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### Thermoregulatory Correlates of Escape Behavior by a Desert Lizard, *Ctenophorus isolepis*

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The effect of temperature on anti-predator behavior may be of critical importance for reptiles (Huey and Hertz, 1984; Greene, 1988). Experimental and field studies indicate that lizards alter their anti-predator behavior in response to body temperature either quantitatively (e.g., Rand, 1964; Bustard, 1968) or qualitatively (Hertz et al., 1982; Crowley and Pietruszka, 1983). Studies thus far have addressed changes in behavior at body temperatures below the preferred temperature. Many reptiles, particularly desert species, are adept at behaviorally thermoregulating within a few degrees of their preferred temperature and experience non-preferred body temperatures only for brief periods early and late in the day (Huey and Slatkin, 1976; Pianka, 1986). However, to maintain their preferred temperature, these species may have to alter their anti-predator behavior in response to changing environmental conditions (Huey and Slatkin, 1976). Here I report that an Australian agamid exhibits such a behavioral shift as environmental temperature increases.

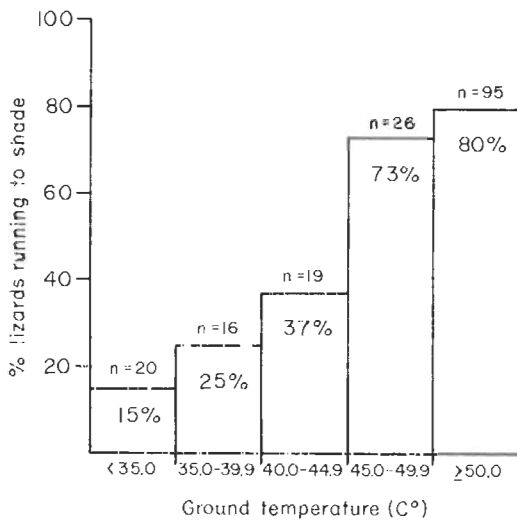


FIG. 1. Percentage of lizards that stopped in the shade at different ground temperatures. Data recorded late in the day, when there was very little non-shaded area, are not included.

The military dragon, *Ctenophorus* (formerly *Amphibolurus*) *isolepis*, is a diurnal and insectivorous lizard of moderate-size (max. 75 mm snout-vent length) found through the desert regions of central and western Australia (Cogger, 1983). Pianka (1971, 1986), working in Western Australia, found that the lizards are active in open spaces between spinifex hummocks, retreating at midday to the open shade adjacent to, but not under, the hummocks. The mean body temperature of 1261 active lizards was 37.8°C, very close to the preferred temperature of 37.0°C reported in laboratory trials (Licht et al., 1966, referred to as *Amphibolurus maculatus* [Pianka, 1971]). *Ctenophorus isolepis* preys primarily upon ants, and is itself preyed upon by varanids and probably by pygopodids, snakes, and raptors (Pianka, 1971). When provoked, it runs quickly, often in a zigzag pattern, and normally retreats into vegetation only when persistently pursued to the point of collapse (Pianka, 1971, in litt.). My observations of *C. isolepis* in central Australia are in accordance with Pianka's findings.

Observations were made on 157 *C. isolepis* in the township of Yulara, Northern Territory (25°S, 126°E) between 24 Sept-5 Oct and 1-7 Nov 1985. The red sand desert is comprised of sand plains and dunes covered with spinifex (*Triodia*), a grass that occurs in dense clumps of spines as great as 2 m in diameter. Bushes (*Acacia* and others) are less common sources of shade. Lizards were spotted as I walked at a slow and fairly constant pace in the narrow spaces between spinifex clumps. I avoided walking routes taken previously; nonetheless, some lizards may have been spotted more than once, though never on the same day. When approached, the lizards fled; data were collected only for lizards that were in front of me when they began to flee. For each lizard, the following were noted: time of day; shaded air temperature

TABLE 1. Frequency of distances run (estimated to the nearest m) at different ground temperatures (°C) in the sun.

Distance	<35.0	35.0-39.9	40.0-44.9	45.0-49.9	>50.0
	N	N	N	N	N
Distance	25	18	25	20	69
1	0.160	0.167	0.080	0.100	0.174
2	0.400	0.500	0.480	0.250	0.203
3	0.080	0.278	0.040	0.250	0.188
4	0.000	0.000	0.000	0.000	0.101
5-9	0.280	0.056	0.280	0.350	0.246
≥10	0.080	0.000	0.120	0.050	0.087

1 cm above the sand in the open; ground temperature where the lizard stopped (measured by placing the thermometer horizontally on the sand so that the entire bulb was barely covered); age (juvenile/adult); sex; distance lizard moved away (visually estimated to the nearest meter less than 5 m, 5-10 m, or further than 10 m); and microhabitat in which the lizard stopped (sun/shade; open/near fringe of plant/under plant). When a lizard stopped in the shade, ground temperature in the open was also recorded. If a lizard stopped several times, only the data for the first run were used except that sun/shade preference was recorded as the first place at which a lizard remained for 30 seconds, or, if it was continually on the move, where it spent most of its time. All temperatures were taken with a cloacal mercury thermometer (Miller and Weber, Inc., maximum 50°C). Some information could not be determined because lizards ran out of sight or off into the distance. Twenty-five lizards were noosed within a minute of being sighted and their cloacal temperatures ( $T_b$ ) quickly taken. Lizard behavior is analyzed with regard to ground temperature ( $T_g$ ), although solar radiation, air temperature, wind speed, and other factors also influence the operative environmental temperature affecting the lizard (Bakken and Gates, 1975).

Males and females did not differ statistically in any of the analyses ( $P > 0.05$ ), so data for the sexes were combined. Mean  $T_b$  for 25 lizards was 37.2 ± 0.5°C. Lizard temperatures were generally lowest in the early morning and highest in mid-to-late afternoon. Even in the relatively cool early morning, however,  $T_b$  was close to the preferred temperature. Lizards that fled to shade had higher body temperatures ( $\bar{x} = 37.7 \pm 0.9$ ,  $N = 11$ ) than lizards that stopped in the sun ( $\bar{x} = 36.8 \pm 0.3$ ,  $N = 12$ ;  $P < 0.05$ , Mann-Whitney test, two-tailed; data for two lizards were excluded because they did not clearly run to sun or shade).

As  $T_g$  in the open increased, lizards showed a greater tendency to escape to the shade (Fig. 1;  $P < 0.0005$ , 2 × 5 contingency table analysis), even though shade is least available at midday (Huey and Pianka, 1977). Usually, lizards went to the open shade at the fringe of a spinifex clump, rarely going into the clump itself. The shade of bushes was also used when available.

The distance covered during the escape run also varied with  $T_g$  in the open. At high  $T_g$  (>45°C), lizards

TABLE 2. Frequency of distances (m) lizards ran to sun or shade at different ground temperatures in the sun ( $^{\circ}\text{C}$ ).<sup>1</sup>

Distance	40.0-44.9 $^{\circ}\text{C}$		45.0-49.9 $^{\circ}\text{C}$		>50.0 $^{\circ}\text{C}$	
	N		N		N	
	7	7	3	8	50	10
	Shade	Sun	Shade	Sun	Shade	Sun
1	0.143	0.000	0.333	0.000	0.200	0.000
2	0.286	0.714	0.000	0.500	0.240	0.400
3	0.143	0.000	0.000	0.125	0.140	0.300
4	0.000	0.000	0.000	0.000	0.120	0.100
5-9	0.286	0.286	0.667	0.250	0.260	0.100
$\geq 10$	0.143	0.000	0.000	0.125	0.040	0.100

<sup>1</sup> Sample sizes are smaller than in Table 1 because a choice between sun and shade was not always available and some lizards did not clearly prefer sun or shade. Probabilities that the distributions within each category or for all data combined are different were calculated using the Kolmogorov-Smirnov two-sample test and were all  $>0.10$ .

ran further than at lower  $T_g$  (Table 1). Although there is a great deal of scatter in the data, a significant relationship exists between  $T_g$  and distance run ( $P < 0.001$ , Kendall's test of rank correlation, two-tailed, normal approximation, distance categories as in Table 1,  $\tau = 0.22$ ). Spinifex clumps at the study site are almost always spaced less than a meter apart; lizards would usually bypass one or more clumps before stopping in either sun or shade. Thus, longer runs did not result from lizards having to run a greater distance to reach shade. In the three highest  $T_g$  categories, lizards that ran to the shade ran further than those that ran to the sun (Table 2), but in none was the difference close to significant (Kolmogorov-Smirnov two-sample test). Lizards also did not appear to run further when running to shade at higher ground temperatures than at lower ground temperatures (Table 2).

Thermoregulatory considerations appear to be a major determinant of where lizards stop after running away from a potential predator. Lizards with higher  $T_b$  go to the shade; those with lower  $T_b$  remain in the sun (see above and Pianka, 1986). Tinkle (1967) demonstrated the consequences of remaining in the open at high  $T_g$  for the North American lizard *Uta stansburiana*, which is somewhat smaller than *C. isolepis* (max. 55 mm snout-vent length). Lizards tethered in the open at  $T_g > 55^{\circ}\text{C}$  generally reached their critical thermal maximum temperature, beyond which the lizards lost the capability to right themselves, within one minute; one juvenile reached this point in 17 seconds. I often recorded differences of  $>20^{\circ}\text{C}$  between  $T_g$  in the sun and shade (and I would have recorded greater differences if the thermometer had a higher scale). Changes in tail and foot posture by *C. isolepis* that moved from sun to shade or vice-versa indicate that the lizards respond to these differences (Losos, 1987).

Whether seeking shade at the edge of spinifex plants renders *C. isolepis* more vulnerable to predation is unclear. The lizards are clumsy and slow when moving through the dense spines of the spinifex (Pianka, 1971; pers. obs.), but they are well-suited to escape in the open, where their relatively long legs allow them to sprint quickly and change direction suddenly

(Pianka, 1986). Consequently, stopping near spinifex might compromise their ability to escape if confronted by a predator. None of five lizards observed in the late afternoon, when there was no unshaded ground and thus no opportunity for thermoregulation, ran to the edge of spinifex plants, which suggests a preference for open ground. However, this preference could be related to territorial or feeding behavior as well (Pianka, 1971).

*Ctenophorus isolepis* also tends to run further away at higher  $T_g$ . A number of possible causes may be responsible for this trend. 1) Subtle differences in the way I moved through the environment at different times of the day might have resulted in different responses by the lizards. 2) Lizards active at different  $T_g$  might not be the same, and might differ in escape behavior. 3) Lizards might have higher  $T_b$  and consequently greater speed or endurance (Bennett, 1980), at higher  $T_g$ . However, *C. isolepis* maintains its  $T_b$  within a narrow range over a wide range of ambient temperatures (Pianka, 1971, 1986). Additionally, the lizards ran quickly and usually stopped within 2-3 seconds, so their  $T_b$  probably did not greatly increase from activity metabolism, conduction or convection while running. 4) Predation pressure might be greater at higher  $T_g$ . At higher  $T_g$ , some predators (e.g., some varanids; King, 1980; Pianka, 1986) might be more active or have greater endurance and speed as a result of higher  $T_b$  (Bennett, 1980; R. B. Huey, in litt.). Running greater distances could increase the probability that a predator will give up or lose sight of the lizard. Whether in the sun or shade, the lizards normally stop on the far side of a spinifex hummock, which makes them difficult to see, particularly at a distance (C. James, in litt.). Pianka (in litt.) and I found that lizards that ran more than 5 m away were more difficult to locate than those that stopped nearby.

The data are not in hand to test these or other hypotheses. The commonly observed bimodal distribution of activity in desert lizards is usually attributed to thermoregulatory limitations (e.g., Mayhew, 1963; Pianka, 1969; Porter et al., 1973), but its consequences rarely have been discussed other than in terms of thermoregulation. Huey and Slatkin (1976) argued that a conflict could exist between optimal thermo-

regulatory and anti-predator behavior. They suggested that the high proportion of thermoconforming lizards in thermally coarse-grained environments such as forests is a result of the increased cost, in vulnerability to predation, that would be associated with moving to and from open areas to thermoregulate closely. In an opposite fashion, *Ctenophorus isolepis* thermoregulates precisely and modifies its escape behavior in response to changes in its thermal environment. Whether these modifications affect the lizard's risk from predation remains to be determined. The potential antagonism between thermoregulatory and anti-predator strategies might have important consequences for desert lizards and other organisms (e.g., Chappell, 1983) and merits further study.

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