs present on San Clemente Island within the past century also prey on these lizards, and *X. riversiana* comprised 40% of the dietary items in a sample of 10 cats from this island (R. Wilson and W. Mautz, unpublished observations). The thermal dependence of escape behavior and aggressive response is likely an important component of predator defense for the lizards, and predator defense is an important aspect of conservation biology for this narrowly distributed and threatened species of *Xantusia*.

MATERIALS AND METHODS

Eleven *X. riversiana* were collected from San Clemente Island, Los Angeles County, California, (Memorandum of Understanding, California Fish and Game, to the senior author) and were returned to the laboratory. They were held in individual cages in a temperature controlled cabinet main-

tained on an LD 12:12 photoperiod at 28 C by day and 20 C by night. Choice of 28 C was based on T_p of *X. riversiana* in a thermal gradient during the daytime activity period (Mautz, 1979b). Lizards were provided with water ad lib. and fed larval *Tenebrio* once a week and two days prior to any experiments. All animals were released in excellent condition at the capture locality at the conclusion of the study.

Two types of locomotor tests were conducted. Sprint speed measurements were made in a linear track 0.1 × 1.5 m floored with plastic lawn (Astroturf) and ruled with 0.25 m marks. Lizards were chased down the track by gently prodding their tails. Sprint trials were videotaped, and speed over each 0.25 m interval was determined from slow motion and stop-action replays. We ran lizards two times in succession, allowed 1 h to rest, and then ran them twice again. The fastest speed over any 0.25 m interval was used in subsequent analyses. We measured exertion running capacity in a circular track 0.20 m wide with a lap distance of 3 m. Lizards were chased around the track by an investigator standing at the center and using a blunt prod. Endpoint was determined as failure of the lizard to run further after 10 rapid taps on the tail with the prod. We measured time and distance run to this endpoint. At the end of the exertion runs, *X. riversiana* frequently assumed defensive postures similar to those adopted by other species of lizards in advance of, or instead of, running (Hertz et al., 1982). The post-run behaviors of the lizards were catalogued and scored as follows: head up (1) or down (0), mouth open (1) or closed (0), attempt to bite (1) or not (0). We summed scores for the three possible conditions for each lizard.

Locomotor tests were performed in a temperature controlled room. On the day of an experiment, lizards were brought into the room (at test temperature) 4 h before running. Body temperature of lizards was measured following each run. Temperature was set at a selected level for two days, and sprint tests were done on Day 1 followed by exertion tests on Day 2 (Bennett, 1980). Initially, sprint performance was

tested at 28 C on consecutive days to establish a baseline of repeatable performance. *Xantusia riversiana* did not exhibit a significant difference in performance between the first two days at this temperature. We randomly ordered five successive test temperatures for sprint and exertion runs (25, 10, 20, 30, and 15 C), and we made final sets of measurements at the warmest temperature, 35 C, and then again at 28 C. On the final exertion test at 28 C, the time to complete each consecutive 3.0 m lap was recorded for each lizard. For determination of thermal performance breadth and optimum, we measured critical thermal maximum (CT_{max}) and minimum (CT_{min}) from separate groups of freshly captured lizards on San Clemente Island. Lizards were held in a plastic container set in a water bath and warmed or cooled predominantly by conductive and convective exchange at 1–2 C/min. Critical temperatures were determined as body temperature at loss of righting response. All animals recovered quickly from these measurements.

Oxygen consumption during locomotion was measured on a variable speed treadmill described elsewhere (John-Alder and Bennett, 1981). Lightweight transparent acetate masks were fitted loosely around a lizard's head, and air was drawn from the mask at 300 ml/min to collect expired air. Room temperature was set at 30 C. Carbon dioxide and water vapor were absorbed with Ascarite and Drierite, respectively, and we analyzed oxygen content of the expired air with an Applied Electrochemistry model S-3A oxygen analyzer. *Xantusia riversiana* readily performed burst sprinting but could not be trained to walk at sustained speeds on the treadmill. Treadmill speed was adjusted during the tests to keep lizards running on the open track, and the lizards became exhausted within 40–108 s. Oxygen consumption (STPD) was calculated from gas fraction recordings (corrected for gas sample transport time delay) for periods during and immediately after sprinting, using appropriate standard equations (Withers, 1977). We analyzed values for the 30 s period of highest oxygen consumption.

Statistical analyses were performed using paired *t*-tests, repeated measures analysis of variance, and regression analysis (Dixon, 1985). Thermal performance breadths, B_{95} (the temperature range for performance exceeding 95% of maximum) and B_{80} (temperature range for performance exceeding 80% of maximum), and optimal temperature, T_o (the midpoint temperature of B_{95}), for sprint speed, exertion distance, and exertion time (Hertz et al., 1983) were determined by the method of convex polygons (van Berkum, 1986).

RESULTS

Xantusia riversiana ran immediately upon release in the linear and circular race tracks at all temperatures tested, and the lizards did not engage in defensive or aggressive displays before running. In trials conducted at 28 C at the beginning and again at the end of the experiment, no locomotor or behavioral variable changed significantly (Table 1). None of the performance variables were significantly correlated with body mass over the narrow range of body sizes examined. Differences among individual animals in performance were highly significant across all temperatures for both sprint speed ($F = 4.3$, $df = 8$, $P < 0.006$) and exertion distance ($F = 3.4$, $df = 8$, $P < 0.004$) tests. Two lizards lost portions of their tails during handling. However, tail loss had no significant effect on sprint speed ($F = 0.2$, $df = 1$, $P < 0.66$) or exertion distance ($F = 0.1$, $df = 1$, $P < 0.71$) across the temperatures 10, 20, 28, 30, and 35 C that included tests of lizards with broken tails. Data from these animals were therefore included in subsequent analyses.

CT_{max} was 39.0 C \pm 0.4 SE ($n = 11$) and CT_{min} was 6.6 C \pm 0.4 SE ($n = 12$). Sprint speed was strongly dependent on body temperature over the lower range of temperatures tested (Fig. 1) but had a broad plateau from 25–35 C, as shown by the value of the B_{80} statistic (Table 2). Optimal sprint speed temperature, 29.2 C (Table 2), was similar to T_p (28.3 C) (Mautz, 1979b). Thermal dependence of total distance run in the circular track (Fig. 2, Table 2) was similar to that of maximum

TABLE 1.—Initial and final locomotor performance of *X. riversiana* at 28 C. Data are $\bar{x} \pm SE$ (range); $n = 11$, and an asterisk indicates a significant paired t -test statistic.

	Initial value $\bar{x} \pm SE$ (range)	Final value $\bar{x} \pm SE$ (range)	t	P
Snout-vent length (cm)	9.53 \pm 0.20 (8.70–10.80)	—	—	—
Mass (g)	25.52 \pm 1.46 (20.40–35.40)	20.52 \pm 1.17 (16.33–28.75)	2.67*	0.011
Maximum running speed over 0.25 m (m/s)	1.57 \pm 0.15 (0.88–2.78)	1.43 \pm 0.07 (1.09–1.92)	1.03	0.33
Exertion time (m)	87.27 \pm 15.03 (54.11–233.17)	82.78 \pm 10.53 (56.11–180.71)	0.63	0.47
Distance run (m)	19.57 \pm 1.95 (12.75–35.34)	21.26 \pm 1.51 (12.18–30.24)	–1.37	0.19
Behavior score	0.45 \pm 0.21 (0–2)	0.91 \pm 0.42 (0–3)	–0.80	0.43

sprint speed. Total time run to exhaustion, however, was remarkably independent of temperature (Fig. 2, Table 2). Most of the lizards were capable of burst runs of about 70–90 s, and the distance that they covered was, in turn, largely dependent on the speed that they could achieve.

A complete profile of speed versus time and speed versus distance was measured in the final exertion run conducted at 28 C. Maximum speed was attained within the first few seconds of running; speed then declined exponentially, and most lizards were exhausted after running 80 s and covering 21 m (Fig. 3). Regression equations of the form $V = a_1 e^{b_1 T}$ and $V = a_2 e^{b_2 D}$ were calculated for each individual animal ($n = 11$) where e is the base of natural logarithms, T is time in seconds, D is distance in meters, and a and b are empirically fit constants. Correlation coefficients for exponential fits for each individual ranged from -0.92 to -0.99 for V as a function of T and -0.89 to -0.99 for V as a function of D . Mean values of constants for time were $a_1 = 0.721 \pm 0.053$ SE and $b_1 = -0.029 \pm 0.005$ SE, and mean values for

distance were $a_2 = 0.915 \pm 0.061$ SE and $b_2 = -0.097 \pm 0.008$ SE. Because two of the 11 lizards had unusually high exertion capacities, data for individuals at times greater than 65 s and distances greater than 19.5 m lie above the curves, which represent an average response of all 11 individuals. These negative exponential relationships corresponded to a half-time decline in speed of 23.8 s and a half-distance decline in speed of 7.2 m.

The intensity of aggressive responses was strongly dependent on body temperature. As temperature declined, aggressive behavior score abruptly increased to a maximum at 20 C (Fig. 4), a temperature below which sprint speed began to decline greatly. At temperatures above 20 C, aggressive responses were uniformly low, and

TABLE 2.—Thermal optima and breadths for locomotor performance of *X. riversiana*.

	T_o (C)	B_w (C)	B_m (C)
Sprint speed ($n = 11$)	29.2	3.3	9.7
Exertion distance ($n = 11$)	28.0	3.7	12.1
Exertion time ($n = 10^*$)	24.5	6.9	17.2

* Exertion time of one individual did not vary consistently with temperature and criteria for convex polygon analysis were not met.

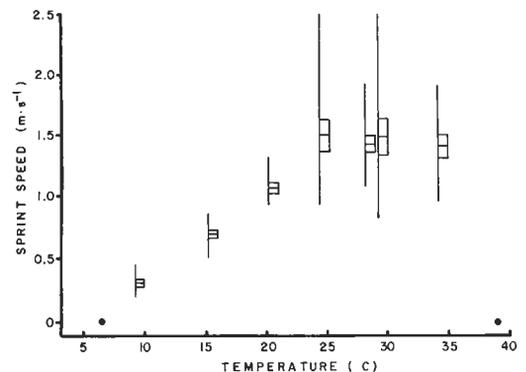


FIG. 1.—Relationship between body temperature and the sprint speed of *X. riversiana* ($\bar{x} \pm SE$ with ranges, $n = 11$). Solid circles are CT_{max} and CT_{min} .

below the 20 C maximum, aggression declined with falling temperature.

Xantusia riversiana attained high levels of oxygen consumption during and immediately following treadmill running. Eight lizards (mean body mass $20.5 \text{ g} \pm 1.6 \text{ SE}$) had satisfactory performance in these tests (defined as runs in which lizards were removed from their housing, masked, and placed on the treadmill all without a pre-run burst of struggling). During running, oxygen fraction of air from the mask was highly variable, and a 30 s steady state period of maximal \dot{V}_{O_2} could not be characterized, so average \dot{V}_{O_2} over the entire period of running was determined. Body temperature just prior to sprinting was $29.5 \text{ C} \pm 0.1 \text{ SE}$ and increased to $31.2 \text{ C} \pm 0.1 \text{ SE}$ after sprinting. \dot{V}_{O_2} during running was $30.8 \text{ ml/min} \pm 4.1 \text{ SE}$ ($n = 8$). Maximum \dot{V}_{O_2} immediately following running ($\dot{V}_{O_{2\max}}$), defined by a 30 s plateau of steady state \dot{V}_{O_2} , was $44.4 \text{ ml/min} \pm 3.5 \text{ SE ml/min}$. $\dot{V}_{O_{2\max}}$ and average \dot{V}_{O_2} during sprinting were respectively 2.3 and 1.6 times larger than the value of $\dot{V}_{O_{2\max}}$ expected for lizards of equivalent body mass (Bennett, 1982).

DISCUSSION

Xantusia riversiana was a moderately fast sprinter over relatively short distances but maintained its sprinting capacity over a wide range of low body temperatures. Maximum sprint speed measured over 0.25 m intervals (Fig. 1) was about half the maximum speed of an agamid lizard (Hertz et al., 1982), 85–90% that of the iguanid *Sceloporus undulatus* (Crowley, 1985), and intermediate among those of five species of nocturnal gekkonids (Huey et al., 1989). In exertion sprint tests, two iguanids, a teiid, and a scincid lizard had greater stamina than *X. riversiana* (Figs. 2, 3), while the exertion distance of the anguid, *Elgaria multicarinata*, was similar (Bennett, 1980).

Thermal performance breadths, B_{95} and B_{80} , for sprint speed of *X. riversiana* (Table 2) were similar to those of five nocturnal geckos and 13 diurnal lizard species compiled by Huey et al. (1989). Optimal sprinting temperature, T_{\circ} , of the xantusiid was lower than those of these other lizards,

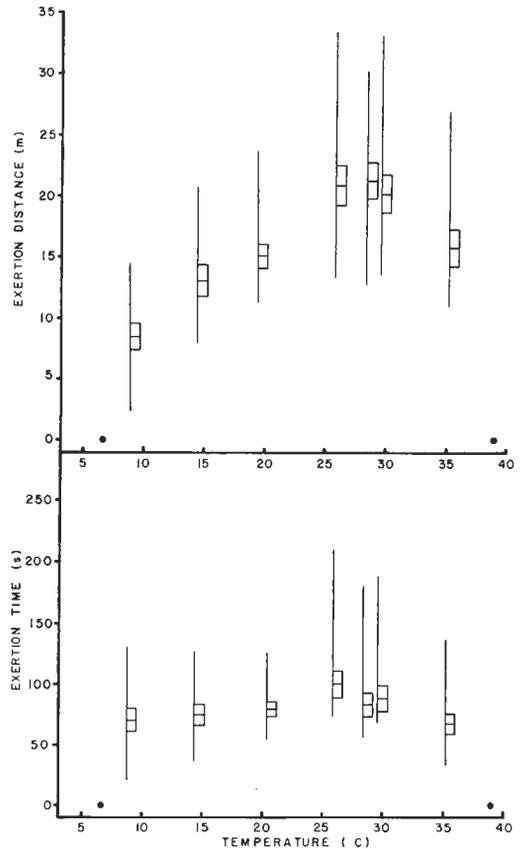


FIG. 2.—Relationship between body temperature and the exertion distance run and running time by *X. riversiana* ($\bar{x} \pm \text{SE}$ with ranges, $n = 11$). Solid circles are CT_{\max} and CT_{\min} .

and the xantusiid represents one of three apparent patterns of temperature dependent locomotor performance among lizards. Diurnal lizards active at relatively high body temperatures and having relatively high preferred body temperatures, T_p , also have high T_{\circ} for sprinting (Huey et al., 1989). Nocturnal geckos and skinks are active at lower body temperatures, have lower preferred temperatures, but also have high sprint T_{\circ} (Huey and Bennett, 1987; Huey et al., 1989). This means that the nocturnal geckos and skinks are active at body temperatures with substantially diminished sprint performance. *Xantusia riversiana* showed a distinctly different pattern; it is a diurnal lizard with a relatively low T_p , low sprint T_{\circ} , and low active body temperatures. Field body tem-

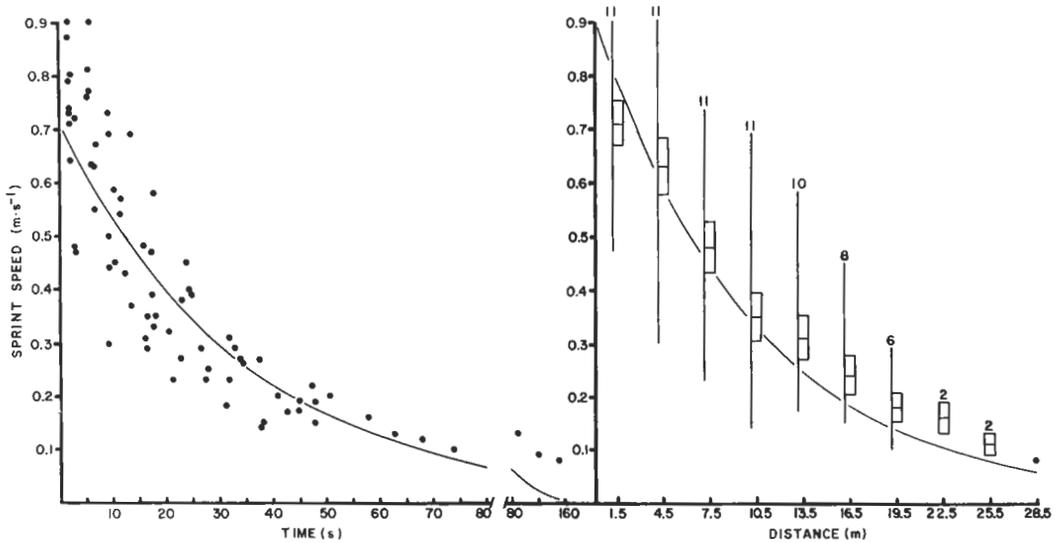


FIG. 3.—Sprint speed of *X. riversiana* over each 3 m lap of the circular track as a function of elapsed time (solid circles for individual lizards) and distance covered ($\bar{x} \pm SE$ with ranges). Mean body temperature was 29.0 C. Numbers are number of lizards completing each lap. Negative exponential curves have intercept and power constants which are averages of values derived from curve fitting to individual lizards (see text).

peratures of this lizard present a problem for interpretation, because the lizards are only rarely and fleetingly glimpsed abroad and are usually discovered by turning rocks or prostrate cactus stems in thickets of scrub vegetation. On sunny days, body temperatures of uncovered lizards ranged up to 13.2 C above air temperature at the site of discovery (Mautz, 1979b). Whether a reclusive lizard under cover is active or not is uncertain; however, body temperatures elevated above adjacent air temperatures imply that the lizards were basking or selecting warm spots within a sheltered site (Huey et al., 1989). If we approximate activity body temperatures as the set of all body temperatures recorded in the field at times in which one or more body temperatures were elevated at least 4 C above discovery site air temperature, the distribution has a mean of 24.4 C \pm 4.5 SD ($n = 45$), a median of 25.1 C, and range of 15.4–32.1 C. Body temperatures of *X. riversiana* in the field during the daily activity period averaged a few degrees less than T_p and T_o and did not exceed 32.1 C.

Sprint performance for another species of *Xantusia*, *X. vigilis*, showed tempera-

ture optima similar to T_p (Kaufmann and Bennett, 1989), but in comparison to other diurnal lizards or nocturnal geckos (Huey et al., 1989), these temperatures were not so clearly shifted toward the lower temperatures observed here for *X. riversiana*. Thermal biology of *X. vigilis* may be distinctive among Xantusiidae, because this desert lizard is found in the most extreme arid habitat of the family and has an elevated T_p (31.1–33.0 C) compared to other xantusiids, including two species of *Xantusia* and two species of *Lepidophyma* (25.6–28.3 C) (Kaufmann and Bennett, 1989; Mautz, 1979b).

Negative exponential curve fitting to the decline of speed with increasing time and distance during maximal exertion (Fig. 3) is an effective method of characterizing sprint performance in terms of an initial maximum speed (intercept) and speed decline constant (exponential term) with time or distance. In the data set for Fig. 3, the initial values of speed were average speeds over the first 3 m run, which included acceleration from standing start. Thus, the intercept speeds are less than maximum sprint speed recorded over 0.25 m intervals on the linear raceways. The exponential

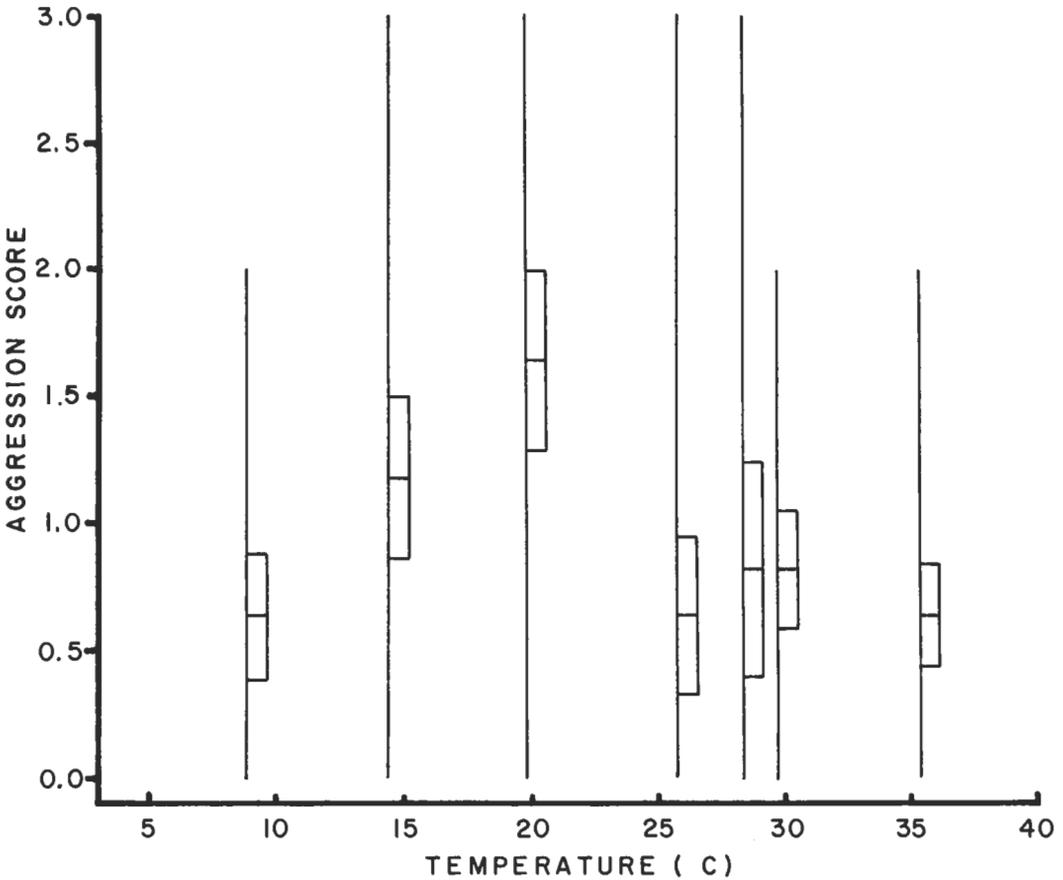


FIG. 4.—Relationship between body temperatures and aggression ($\bar{x} \pm SE$ with ranges, $n = 11$) for *X. riversiana*.

terms are a measure of performance that can be used in comparative analyses. A finer resolution of sprint speeds over short intervals at the beginning of test sprints might yield improved intercept estimators of maximum sprint speed.

It is curious that *X. riversiana* had a temperature dependent aggressive response (Fig. 4) that was only revealed when the lizards were exhausted after a long sprint. Two agamid lizards and an iguanid lizard displayed aggressive responses (biting or threat of biting) instead of running at low body temperatures and reduced sprint performance (Crowley and Pietruszka, 1983; Hertz et al., 1982). Sprinting and aggressive responses were thus complementary defenses across a broad range of body temperatures in these species. Sprint performance and aggressive behav-

ior of *X. riversiana* is an example of interacting factors, exhaustion and temperature, influencing aggressive response (Hertz et al., 1982). Because *X. riversiana* restricts activity to dense thickets of vegetation and loose rocks, escape from predator attack is available over short distances, and running is likely an effective defense even at low body temperatures. While the lizards can find refuge in their habitat long before sprinting to exhaustion (Fig. 2), the extended sprints observed in the laboratory also represent the capacity of the lizards to struggle against restraint by predators. The aggressive response (Fig. 4) may then function over lower body temperatures at which the capacity for high speed running and high intensity struggling against restraint is suboptimal (Figs. 1, 2).

The high values of V_{O_2max} recorded for

X. riversiana following sprinting and of average \dot{V}_{O_2} recorded during sprinting was surprising, because standard \dot{V}_{O_2} of xantusiid lizards is exceptionally low (Mautz, 1979a). Standard \dot{V}_{O_2} of a 20.5 g *X. riversiana* at 30 C is estimated to be 1.57 ml/h, and factorial aerobic scope is therefore 29. The only other lizard known with a comparable factorial aerobic scope is the small varanid lizard, *Varanus gilleni* (Bickler and Anderson, 1986). While the large factorial aerobic scope of the varanid resulted from a very large $\dot{V}_{O_{2max}}$, the large scope of the xantusiid resulted from a large $\dot{V}_{O_{2max}}$ and exceptionally low standard \dot{V}_{O_2} . The high $\dot{V}_{O_{2max}}$ of *X. riversiana* indicates that these lizards have no special limits on short term \dot{V}_{O_2} attained during activity that are imposed by the physiological or biochemical factors mediating the extremely low standard \dot{V}_{O_2} of xantusiid lizards (Mautz, 1979a). These observations are consistent with the hypothesis that low standard \dot{V}_{O_2} in Xantusiidae may be a derived state among lizards related to low energy utilization and reclusive behavior in small home ranges (Mautz, 1979a, 1991).

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