# Postures of the Military Dragon (*Ctenophorus isolepis*) in Relation to Substrate Temperature

Jonathan B. Losos

Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, U.S.A.

The ability of lizards to behaviorally thermoregulate by changing position or posture has been recognized since the pioneering work of Cowles and Bogert (1944). Many subsequent workers have inferred that lizards make postural adjustments to alter heat flux (e.g., Fitch, 1956; Heath, 1965; Bartholomew, 1966; Mayhew, 1968; Heatwole, 1970; Brattstrom, 1971; DeWitt, 1971; Louw and Holm, 1972), but in only a few cases has the relationship between temperature and posture been quantified (e.g., Bradshaw and Main, 1968; Muth, 1977). Bradshaw and Main (1968) found little difference in the thermoregulatory behavior of four Australian agamids in the genera *Pogona* and *Ctenophorus* (generic assignations following Storr et al., 1983) despite marked differences in size and ecology. Here I report on thermal correlates of postural changes in a closely related species, the military dragon, *Ctenophorus isolepis*.

Observations were made on 266 *C. isolepis* encountered in the desert in the township of Yulara, Northern Territory, Australia (25°S, 126°E) during 24 Sept-5 Oct and 1-7 Nov 1985. Lizards were spotted and flushed as I walked in the narrow spaces between spinifex clumps. The following information was noted for each lizard: shaded air temperature 1 cm above the sand in the open, ground temperature at the spot where the lizard stopped (measured by placing the termometer so that the bulb was just covered by sand), and body postures adopted after the lizard stopped. When a lizard stopped in the shade, ground temperature in the open was also recorded. Temperatures were taken with a cloacal thermometer (Miller and Weber, Inc.), which has a maximum reading of 50 C°. Some data could not be determined because lizards ran partially or completely out of sight. Lizard behavior is analyzed with regard to ground temperature ($T_g$), though air temperature, wind speed, and other factors also influence the operative environmental temperature affecting the lizard (Bakken and Gates, 1975).

Four distinct lizard postures appear to indicate the importance of $T_g$: (1) In the early morning, when $T_g$ was low, lizards lay completely flat on the ground. (2) More commonly in the morning, and in the late afternoon and the shade at midday, lizards sat with forelegs semi-extended, lifting the forequarters off the sand. Feet, hindlegs, and tail were in contact with the ground. (3) At higher ground temperatures, the toes of all four feet were also lifted off the sand, so that only the palms of the feet were touching the surface. Some or all of the tail was also lifted off the ground. On some occasions, the rump was also raised above the sand so that the weight of the body rested on the base of the tail and palms of the feet (see Pianka [1985] fig. 10). (4) When ground

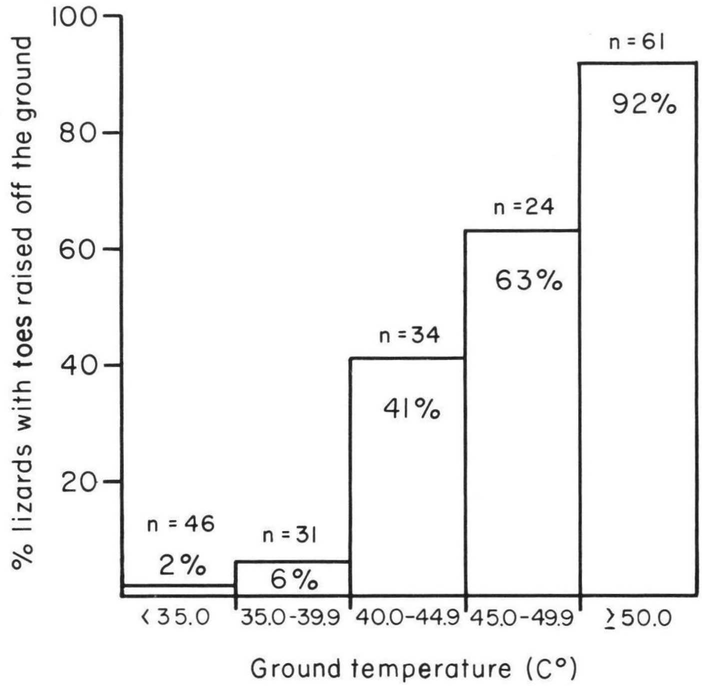


**Figure 1**. Percentage of lizards that lifted their toes at different ground temperatures. The responses of lizards that stopped in both sun and shade, and thus experienced different ground temperatures, are recorded for both locations.

temperatures were very high (>50 C°), all four legs were extended, lifting the body entirely off the sand. The tail was rigid and held above the ground as well. Only the palms of the feet touched the ground. On one occasion, a lizard lifted a foot completely off the ground.

The effect of $T_g$ on posture can be seen by examining the incidence of toe- and tail-lifting at different $T_g$. Data for lizards in the sun and in the shade were similar and are combined for these analyses. In both cases, the frequency in which the appendage is lifted is dependent on $T_g$ where the lizard stopped (chi-square test, $p < .0005$; figs. 1 and 2).

Comparisons of foot and tail posture of lizards that first stopped in the sun and then moved to the shade or vice versa, and of lizards that were only partially in the shade, also indicate that lizards respond to $T_g$. Of 37 lizards that had their feet up when in the sun, 25 placed them flat on the ground while in the shade. None of the 27 lizards that had their feet down in the sun raised them in the shade ($p < .01$, G-test). Similarly, 30 of 41 lizards had their tails up in the sun and down in the shade, while none of the 23 lizards with tail down in the sun raised it in the shade ($p < .01$, G-test).

Fourteen lizards with part of the tail in the sun had the exposed portion raised and

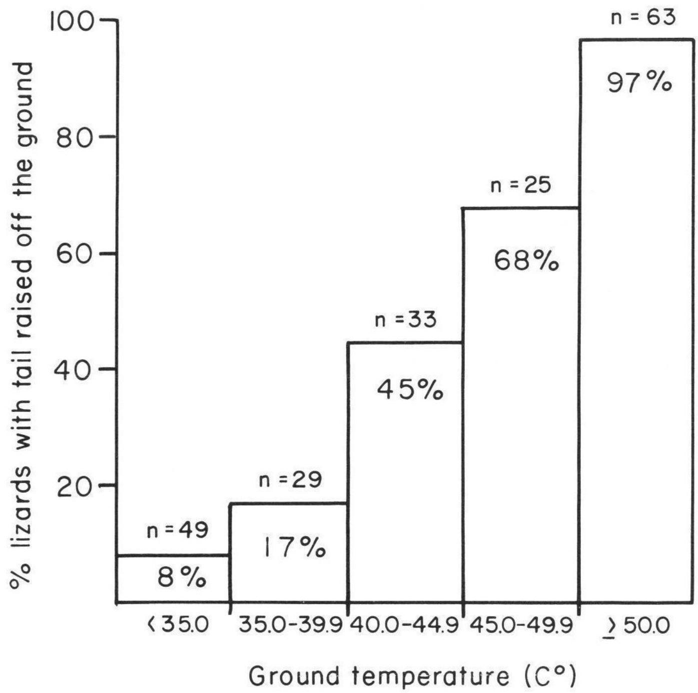


**Figure 2**. Percentage of lizards that lifted their tails at different ground temperatures. Data for lizards that stopped in both sun and shade are treated as in figure 1.

the shaded portion flat on the substrate. The opposite situation was never observed (probability estimates cannot be calculated because the total number of lizards which stopped with their tails partially in the shade is not known). Usually the match between where the shade began and where the tail rose above the surface was quite precise. In most instances, the distal portion of the tail projected into the sun and was raised; in two cases the distal part of the tail was in the shade and on the ground, while the more proximal portion was in the sun and raised. Similarly, in two instances lizards were observed with one foot exposed to the sun with toes raised, while toes on the other feet in the shade were contacting the substrate.

By raising its body and/or appendages off the substrate a lizard alters its rate of heat flux in two ways: it minimizes conduction with the ground, and exposes itself to lower air temperatures and greater wind velocity, which increase convective heat loss (Porter et al., 1973). Similar thermoregulatory postural adjustments have been noted for many lizards (see above), but rarely has the relationship between temperature and posture been quantified. Bradshaw and Main (1968) reported mean body and environmental temperatures associated with raised body postures in three species of *Ctenophorus*. However, such statistics are sensitive to differences in the sample sizes at different temperatures (Bradshaw and Main, 1968) and do not consider the number of lizards at a given temperature not adopting a raised posture. Reporting the proportion of lizards exhibiting postures at different temperatures, as I have done, provides a more accurate description of the effect of $T_g$ on posture. An even more precise approach that relates the physiology and behavior of a lizard is to record body temperature and determine the temperatures at which a lizard adopts a series of thermoregulatory postures (e.g., Muth, 1977, for *Callisaurus draconoides*). The method reported here can only indirectly reveal the relationship between body temperature and posture, but has the advantages of not disturbing the lizards by attaching sensors and providing useful data that can easily be collected in the course of other studies (e.g., Losos, in press).

The thermoregulatory postures exhibited by *C. isolepis* are virtually identical to those of *C. caudicinctus, C. inermis*, and *C. ornatus* (Bradshaw and Main, 1986). The only apparent difference involves the manner in which the tail is elevated above the ground: *C. ornatus*, and, by implication (see Bradshaw and Main, 1968), *C. caudicinctus* and *C. inermis*, curl the tail over the back, but *C. isolepis* lifts the tail and holds it rigidly. The much larger bearded dragon, *Pogona barbata*, exhibits the same postures, but differs in alternately lifting its forelegs off the ground and wiggling its tail at high temperatures (Brattstrom, 1971). Recent work by Moody (1980) has begun to unravel the interrelationships among the Agamidae. Further work on other members of the family will indicate to what extent thermoregulatory behaviors are influenced by phylogeny, ecology, and body size.

**Acknowledgements.** I thank the Conservation Commission of the Northern Territory and Yulara Township for permission to conduct this work; Ken Johnson, Steve Morton, and the Yulara Development Corporation for assistance in the field; John Carothers, Harry Greene, Paul Hertz, Ray Huey, Craig James, Claudia Luke, Eric Pianka, Robert Pietruszka, and Kevin de Queiroz for commenting on earlier drafts; George Roderick and Nancy Staub for statistical advice; and Gene Christman and Claudia Luke for drawing the figures. Above all, I thank Mike Gillam for his friendship and support, without which this work could not have been completed. This research was supported by a Berkeley Fellowship from the University of California, Berkeley; the Carl Koford Fund of the Museum of Vertebrate Zoology; and National Science Foundation grant BSR 83-00346 (to Harry Greene).

## References

Bakken, G.S., Gates, D.M. (1975): Heat transfer analysis of animals: some implications for field ecology, physiology and evolution. In D.M. Gates and R.B. Schmerl, eds., Perspectives of Biophysical Ecology. Springer-Verlag: New York. Pp. 255-290.

Bartholomew, G.A. (1966): A field study of temperature relations in the Galapagos marine iguana. Copeia **1966**: 241-250.

Bradshaw, S.D., Main, A.R. (1968): Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. J. Zool., Lond. **154**: 193-221.

Brattstrom, B.H. (1971): Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. Copeia **1971**: 484-497.

Cowles, R.B., Bogert, C.M. (1944): A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. **83**: 265-296.

DeWitt, C.B. (1971): Postural mechanisms in the behavioral thermoregulation of a desert lizard, *Dipsosaurus dorsalis* (Iguanidae). J. de Physiol. **63**: 242-245.

Fitch, H.S. (1956): An ecological study of the collared lizard (*Crotaphytus collaris*). Univ. Kans. Pub. Mus. Nat. Hist. **8**: 213-274.

Heath, J.E. (1965): Temperature regulation and diurnal activity in horned lizards. Univ. Cal. Pub. Zool. **64**: 97-136.

Heatwole, H. (1970): Thermal ecology of the desert dragon *Amphibolurus inermis*. Ecol. Mon. **40**: 425-457.

Losos, J.B. (in press): Thermoregulatory correlates of escape behavior by a desert Lizard, *Ctenophorus isolepis*. J. Herp.

Louw, G.N., Holm, E. (1972): Physiological, morphological and behavioural adaptations of the ultra-psammophilous, Namib desert lizard, *Aporosaura anchietae* (Bocage). Madoqua **1**: 67-85.

Mayhew, W.W. (1968): Biology of desert amphibians and reptiles. In G.W. Brown, ed., Desert Biology, Vol. 1. Academic Press: New York. Pp. 193-356.

Moody, S.M. (1980): Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Ph.D. dissertation, Univ. Mich. 373 pp.

Muth, A. (1977): Body temperatures and associated postures of the zebra-tailed lizard, *Callisaurus draconoides*. Copeia **1977**: 122-125.

Pianka, E.R. (1985): Some intercontinental comparisons of desert lizards. Nat. Geo. Res. **1**: 490-504.

Porter, W.P., Mitchell, J.W., Beckman, W.A., DeWitt, C.B. (1973): Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their micro-environment. Oecologia **13**: 1-54.

Storr, G.M., Smith, L.A., Johnstone, R.E. (1983): Lizards of Western Australia. II. Dragons and Monitors. Western Australian Museum: Perth. 113 pp.

*Received: November 12, 1986*