

PHYSIOLOGICAL CONSEQUENCES OF THERMOREGULATION IN A TROPICAL LIZARD (*AMEIVA FESTIVA*)¹

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Ameiva festiva, a teiid lizard from Costa Rica, alternately basks in the sun at the edge of forests and then forages in the shade of the forest. We used this natural analog of behavior in a laboratory shuttle-box to examine the effect of thermoregulatory behavior on physiological and ecological performances of lizards in nature. We observed body temperatures (by radiotelemetry) and locomotor behavior in the field and measured the thermal dependence of sprint speed, stamina, and aerobic scope in the laboratory. The mean upper and lower threshold temperatures for shuttling in the field were 39.4 ± 0.97 C (95% confidence interval) and 34.5 ± 1.11 C (95% confidence interval), respectively, and corresponded to very high levels of sprint speed (90% of maximum speed), stamina, and aerobic scope. Nevertheless, the lizards apparently rarely use these high levels of locomotor capacity. Although these lizards are active foragers, their speed and duration of movement in the field fall far below the levels of speed and stamina that they achieved in the lab when measured at temperatures that they regularly experienced in the field. The only time that we observed an individual use its (apparently) full locomotor capacities was in a single high-speed, long-distance attempt at escape from a predator. Thus the locomotor capacities of *Ameiva festiva* may be analogous to the principle of excessive construction (sensu Gans), whereby the phenotypic capacities of animals are not shaped by routine activities but instead by rare events that may be critical to an animal's survival.

INTRODUCTION

Inspired by the discovery of behavioral thermoregulation by reptiles (Cowles and Bogert 1944; Avery 1982), numerous physiological ecologists have documented a general correlation between the thermal optima for physiological functions and species-specific body temperatures (Licht

1967; Dawson 1975; Bennett and Dawson 1976; Bennett 1980, 1984; Huey 1982; Avery 1984; Stevenson, Peterson, and Tsuji 1985). Typically, the thermal optimum of a given function is compared with either (1) the "preferred" or "selected" body temperature, which represents the mean body temperature selected by lizards in a laboratory thermal gradient (Licht et al. 1966; Pough and Gans 1982), or (2) the mean body temperature of lizards active in nature (Hertz, Huey, and Nevo 1983; Crowley 1985; van Berkum 1986).

The view that reptiles attempt to regulate at a single body temperature is, however, an oversimplification (Heath 1970). Research with lizards in laboratory shuttle-boxes suggests that a "dual-threshold" model is a better descriptor of reptilian thermoregulation (Berk and Heath 1975; Barber and Crawford 1977; Dreisig 1984; see also Bowker and Johnson 1980). Thus a lizard may seek a warm environment if its body temperature (T_b) is below a lower threshold or seek a cool environment if its T_b is above a higher threshold. These thresholds appear to be stochastic (Barber and Crawford 1977) and may vary with

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physiological and ecological circumstances (Cabanac 1979; Kluger 1979; Huey 1982; Withers and Campbell 1985).

The dual-threshold concept of behavioral thermoregulation prompted us to readdress the effect of thermoregulatory behavior on physiological and ecological performance of lizards in nature. Specifically, we wished to establish (1) the levels of performance with which the upper and lower thresholds are associated and (2) the behavioral circumstances under which the lizards take advantage of high levels of performance.

We investigated the thermal biology of *Ameiva festiva* (Teiidae), a widely foraging lizard from the lowland tropics of Central America. This lizard is ideally suited for analysis of the physiological consequences of thermoregulation. Individuals alternately bask in the sun at the edge of forests and then forage in the shade of the forest itself (Hillman 1969; Pough 1983). This clearly defined shuttling between sun and shade is a natural analog of the behavior of lizards in laboratory shuttle boxes. The active foraging movements of this species suggested that locomotion would be the most appropriate physiological system to investigate. We therefore gathered field observations on locomotor behavior, field measurements of T_b and threshold temperatures (by radiotelemetry), and laboratory data on the thermal dependence of sprint speed, stamina, and aerobic scope.

MATERIAL AND METHODS

FIELD STUDIES

We conducted these studies in the Sarapiquí Valley (Atlantic lowlands [elevation 50 m]) of Costa Rica at Finca La Selva, a biological station of the Organization for Tropical Studies, and at Finca El Bejuco during late August through early September 1982 and during April 1984.

To monitor T_b 's of lizards in the field, we captured four large (34.5–44.9-g) male *Ameiva festiva*, implanted temperature-sensitive transmitters, and released the lizards within their territories. Two lizards were studied in August 1982 during the *veranillo* (short dry season); and two were studied in April 1984 at the end of the regular dry season, which corresponds to the hottest time of year. The transmit-

ters (Mini-Mitter model T embedded in ELVAX) weighed ~ 2.3 g (10×20 mm). They were calibrated in water (15–45 C) before implantation and recalibrated after the field studies. No drift was detected.

Transmitters were surgically implanted under cold anesthesia. A 1-cm incision was made in the lateral skin of the abdomen, the abdominal muscles were gently teased apart, and the peritoneal mesentery was cut to allow insertion of the transmitter into the peritoneum. Because the superficial and deep lateral abdominal muscles run perpendicular to each other, the opening in the muscles closed naturally and did not require sutures. The incision in the skin was sutured with silk. All lizards were basking and feeding within 15 h of surgery. Wounds largely were healed within a week, when the lizards were released. At least 3 days elapsed before we began to monitor field T_b . Released lizards appeared to behave normally and were observed basking, foraging, and even copulating.

We followed two lizards in the dry season for 2:55 h and 4:50 h and two lizards in the wet season for 2:29 h and 12:08 h. Each lizard was followed on two or three occasions, and continuous observation periods ranged from 0:55 h to 4:36 h. Observations of movement rates and thermoregulatory behavior were made by following lizards at distances of 10–20 m (some additional observations of movement rates were made on nontelemetered lizards). In general, the lizards seemed unconcerned by our presence. Several times per minute we also recorded rates of transmitter clicks, which were later converted to T_b .

Calculations of distributions of field T_b were based on temperatures at 5-min intervals. The lower threshold temperature was recorded when we observed an undisturbed lizard stop foraging and initiate basking, and the upper threshold was measured when we observed a lizard cease basking and start foraging. Thresholds were only recorded during sunny periods to ensure that these behavioral shifts were based on lizard T_b , not on weather changes. Thresholds were not recorded if the new behavior lasted for less than 1 min (see fig. 1) or if we failed to observe the behavioral shift (see Heath 1964). We calculated the durations of all foraging and basking bouts

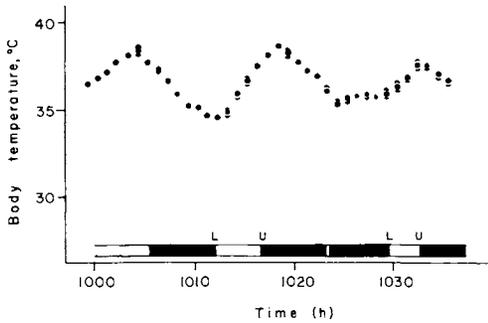


FIG. 1.—Body temperature measured by radiotelemetry of an adult male *Ameiva festiva* during a typical 35-min period under sunny skies (La Selva, Costa Rica, August 28, 1982). The lizard was shuttling between the edge and interior of a second-growth forest. The bar at the bottom of the graph illustrates the behavior of the lizard: solid sections indicate foraging, open sections indicate basking, and the stippled section indicates that the lizard was not under direct observation. Lower (L) and upper (U) threshold temperatures are indicated. The apparent thresholds at 1004 hours and 1023 hours were excluded from the analysis because the probable behavioral change (1004 hours) was not observed and because the lizard basked (1023 hours) for less than 1 min (see Material and Methods).

that were observed in their entirety, including those observed when the sun was partially obscured.

Operative temperature (T_e , i.e., the equilibrium T_b of a lizard model; Bakken 1976; Tracy 1982) was measured between 1020 and 1407 hours on sunny days (April 22 and 23, 1984) using *Ameiva*-sized models (PVC pipes) that had been painted flat gray. Models were placed on the ground either in full sun or in full shade to approximate the maximum and minimum potential T_b 's on the edge of and in the forest, respectively. Calibration of models against tethered lizards was not attempted because equilibrium temperatures of models in full sun always exceeded the lethal limits of *Ameiva*. Therefore our estimates of T_e must be considered to be crude.

LOCOMOTOR STUDIES

Lizards were captured in Costa Rica between September 2 and 10, 1982, and transported to the United States, where they were maintained in terraria under semi-natural cycles of temperature and light (6 h/day at 35 C, 18 h/day at 25 C, 12L:12D) and provided with ample food and water.

Stamina was measured in the laboratory

of A. F. Bennett at the University of California, Irvine, on September 13–19, 1982. General procedures are detailed in John-Alder and Bennett (1981). In brief, lizards were placed on the moving belt of a treadmill, and stamina was assessed as the elapsed time until the lizard was unable to maintain position and had fallen off the treadmill twice. An experiment was terminated if the lizard was still moving after 30 min, since this time greatly exceeds the actual length of movement bouts in nature (see Results). T_b 's were maintained at either 32 ± 0.5 C or 36 ± 0.5 C. Nine lizards were used (mean mass = 26.5 ± 4.89 g [95% confidence interval], range = 18.1–34.5 g; mean snout-vent length = 99.2 ± 6.39 mm, range = 88–110 mm).

Sprint speed was measured both in the United States (September 27–October 10, 1982) and in Costa Rica (April 29–May 25, 1982), and data are combined for analysis here. The nine lizards from the above experiment were raced at the University of Washington after being maintained on the environmental regime described previously. Eleven other lizards (mean mass = 25.63 ± 7.06 g, range 11.3–43.4 g; mean snout-vent length = 96.7 ± 8.62 , range 77–117 mm) were raced in Costa Rica after being maintained in outdoor cages (with access to sunlight or to heat lamps) with natural photoperiods. Procedures and apparatus for measuring sprint speed follow Hertz et al. (1983). Lizards were raced six times (United States) or five times (Costa Rica) per temperature and at one temperature per day every 2 days (United States) or 3 days (Costa Rica) at the following sequence of temperatures: 36, 32, 39, 28, 41 C for U.S. experiments; 36, 40, 27, 21, 43 C for Costa Rican experiments. Critical thermal limits (Hertz et al. 1983) were measured only on the Costa Rican specimens.

Statistics that describe the thermal dependence of sprint speed (below) were obtained by determining the maximum speed over 0.5 m for each lizard at each temperature (see Hertz et al. 1983). Using critical thermal limits as endpoints (0 m/s), we then fitted straight lines to speed versus body temperature data for each lizard using a minimum-polygon algorithm, modified so that no more than one consecutive temperature interval was skipped (van Berkum

1985). Two measures of performance breadth (i.e., the range of temperatures over which the lizard ran at 80% and 95% of maximum speed; Hertz et al. 1983) were estimated to describe the range of temperatures over which lizards ran well.

METABOLIC RATE

Standard metabolic rate (SMR; see Garland 1984) was measured at night for quiescent lizards at 30, 35, and 38 C (no test was run at 40 C to avoid stressing the lizards) using methods described in Garland (1984). Oxygen consumption during forced locomotion was determined for lizards walking or running on a treadmill at 30, 35, 38, and 40 C. The apparatus, procedures, and data analysis follow John-Alder (1983) with the following modifications: the treadmill was initially set at a low, sustainable speed and was thereafter increased in steps of 0.1–0.2 km/h until no further increments in O₂ consumption were noted or until the lizards could no longer maintain position on the treadmill. Rate of airflow through the mask was 700–750 ml/min, ensuring complete collection of expired gases.

STATISTICS

Data are reported as mean \pm 95% confidence interval. We used .05 as the critical probability value for statistical significance.

RESULTS

USE OF STAMINA AND SPEED IN THE FIELD

Foraging lizards in nature typically moved for short periods before resuming basking. Their foraging bouts ($n = 25$) averaged only 6.0 ± 2.60 min, not significantly longer than their basking bouts ($n = 27$, mean = 4.3 ± 1.88 min). Both foraging and basking bouts varied considerably in duration (range for both behaviors 1–24 min).

Foraging lizards moved slowly and averaged only 0.16 ± 0.056 km/h ($n = 7$) while actually moving, a low speed that is typical of other foraging teiid lizards (Garland 1985). On occasion, however, they would move more quickly (0.65 ± 0.172 km/h, $n = 3$), as when crossing an open trail through the forest; but these movements were brief (maximum 1.5 min) and

were much slower than maximal burst speeds (below). Prey capture by *Ameiva* is difficult to observe because they normally forage under debris on the forest floor. Our impression from observing swallowing movements was that prey of some sort were found under most objects that the lizards searched. We saw only two vigorous chases (after a butterfly [unsuccessful] and a grasshopper [successful]) during 25 h of observations on these lizards. Data on stomach contents are needed to substantiate our suspicion that vigorously chased prey constitute a minor part of the normal *Ameiva* diet.

Ameiva do sprint during some social interactions. On several occasions we saw lizards of unknown sex involved in high-speed chases. Nevertheless, during the single complete courtship and copulation (total encounter lasted 6 min) that we observed, neither the male nor the female moved quickly.

Ameiva also sprint when attempting to evade predators. In one case, a small *Ameiva festiva* sprinted in a straight line for at least 6 m before being captured by a snake (*Pseustes poecilonotus*). *Ameiva* will also sprint when disturbed by humans. The average distance that they ran when approached by a slowly walking human was 1.45 ± 0.19 m ($n = 15$).

FIELD BODY TEMPERATURES

Ameiva festiva regulate T_b 's during activity (table 1, fig. 1). During the morning they emerge, at a low T_b (26 C), from shallow nocturnal retreats in the leaf litter and move to sunny spots to begin basking. Once they reach the upper threshold T_b (39.4 ± 0.97 C), they begin foraging on the shaded floor of the forest. They resume basking when their T_b 's drop to the lower threshold (34.5 ± 1.11 C). These set-point temperatures are not fixed but have a range of 5–6 degrees C and actually overlap (table 1).

Mean activity temperature (radio telemetry) in the hot season (37.1 C) was higher than it was in the cooler *veranillo* (35.1; $t = 4.66$, $df 161$, $P < .001$). For both seasons together the mean activity temperature was 35.9 C (table 1). The central 50% of all records of T_b in our sample was within a narrow range (34.3–37.8 C). In contrast, mea-

TABLE 1
 T_b STATISTICS FOR FREE-RANGING *Ameiva festiva*

BEHAVIORAL CATEGORY	T_b (°C)			n_r	n_i
	Mean \pm 95% Confidence Interval	Range			
Emergence	26.4	26.3–26.4		3	3
Upper threshold	39.4 \pm .97	36.4–42.6		14	3
Lower threshold	34.5 \pm 1.11	31.6–37.2		11	3
Median activity	36.3	NA		163	4
Mean activity	35.9 \pm .45	27.3–41.9		163	4
Feeding	37.4 \pm 2.03	32.5–39.8		8	2
Copulating	NA	33.0–33.2		1	1
Q ₁	34.2	NA		163	4
Q ₃	37.8	NA		163	4

NOTE.— n_r = number of records; n_i = number of individuals. Q₁ and Q₃ (lower and upper interquartile temperatures, respectively) delimit the central 50% of all records of T_b . NA = not applicable.

surements of T_e 's (of lizard models) suggest that the potential range of T_b is great: T_e 's were 56.9 \pm 9.04 C ($n = 4$) in sun and 28.8 \pm 1.52 ($n = 6$) in shade.

LABORATORY STUDIES OF STAMINA

Ameiva have considerable stamina on treadmills (table 2). At both 32 and 36 C, most individuals maintained a speed of 0.5 km/h for 30 min, which was considerably faster and longer than they move while foraging in nature (above). Moreover, nine of 10 lizards ($T_b = 32$ C) maintained a speed of 0.8 km/h for 30 min. Temperature did not significantly affect stamina at a low speed of 0.5 km/h (Fisher exact test, $P > .75$). However, temperature does affect stamina at high speed: *Ameiva festiva* that were vigorously active in a small chamber lost their righting response after 11.7 \pm 2.60 min at 36 C but only after 4.8 \pm 0.96 min

TABLE 2

STAMINA OF *Ameiva festiva* MOVING ON A
TREADMILL AT DIFFERENT SPEEDS

T_b (°C)	SPEED (km/h)	NUMBER	
		Finishing	Exhausting
32	.5	12	1
36	.5	9	4
32	.8	9	1

NOTE.—Runs were 30 min long.

at 26 C ($n = 14$; K. R. Morgan, personal communication).

LABORATORY STUDIES OF SPEED

Sprint speeds of *Ameiva* were strikingly temperature sensitive and were maximal within the threshold range of temperatures (table 3, fig. 2). The mean optimal sprint temperature (37.6 C) was close to the mean field T_b (35.9 C). The mean upper and lower threshold temperatures corresponded to average performance levels of 89.1% and 91.4%, respectively, of maximum speed (fig. 2).

Thermoregulation enhanced sprint capacities of these lizards (table 3): 54.0% of all T_b 's of active lizards were within the range of temperatures (3.8 degrees C) over which lizards sprint at better than 95% of maximum speed, and 87.7% of all records were within the 80% performance range (9.3 degrees C).

METABOLIC RATE AND SCOPE

The thermal dependence of standard metabolic rate, maximum oxygen consumption, and aerobic scope are given in table 4. Values generally increased from 30 to 38 C. In particular, aerobic scope was higher at 35 and 38 C than at 30 C (repeated-measures ANOVA, $P < .01$). Thus aerobic scope was maximal within the threshold range of temperatures.

DISCUSSION

In this Discussion we address several issues. Do *Ameiva festiva* regulate T_b 's in nature? What are the thermoregulatory threshold temperatures? What levels of performance correspond to the threshold temperatures? Under what circumstances do lizards take advantage of enhanced locomotor capacity?

THERMOREGULATION IN NATURE

Ameiva festiva thermoregulated carefully (table 1, fig. 1) in a complex thermal environment. Their shuttling between the edge and the interior of the forest was controlled, such that 50% of all records of T_b were within a 3.5 degree C range even though T_e 's in these environments differed by 28.1 degrees C. Apparently *Ameiva* are rarely at equilibrium temperatures during normal activity.

The shuttling behavior of *Ameiva* was consistent with a dual-threshold model of thermoregulation (Introduction). The average lower and upper threshold tempera-

tures in nature were 34.5 C and 39.4 C, respectively. Lower and upper threshold temperatures overlapped in *Ameiva* (table 1), but not in *Dipsosaurus* tested in the laboratory (Berk and Heath 1975).

CONSEQUENCES OF THERMOREGULATION

Thermoregulation by *Ameiva festiva* had a profound effect on physiological capacity, at least with respect to locomotor physiology. For example, thermoregulation maximized sprint capacity of *Ameiva festiva*. The mean field T_b recorded here and in the literature (our data, 35.9 C; Hirth 1965, 36.2 C; Hillman 1969, 37.7 C) was similar to the optimal temperature for sprinting (37.6 C). Moreover, a lizard that is always active at temperatures within the threshold range should be able to run to within 10% of maximal speed (fig. 2).

Thermoregulation also maximized aerobic scope and probably stamina. Aerobic scope was higher at 35 C and 38 C than at 30 C (table 4). High-speed stamina (length of time lizards could sustain activity when being chased in a container) was 2.6

TABLE 3
THERMAL DEPENDENCE OF SPRINT SPEED OF *Ameiva festiva*

Parameter	Mean ± 95% Confidence Interval
A. Temperature (°C) at Various Performance Levels	
Optimal temperature (M_{95})	37.5 ± .94
Lower 95%*	35.4 ± 1.55
Lower 80%*	30.8 ± 1.53
Upper 95%*	39.6 ± .67
Upper 80%*	40.9 ± .65
CTMin	15.5 ± .42
CTMax	43.7 ± .22
B. Predicted Relative Performance at Specific Body Temperatures	
Median T_b939 ± .026
Mean T_b933 ± .027
Lower set point T_b900 ± .031
Upper set point T_b915 ± .052
Q_1891 ± .033
Q_3947 ± .029
Lowest recorded field T_b661 ± .071
Highest recorded field T_b585 ± .103

NOTE.— $n = 20$ for sprint data; $n = 11$ for critical thermal limits.

* The lower (higher) temperature at which a lizard ran at the indicated percentage of maximum speed.

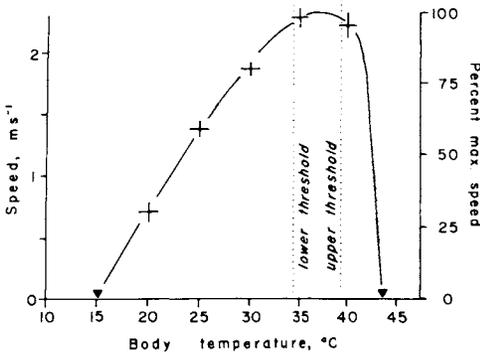


FIG. 2.—Speed of *Ameiva festiva* at various body temperatures. The figure plots the mean \pm SD for each temperature. The range of body temperatures between the upper and lower threshold temperatures is delimited by vertical dotted lines.

times higher at 36 C than at 26 C (K. R. Morgan, personal communication). Low-speed stamina within 30 min showed no effect of temperature between 32 C and 36 C (table 2).

INTEGRATION OF PHYSIOLOGY AND ECOLOGY

When do lizards actually use the enhanced locomotor capacity resulting from thermoregulation? Although our data on the natural history of *Ameiva* are limited, we can partially answer this question.

Ameiva festiva might use enhanced stamina to extend their foraging activities, but field observations suggest that this is definitely not the case. All foraging bouts were much slower (mean = 0.16 km/h) and much shorter (mean = 6.0 min) than what

the lizards are capable of sustaining, even at low T_b (0.8 km/h for 30 min at 32 C). In routine foraging, therefore, *Ameiva* did not even begin to approach their endurance capacities. This pattern holds for the teiid *Cnemidophorus tigris* as well (Garland 1985).

Ameiva might use enhanced sprint capacity to capture prey (Webb 1976). However, we saw *Ameiva* rapidly chasing prey only twice in 25 h, suggesting that enhanced speed should have little effect on feeding success. Nevertheless, an understanding of the relationship between speed and feeding requires knowledge of the relative importance of evasive versus non-evasive prey in the diets of *Ameiva*.

Although *Ameiva* are thought to be non-territorial (Hirth 1963), they occasionally chased each other at high speed. Consequently, thermoregulatory enhancement of speed or stamina (Garland 1985) might affect social or reproductive dominance, but this hypothesis requires direct testing.

Ameiva definitely run at very high speed from predators such as snakes (above). At La Selva the number of species of potential predators (snakes, hawks, and carnivores) is very high, and many snakes are found with *Ameiva festiva* in their guts (H. W. Greene, personal communication). The actual frequency of predation attempts on *Ameiva* is unknown, but the thermoregulatory enhancement of sprinting is clearly adaptive at such times (Christian and Tracy 1981; Huey and Hertz 1984; Webb 1985).

Overall, our data indicate that locomotor

TABLE 4
STANDARD METABOLIC RATE (SMR), OXYGEN CONSUMPTION DURING FORCED LOCOMOTION ($\dot{V}O_2fl$), AND AEROBIC SCOPE AS A FUNCTION OF BODY TEMPERATURE FOR *Ameiva festiva*

TEMPERATURE	MEANS \pm 95% CONFIDENCE INTERVAL (ml O ₂ g ⁻¹ h ⁻¹)		
	SMR	$\dot{V}O_2fl$	Aerobic Scope
30	.149 \pm .012	2.316 \pm .208	2.167 \pm .208
35	.235 \pm .028	2.771 \pm .402	2.536 \pm .423
38	.395 \pm .038	2.912 \pm .395	2.516 \pm .388
40	...	2.824 \pm .376	...

NOTE.—n = 8.

capacity of *Ameiva festiva* was enhanced by thermoregulation but that this enhanced capacity was rarely used. Locomotor efforts expended during most foraging and prey-capture activities did not approach the actual capacities of these lizards. Nevertheless, enhanced locomotor capacity may be crucial to *Ameiva* when attacked by predators or during some social encounters. In effect, thermoregulation may be a safety factor that enables these lizards to "be prepared."

The scenario that we propose is analogous to the principle of excessive construction. Gans (1979) notes that the phenotypic capacities of animals often exceed their routine needs (hence the term "excessive construction"). He proposes that the phenotypic capacities of animals are not shaped by routine activities but instead by rare

events that may be critical to an animal's survival. The "excessive" locomotor capacity resulting from thermoregulation by *Ameiva* might similarly be adaptive, primarily in emergencies such as attacks by predators.

The enhancement of physiological capacity that results from thermoregulation may not be "excessive" for all physiological systems. More efficient digestion or growth (Harlow, Hillman, and Hoffman 1976; Harwood 1979; Avery 1984), for example, should be adaptive during routine rather than in emergency situations. Obviously, attempts to evaluate the importance of thermoregulation to the physiological ecology of ectotherms must consider the functions of particular physiological systems (Stevenson et al. 1985).

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