

TEMPERATURE RELATED AGGRESSION AND PREDATOR AVOIDANCE
IN THE EASTERN COLLARED LIZARD (CROTAPHYTUS COLLARIS)

by

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Introduction

From the chemical to the organismic level of organization, temperature is an important parameter in virtually all biological activities. Additionally, the range of temperatures in which animal's biochemical systems operate most efficiently is relatively narrow (Goin et al. 1978). Maintenance of a constant internal environment (homeostasis) within these thermal limits is an integral component of most organism's repertoire of survival strategies.

Two main modes of dealing with the thermal problems facing animals have evolved. Endothermy is characterized by an essentially unvarying body temperature sustained by the production of heat from oxidative metabolism. The vast majority of animals, however, depend on external sources of heat to achieve homeostasis. Ectothermic organisms, including reptiles, amphibians, fish, and most invertebrates, have such low rates of metabolic heat production and high rates of heat loss through conduction that their internal temperatures are generally independent of heat produced from metabolism (Bartholomew 1977). Because of their dependence on external temperatures, ectotherms are affected more by extreme environmental fluctuations in temperature than endotherms are. Rates of metabolism in some ectotherms are known to double in response to an increase in body temperature of 10 C ($Q_{10} = 2$; Cloudsley-Thompson 1971). Elevated body temperatures (> 50 C) cause protein denaturation and a general breakdown in chemical integrity (Goin et al. 1978). Therefore, ectotherms are posed with the problem of keeping their body temperatures within operational norms, even when the ambient temperature is not in the thermal tolerance range.

The evolutionary response by ectotherms to maintaining homeostasis in

a thermally complex environment is through the use of behavioral, and to a lesser extent, physiological, thermoregulation. Since maximum potential resting metabolic rates in ectotherms are relatively low, physiological thermoregulation by way of internal heat production is not as important as in endotherms. Restricted physiological thermoregulation has been noted in reptiles, however, mainly in the form of cardiovascular adjustments and evaporative cooling by panting. Large reptiles, by virtue of their small surface area to volume ratio, are able to thermoregulate to a limited extent through the use of metabolic heat, but the majority are too small for this process to be thermally effective (Cloudsley-Thompson 1971). For example, under experimental conditions, the lizard Dipsosaurus dorsalis is incapable of lowering or raising its body temperature by more than 1 degree C by physiological means alone (Soule 1963).

Insufficient metabolic heat production in most ectotherms requires that they adopt behavioral means of internal temperature regulation. Examples of behavioral thermoregulation can be found in numerous taxa spanning disparate environments. Centrarchid fish accurately select preferred water temperatures along a thermal gradient (Magnuson and Beitinger 1978), as do aquatic amphibians (Bartholomew 1977). The behavioral thermoregulatory abilities of aquatic animals are restricted by the thermal stability of the surrounding medium and limited influence of solar radiation. The temporal and spatial thermal variability of terrestrial habitats require more rapid and precise responses to fluctuating daily temperatures than in aquatic environments (Bennett 1983). Among the vertebrates, behavioral thermoregulation is best developed in terrestrial reptiles, with diurnal lizards exhibiting the most complex strategies. By controlling exposure to the sun's radiation

through posturing, shuttling between patches of sun and shade (heliothermic behavior), and varying the duration of contact with warm or cool substrates (thigmothermic behavior), lizards are able to regulate their body temperatures within a narrow range (Magnuson and Beitinger 1978). By moving between warm and cool areas, whiptail lizards (genus Cnemidophorus) display ranges in body temperature as small as 1.33 degrees C, with the degree of precision directly related to the frequency of moving between the two areas (Bowker and Johnson 1979). Members of the genus of small South American lizards, Liolaemus, attain body temperatures as much as 30 degrees C above ambient air temperature when exposed to direct solar radiation coupled with low air and substrate temperatures, a condition that commonly occurs shortly after sunrise at the high altitudes this lizard inhabits (Bartholomew 1977).

The ability of diurnal lizards to regulate body temperature behaviorally in thermally variable habitats has adaptive value in that it provides control over temperature dependent metabolic processes, contributes to the maintenance of homeostasis, and allows for the avoidance of potentially lethal temperatures (Huey and Slatkin 1976; Dawson 1983). There are, however, costs associated with the physiological benefits accruing from behavioral thermoregulation. In addition to the energetic cost of locomotion when shuttling from sunny to shady patches, lizards make themselves more conspicuous to predators by moving. The need to maximize exposure to the sun's rays on a cool day means spending more time in the open, increasing the chance that a predator will see them (Christian and Tracy 1981). Those microhabitats that are appropriate for thermoregulation might not be suitable for foraging. After heating up in one area, a lizard may have to spend time and energy moving to an area

where food can be acquired. Thus, costs of behavioral thermoregulation may reduce the net physiological advantage associated with this strategy. Thermoregulation in lizards is a discrete requirement that generally takes time away from other needs, such as foraging for food, finding a mate, avoiding predation, and territory defense. Satisfying conflicting demands represents a trade-off between the costs and benefits of performing these various activities, which are all of central importance to the inclusive fitness of the individual (Krebs and Davies 1981). Animals that are able to optimize their behavior at a point balancing conflicting needs will be at a selective advantage. Therefore, an optimal behavior can be viewed in terms of activity that maximizes the fitness of an individual (Pulliam 1976). An example of balancing costs and benefits with respect to thermoregulation is the Puerto Rican lizard Anolis cristatellus, which, when time and energy costs of thermoregulating are high because of inaccessibility of basking sites, chooses to remain immobile at a lower body temperature rather than attempt to maintain an optimal body temperature (Huey 1974).

Optimality theory implies that natural selection should favor animals that choose the behavior that maximizes net gains in some currency when presented with conflicting demands (McCleery 1978). Based on this concept, hypotheses concerning evolutionary decision-making in animals can be generated and tested. This paper is concerned with temperature related behavior in the collared lizard, Crotaphytus collaris, a common, diurnal iguanid found primarily in rocky habitats in the western United States. Males are territorial and highly aggressive towards intruding conspecifics during the May-June breeding season. A territorial male will actively attack and chase a rival from the area, but the first line of defense is a

display consisting of head-bobbing, distension of the brightly colored gular pouch, back-arching, and a lateral compression of the body that increases the apparent size of the resident. This display is done while the territory owner is in a stiff-legged posture (Greenberg 1945; Collins 1982).

Mating success in C. collaris is probably linked to the successful establishment and defense of a territory (Yedlin and Ferguson 1973), so there should be strong selective pressure on males to effectively defend a territory. The notion of cost-benefit relationships and optimality theory suggests that there should be a temperature or temperature range where it would benefit territorial males to be most aggressive in defending against other males. This hypothesis is tested in an initial experiment. If the hypothesis is valid, there should be a difference in the intensity of aggressive behaviors of males at different body temperatures. At the lower end of the lizards' temperature tolerance range, they should be too sluggish to effectively defend against intruders, while at the upper end they will be too heat stressed to respond. Stated in terms of a trade-off, the costs of defense at the upper and lower temperature extremes will exceed the benefits of active territorial defense. Lizards in the field should thermoregulate to body temperatures that maximize benefits and minimize costs when defending against rivals.

Numerous examples of the relationship between low body temperature and inhibited behavioral abilities in reptiles appear in the literature (Heckrotte 1967; Greenwald 1974; Bennett 1980; Hertz et al. 1982; Stevenson et al. 1982; Arnold and Bennett 1984). A second experiment tests the hypothesis that lizards, because their behavior is thermally dependent, should adopt different predator avoidance strategies at varying

body temperatures. Specifically, a lizard at a cool body temperature that is unable to run fast, would be more likely to choose an aggressive defense against a predator than would a relatively fleet individual at a higher body temperature. This would only be true of lizards that are capable of inflicting damage to a predator (Crowley and Petruszka 1983). There should be some intermediate temperature where a switching of defense behaviors occurs.

Study Animals and Housing

Lizards used in this study were caught on limestone outcroppings in the Tuttle Creek Dam area near Manhattan, Kansas, and along rural Riley county road cuts from May through July of 1984 and 1985. Captured lizards were weighed with a Pesola balance, and snout-vent length measurements were taken. When not being used in an experiment, individuals were housed separately in 10 or 20 gallon terraria with a sand substrate. Terraria sides were covered with paper to prevent interactions before experiments. The ambient temperature was 25.5 C. A photoperiod of 14L:10D was selected because it represented the natural photoperiod during the month of peak reproductive activity (June; Yedlin and Ferguson 1973). Lizards were maintained on a diet consisting of crickets, grasshoppers, cockroaches, beetles, and water. To avoid possible effects of hunger level on behavior, lizards were not fed until after trials were complete on days when experiments were conducted.

Territorial Aggression - Methods

Temperature based aggressive encounters between territorial males and introduced rivals were observed in laboratory during the collared lizards' breeding season. Interactions took place in five 20-gallon terraria (76 cm long x 31.5 cm wide x 30.5 cm high), each with a sand substrate maintained at a different temperature within the thermal activity range of C. collaris (21.0 C - 45.0 C; Fitch 1956).

In the absence of solar heat, it is reasonable to assume that body temperatures of lizards will approximate substrate temperatures (Cloudsley-Thompson 1971). To confirm this assumption, cloacal temperatures were measured for seven lizards exposed to various substrate temperatures within their thermal activity range (Table 1). Lizards were flattened against the substrate for 15 minutes to allow them to equilibrate. A metal sleeve restricted movement and kept the venter in contact with the sand. Measurements were taken with a YSI Tele-thermometer and lizards were handled with rubber gloves to prevent heat conduction. Substrate temperature was found to be a good estimate of body temperature when the latter was in the lower extreme of the thermal activity range. Although body temperature increased with substrate temperature, the absolute difference between the two increased when substrate temperatures were high. A regression analysis was applied to the temperature data to provide means by which body temperatures could be predicted from substrate temperatures.

The body temperatures selected to be tested were 25.0 C, 27.0 C, 29.0 C, 32.0 C, and 34.0 C. Preliminary tests revealed that lizards kept at a substrate temperature in excess of 40.0 C would often employ panting and a siff-legged posture to keep their body temperatures near their thermal

Table 1. Cloacal body temperatures of seven individuals at various substrate temperatures.

<u>SUBSTRATE</u>	<u>BODY</u>
<u>TEMPERATURE (C)</u>	<u>TEMPERATURE (C)</u>
24.0	24.4
24.0	24.3
24.0	24.2
24.0	24.0
24.0	24.7
28.0	28.1
28.0	28.4
28.0	27.1
28.0	28.1
28.0	28.3
30.0	29.1
30.0	29.7
30.5	29.4
31.0	30.0
31.0	29.9
32.0	31.3
34.0	31.6
34.0	32.4
34.0	33.5
35.0	33.8
35.5	33.3
36.0	32.6
37.0	34.5
40.0	34.8
40.5	37.7
41.0	37.7
41.0	34.5
41.0	38.9
42.0	37.3
42.0	38.6

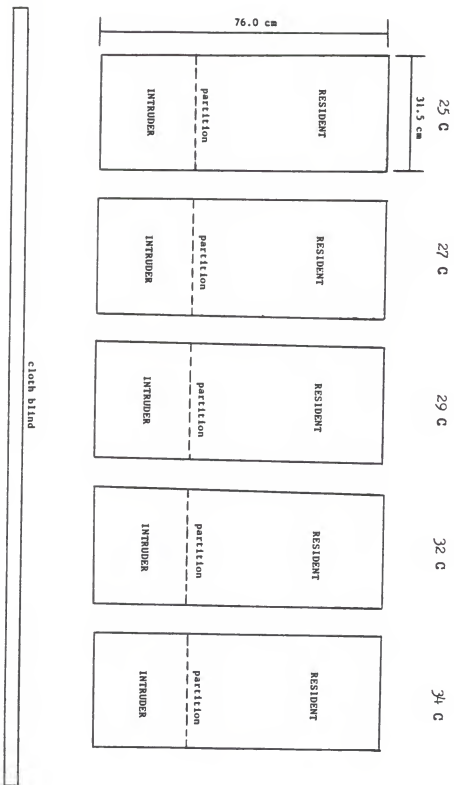
preferenda. To reduce the effect of these thermoregulatory behaviors, the maximum body temperature tested was 34.0 C. Substrate temperatures of four of the five terraria were maintained using an 18.3 m soil heat cable. Appropriate lengths of the cable were coiled under the terraria to obtain the desired temperature. The substrate of the coolest terrarium was maintained by ambient room temperature.

Sides of the terraria were covered with white paper so lizards could not see each other. To restrict observer effect, a cloth blind was positioned in front of the five terraria. A mirror suspended over the terraria permitted observations without looking directly into the tanks (Fig. 1).

A male lizard was introduced into each of the five terraria and allowed 48 hours to acclimate. Initial presentation of a rival male resulting in characteristic displays by the resident indicated that it had adopted the terrarium as a territory. Once residency was established an intruder lizard was introduced by placing it behind a cardboard partition located 30 cm from the end opposite the resident (Fig. 1). After a 15 minute period to let the intruder adjust, the partition was carefully raised. All interactions between the resident and intruder, and the time they occurred, were recorded for a 30 minute period, followed by removal of the intruder. Data collected during a 30 minute trial included the following 10 behavioral characteristics.

1. Number of headbobs by the resident
2. Number of headbobs per bobbing episode
3. Number of maximum displays by resident - A display by a resident was considered maximum when it was performed in the stiff-legged posture.
4. Number of moderate displays by resident - A moderate display was

Fig. 1. Diagram of design for territorial aggression experiment showing substrate temperatures, terraria dimensions, and approximate position of intruder introduction.



similar to a maximum display except the legs were bent.

5. Number of minimum displays by resident - A display qualified as minimum if the ventral surface of the lizard came in contact with the substrate.

6. Number of provoked displays by resident - A display by the resident was considered provoked if it appeared to result from a movement by the intruder.

7. Number of unprovoked displays by resident

8. Number of bites by the resident

9. Number of aggressive encounters resulting in the intruder fleeing

10. Total number of aggressive interactions - Aggressive interactions included displays and/or bites.

Number of headbobs was chosen as a measure of aggression because it is an easily quantifiable component of the defensive displays of C. collaris. Displays were categorized as maximum, moderate, or minimum to determine if lizards showed varied display intensities at different temperatures. Displays were also distinguished based on whether they were provoked by an intruder, or initiated without provocation by the resident. The latter category was considered to indicate greater aggression. Number of bites obviously reflects relative aggression, as does the tendency for an intruder to flee from a resident's attack or display. Total number of aggressive interactions between two lizards was selected to summarize number of bites and displays into a single measure.

To prevent overuse, intruders were never introduced to a resident more than twice in one day and at least two hours were allowed between trials for a particular resident. Intruders were housed at ambient temperature to prevent their behavior from varying upon introduction to a terrarium.

Five intruders were tested against each of the residents at each of the temperatures, yielding 25 encounters per resident and per temperature. The sequence in which intruders were introduced to residents was random. When five trials at any one temperature were completed, the residents were randomly switched to another temperature, where they interacted with the same five intruders. The same procedure was followed with a new group of five residents and intruders. Therefore, data collection was based on the interactions between 10 residents at five temperatures, and 10 intruders. A list of lizards used in this experiment, and relevant information pertaining to each, is given in Table 2.

The Friedman Rank Sums nonparametric test was applied to the data. When significant differences between temperatures were indicated, a separation procedure (distribution-free multiple comparisons based on Friedman Rank Sums; Hollander and Wolfe 1973) was employed.

The four behavioral characteristics that were most appropriate for measuring aggression were analyzed to determine if the size of an intruder had an effect on the defensive response of the resident. The Student's t-test was the statistic applied to this data.

Table 2. Weight (gms) and snout-vent length (mm) of lizards used in territory defense experiment.

<u>LIZARD NO.</u>	<u>WT</u>	<u>SVL</u>
1b	37	106
2b	31	102
3b	33	101
4b	35	105
5b	29	99
6b	32	103
7b	28	101
8b	35	105
9b	29	102
10b	27	101
11b	32	105
12b	40	108
13	35	106
14b	42	110
16b	36	105
17	37	105
21	36	106
22	28	100
23	27	100
24	32	104

Territorial Aggression - Results

Temperature Effect

The data suggest that body temperature affects the intensity of territorial defense in male C. collaris. When presented with a rival, residents were more aggressive at moderate and high body temperatures than at low temperatures. Of the ten behavioral characteristics analyzed, four were statistically significant. It should be noted that residents showed varying degrees of stress and fatigue after the fourth temperature switch. Because the fatigue seemed to inhibit their responses to intruders, data gathered during the fifth trials of both groups of residents were not used in the analysis. The technique for missing values described in Sokal and Rohlf (1981) was applied to compensate for the unusable data.

1. Number of headbobs by the resident (Table 3). Analysis indicates that there are statistically significant differences between individuals at different body temperatures with respect to number of headbobs (Fig. 2; Friedman's Rank Sums: $S = 28.00$, $P < .001$). The frequency of headbobbing is relatively low at 25.0 C and 27.0 C, but it more than doubles at 29.0 C, while decreasing somewhat at 32.0 C and 34.0 C (Fig. 2).

2. Number of headbobs per bobbing episode (Table 4). This behavioral trait is apparently fixed. Once initiated, a headbobbing event runs to completion, comparatively independent of body temperature. Consequently, the number of headbobs per episode was not statistically significant at the .05 level (Fig. 3; $S = 12.95$). There was, however, a small increase in the mean value at 29.0 C, 32.0 C, and 34.0 C, suggesting limited thermal dependence (Fig. 3).

3. Number of maximum displays by the resident (Table 5).

Table 3. Total number of headbobs by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	54	107*	148	182	109
3b	60	72	132	163*	121
4b	53*	32	196	152	118
5b	55	105	195	157	175*
6b	41	94	179*	101	111
12b	88	77	112	153	150*
13	78	52	154*	80	57
14	109*	35	225	112	171
16	75	126*	186	206	88
17	35	104	131	188*	195
Mean (\bar{x})	64.8	80.4	165.8	149.4	129.5

Fig. 2. Mean number of headbobs by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; 25 C and 27 C = a, 29 C and 32 C = bc, 34 C = abc).

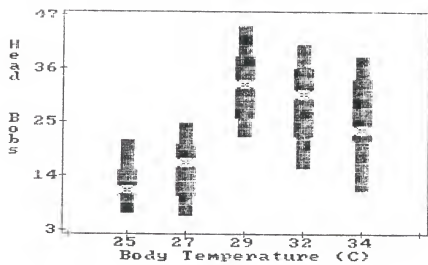


Table 4. Number of headbobs per bobbing episode by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	2.5	4.2*	4.2	4.9	3.9
3b	3.5	3.8	5.1	5.6*	3.8
4b	4.2*	2.9	3.8	4.4	4.0
5b	4.4	4.7	4.6	4.1	5.4*
6b	3.6	3.2	5.1*	4.0	3.4
12b	3.1	3.1	3.5	4.5	4.1*
13	3.7	3.5	5.1*	3.8	3.2
14	3.8*	1.4	4.7	3.7	4.1
16	3.5	4.3*	4.8	4.6	2.9
17	2.4	3.6	4.1	5.1*	4.5
Mean (\bar{x})	3.5	3.5	4.5	4.5	3.9

Fig. 3. Number of headbobs per bobbing episode by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No Diff.).

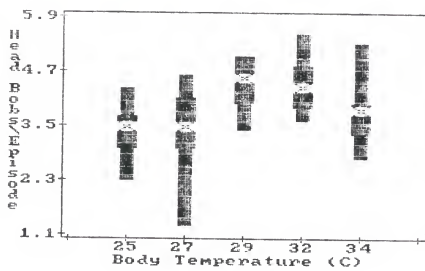


Table 5. Total number of maximum displays by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	15	9*	27	20	12
3b	15	8	11	20*	13
4b	17*	1	40	25	23
5b	3	13	33	35	29*
6b	6	13	31*	10	29
12b	13	5	16	22	20*
13	5	6	19*	4	7
14	15*	4	43	13	22
16	8	10*	26	36	7
17	1	18	17	28*	38
Mean (\bar{x})	9.8	6.3	26.3	21.3	20.0

Statistical differences between body temperatures were found for this characteristic (Fig. 4; $S = 19.84$, $P = .025$). Maximum displays by residents were most common at 29.0 C, with a slight decrease at 32.0 C and 34.0 C.

4. Number of moderate displays by the resident (Table 6). Unlike maximum displays, this behavior was statistically indistinguishable between body temperatures at the .05 level (Fig. 5; $S = 10.99$). Means also differed from those obtained for maximum displays in that they increased with temperature rather than peaking at 29.0 C.

5. Number of minimum displays by the resident (Table 7). Statistical differences between temperatures were not found for this behavior (Fig. 6; $S = 5.96$). Based on histogram patterns, low intensity displays are not dependent on body temperature.

6. Number of provoked displays by the resident (Table 8). Analysis did not reveal statistically significant differences between temperatures (Fig. 7; $S = 2.03$), suggesting that residents are equally likely to display in response to an intruder's movements at all body temperatures tested.

7. Number of unprovoked displays by the resident (Table 9). This behavioral trait showed highly significant differences between body temperatures (Fig. 8; $S = 27.29$, $P = .005$). The tendency for the resident to initiate a display increases threefold at 29.0 C compared to the two lower temperatures. A gradual drop-off is evident at 32.0 C and 34.0 C.

8. Number of bites by the resident (Table 10). Number of bites was not statistically significant at the .05 level (Fig. 9; $S = 12.14$), probably because biting was a relatively rare event during the staged interactions. The inordinately high value for number of bites at 29.0 C

Fig. 4. Mean number of maximum displays by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).

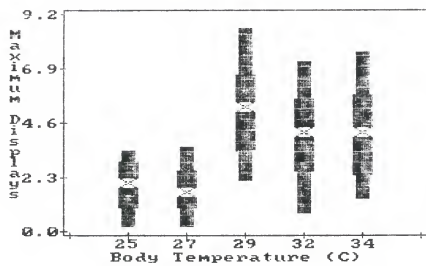


Table 6. Total number of moderate displays by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	2	6*	1	11	13
3b	2	6	15	13*	19
4b	3*	6	10	6	10
5b	7	7	9	11	14*
6b	5	9	11*	8	12
12b	15	16	14	11	21*
13	12	7	14*	12	13
14	10*	6	5	13	18
16	14	13*	11	10	13
17	8	8	13	11*	5
Mean (\bar{x})	7.8	8.4	10.3	10.6	13.8

Fig. 5. Mean number of moderate displays by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).

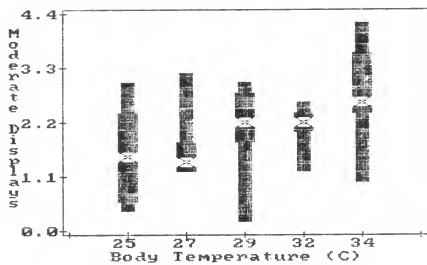


Table 7. Total number of minimum displays by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	0	3*	1	1	3
3b	1	4	0	4*	3
4b	1*	2	2	3	3
5b	3	1	1	0	1*
6b	0	8	4*	8	1
12b	0	3	1	1	1*
13	4	2	4*	7	1
14	1*	0	0	4	2
16	0	2*	2	0	1
17	0	2	2	3*	0
Mean (\bar{x})	1.0	2.7	1.7	3.1	1.6

Fig. 6. Mean number of minimum displays by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).

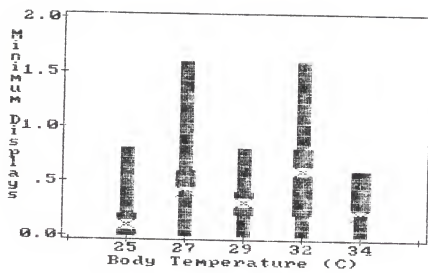


Table 8. Total number of provoked displays by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	2	10*	11	9	9
3b	0	2	5	7*	22
4b	12*	6	6	16	16
5b	13	19	10	5	18*
6b	6	22	13*	6	9
12b	24	22	19	8	27*
13	19	13	26*	26	21
14	22*	3	34	11	29
16	17	13*	4	8	13
17	9	17	9	11*	7
Mean (\bar{x})	12.4	12.7	13.7	10.7	17.1

Fig. 7. Mean number of provoked displays by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).

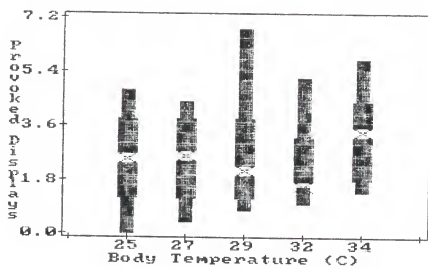


Table 9. Total number of unprovoked displays by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	15	18*	25	39	20
3b	19	12	21	31*	13
4b	14*	3	46	18	20
5b	0	3	47	39	30*
6b	5	8	38*	20	35
12b	4	2	26	26	14*
13	2	1	18*	3	0
14	3*	7	14	18	13
16	5	14*	35	39	8
17	0	11	23	33*	36
Mean (\bar{x})	6.7	7.9	29.3	26.6	18.9

Fig. 8. Mean number of unprovoked displays by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; 25 C and 27 C = a, 29 C and 32 C = b, 34 C = ab).

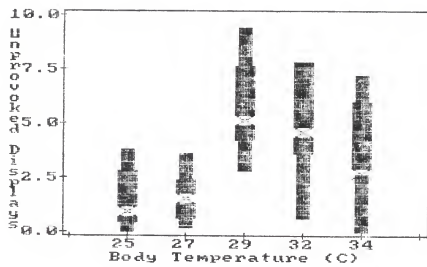
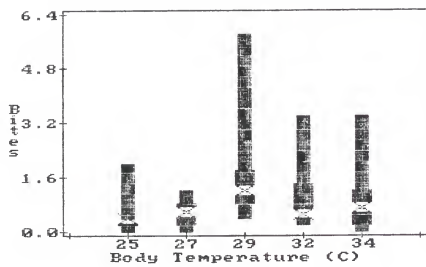


Table 10. Total number of bites by residents during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	2	2*	9	2	0
3b	1	1	2	2*	1
4b	10*	6	29	4	3
5b	2	3	4	7	5*
6b	2	3	9*	1	6
12b	2	4	4	3	4*
13	0	0	6*	2	1
14	1*	0	6	2	6
16	2	5*	4	17	2
17	0	3	8	10*	17
Mean (\bar{x})	2.2	2.7	8.1	5.0	4.5

Fig. 9. Mean number of bites by all residents during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).



is attributable to an excessive display of aggression by resident 4b when it occupied a terrarium at this temperature (Table 10). There was, however, a general trend suggesting an increase in the frequency of bites at moderate and high temperatures (Fig. 9).

9. Number of encounters resulting in the intruder fleeing (Table 11). This measure of aggression was marginally insignificant at the .05 level (Fig. 10; $S = 15.75$), probably, as with number of bites, because it occurred so infrequently. Intruders were more inclined to flee at 29.0 C than at any other temperature.

10. Total number of aggressive interactions (Table 12). Significant differences between body temperatures were found for the total number of aggressive interactions between residents and intruders (Fig. 11; $S = 22.64$, $P < .01$). More aggression occurred at the three higher temperatures than at the two lower ones, a pattern that was also evident for the other three behavioral characteristics that were statistically significant.

Intruder Size Effect

The size of an intruder was found to influence the aggressive response of residents. The mean number of headbobs elicited from all residents across all temperatures was greater for three large intruders (mean weight = 36g) than for three small intruders (mean weight = 28g; Fig. 12; $t = 3.95$, $P < .01$). Similar results were obtained for mean number of maximum displays (Fig. 13; $t = 2.96$, $P < .02$), mean number of unprovoked displays (Fig. 14; $t = 3.42$, $P < .01$), and mean number of aggressive interactions during agonistic encounters (Fig. 15; $t = 4.23$, $P = .001$) with the same intruders.

Individual Variation

Table 13 summarizes mean resident response for four of the behavioral

Table 11. Total number of aggressive interactions resulting in the intruder fleeing during 30 minute encounters with five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	4	8*	14	9	4
3b	3	5	3	7*	8
4b	3*	0	15	1	8
5b	1	14	17	12	15*
6b	3	10	14*	4	13
12b	1	0	7	2	4*
13	3	1	6*	2	0
14	2*	1	7	3	10
16	0	6*	4	17	2
17	0	5	8	7*	8
Mean (\bar{x})	2.0	5.0	9.5	6.4	7.2

Fig. 10. Mean number of aggressive interactions resulting in the intruder fleeing during one 30 minute encounter for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.).

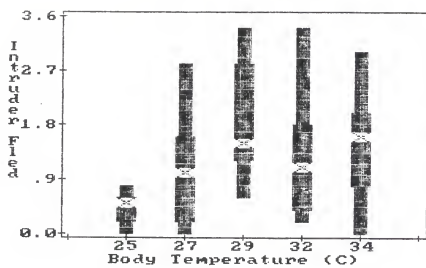


Table 12. Total number of aggressive interactions during 30 minute encounters between residents and five intruders at five temperatures. Asterisks indicate estimates based on the technique for missing values described in Sokal and Rohlf (1981).

	<u>BODY TEMPERATURE (C)</u>				
	25	27	29	32	34
<u>RESIDENT NO.</u>					
2b	25	29*	43	42	28
3b	18	20	28	40*	36
4b	34*	9	80	38	32
5b	15	25	52	45	47*
6b	13	29	54*	27	46
12b	30	28	35	37	45*
13	19	15	44*	25	22
14	29*	10	54	33	48
16	24	33*	43	63	22
17	9	31	40	50*	54
Mean (\bar{x})	21.6	22.9	47.3	40.0	38.0

Fig. 11. Mean number of aggressive interactions during one 30 minute encounter with an intruder for each temperature. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; 25 C and 27 C = a, 29 C = b, 32 C and 34 C = ab).

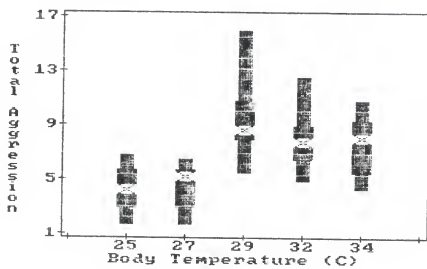


Fig. 12. Mean number of headbobs by all residents during encounters with small intruders (n = 3, mean weight 28 gms) and large intruders (n = 3, mean weight 36 gms). Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles.

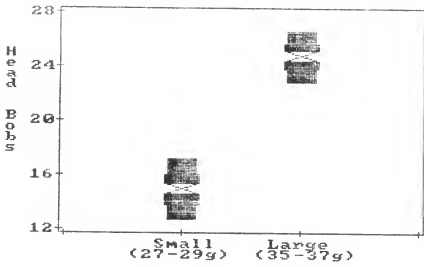


Fig. 13. Mean number of maximum displays by all residents during encounters with small intruders (n = 3, mean weight 28 gms) and large intruders (n = 3, mean weight 36 gms). Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles.

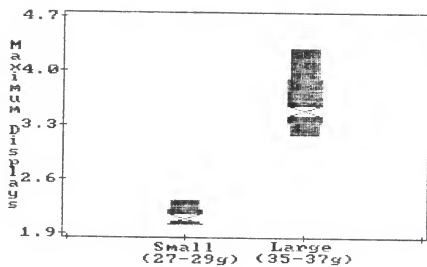


Fig. 14. Mean number of unprovoked displays by all residents during encounters with small intruders (n = 3, mean weight 28 gms) and large intruders (n = 3, mean weight 36 gms). Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles.

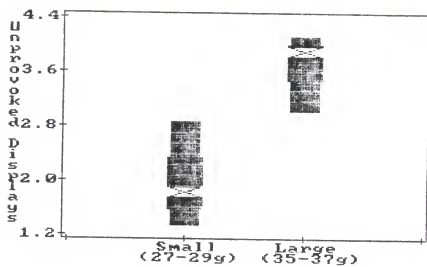


Fig. 15. Mean number of aggressive interactions during encounters with small intruders (n = 3, mean weight 28 gms) and large intruders (n = 3, mean weight 36 gms). Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentile.

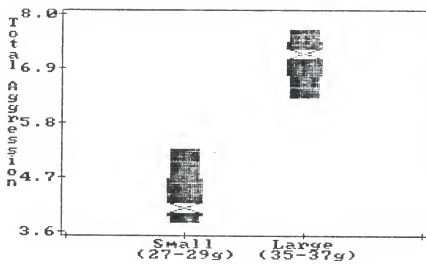


Table 13. Mean responses of all residents for four relevant measures of aggression during 30 minute interactions with intruders.

	<u>BEHAVIORAL CHARACTERISTIC</u>			
	HEAD-	MAXIMUM	UNPROVOKED	TOTAL
	BOBS	DISPLAYS	DISPLAYS	AGGRESSION
<u>RESIDENT NO.</u>				
2b	120.0	16.6	23.4	33.4
3b	109.6	11.4	19.2	28.4
4b	110.2	21.2	20.2	38.6
5b	137.4	22.6	23.8	36.8
6b	105.2	17.8	21.2	33.8
12b	116.0	15.2	14.4	35.0
13	84.2	8.2	4.8	25.0
14	130.4	19.4	11.0	34.8
16	136.2	17.4	20.2	37.0
17	130.6	20.4	20.6	36.8

characteristics that proved to be appropriate measures of aggression in this study. Clearly, some variation in intensity of the response to an intruder is attributable to differences in individuals. For example, resident 5b exhibited the highest mean for three of the four behaviors, while resident 13 produced the lowest values for all four characteristics. Individual variation is apparently secondary to the effect of temperature on aggression since most residents showed relative similarities in these behaviors for particular temperatures, if not absolute similarities (Tables 3, 5, 9, and 12).

Predator Avoidance Behavior - Methods

Tests for predator avoidance behavior at different temperatures were conducted in an oblong, metal arena (176 cm long x 60 cm wide x 56 cm deep) with a sand substrate (1.5 cm deep). Substrate temperature was adjusted with a rheostat control on a heat lamp placed under one end of the elevated tank. Temperatures used in the 1984 trials were 21.0 C, 25.0 C, 27.0 C, 32.0 C, 34.0 C, and 38.0 C. In the 1985 trials temperatures were adjusted to 25.0 C, 27.0 C, 29.0 C, 32.0 C, and 34.0 C. Observations from the first summer's trials indicated that adequate data could be gathered without using the extreme temperatures and that more uniform increments between temperatures would be appropriate.

A trial consisted of placing a lizard directly over the heated area of the substrate. A metal sleeve placed over the lizard restricted movement by keeping the lizard flattened and oriented towards the opposite end of the tank. Preliminary cloacal temperature measurements with a YSI Tele-thermometer indicated that a lizard flattened against the heated substrate reached the desired body temperature in less than 15 minutes for even the highest substrate temperature. After this period the metal sleeve was carefully removed, leaving the lizard exposed on the sand. From a position behind the animal, the lizard was firmly pinched at the base of the tail with a pair of tongs to simulate a predator attack (Fig. 16). Simulated attacks were continued every five seconds for up to 15 attacks or until the lizard fled its original position. The number of bite attempts, and the distance run before stopping the first time were recorded. Each lizard (four in 1984, and 10 in 1985; Table 14) was tested at each of the experimental temperatures in a random sequence to identify individual variation in the response to different temperatures. Data were

Fig. 16. Diagram of design for predator avoidance experiment showing arena dimensions, heat source, and position of cover sleeve (point of simulated attack).

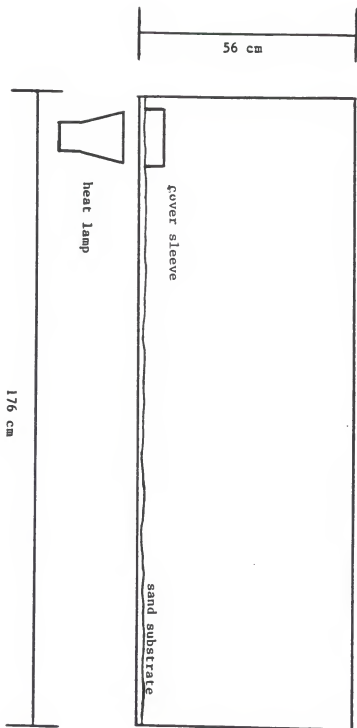


Table 14. Weight (gms), snout-vent length (mm), and sex of lizards used in predator avoidance experiment (1984 and 1985).

<u>1984</u>			
<u>LIZARD NO.</u>	<u>WT</u>	<u>SVL</u>	<u>SEX</u>
2a	32	102	m
11a	39	108	m
12a	32	100	m
14a	25	101	f

<u>1985</u>			
<u>LIZARD NO.</u>	<u>WT</u>	<u>SVL</u>	<u>SEX</u>
8b	35	105	m
9b	29	102	m
10b	27	101	m
13	35	106	m
14b	42	110	m
16b	36	105	m
17	37	105	m
18	23	98	f
19	22	97	f
20	22	98	f

analyzed using the Friedman Rank Sums nonparametric test, and treatment effects separated using distribution-free multiple comparisons based on Friedman Rank Sums (Hollander and Wolfe 1973).

Predator Avoidance - Results

Data from both years reveal that body temperature is an important factor influencing the choice of predator avoidance strategies in C. collaris. Lizards tended to be more aggressive in their responses to pinching at low body temperatures, while at moderate and high temperatures they were more likely to flee (Table 15). Attacks that did not result in the lizard fleeing were accompanied by an attempt to bite the tongue. Analysis of number of bite attempts indicates that there were significant differences between temperatures with respect to aggressive tendencies, and that the number of attempts was inversely related to temperature (Fig. 17; Friedmans Rank Sums: 1984, $S = 10.53$, $P < 0.05$; 1985, $S = 19.60$, $P < 0.01$). The only apparent exception to this generalization appeared in the 1984 data set when the number of bite attempts at 34.0 C exceeded those at 29.0 C. This variation was not quite statistically significant, however, and can be attributed to the small sample size for that year. Therefore it appears that there is a levelling-off for attempted bites after 29.0 C.

From 21.0 C to 29.0 C lizards showed an increased inclination for fleeing from predator attacks as body temperature increased. Furthermore, the distance fled was generally greater at the higher temperatures (Fig. 18). Significant differences between temperatures for distance fled were found for 1985 data ($S = 17.71$, $P < 0.05$). Data from 1984 were not quite significantly different at the 0.05 level ($S = 8.57$), probably because of the small sample size ($n = 4$). Trends for both sets of data were similar except that those from 1984 seem to plateau at 25.0 C, while in 1985 the plateau does not occur until 29.0 C.

Distance run and number of attempted bites were inversely related, although the plateau effect suggests that the relationship is not linear.

Table 15. Number of bite attempts (BA) and distance run (DR) in cm for lizards at different body temperatures after simulated predator attacks.

<u>1984</u>												
<u>BODY TEMPERATURE (C)</u>												
21 25 27 29 34 38												
<u>LIZARD NO.</u>	<u>BA</u>		<u>DR</u>		<u>BA</u>		<u>DR</u>		<u>BA</u>		<u>DR</u>	
2a	2	59	12	125	2	146	1	157	4	69	1	156
11a	7	82	2	145	3	143	1	137	3	111	1	51
12a	7	90	5	113	2	123	2	100	1	156	3	159
14a	15	0	6	112	6	77	2	104	12	57	2	34
Mean (\bar{x})	7.8	57.8	6.3	123.8	3.3	122.3	1.5	125.0	5.0	98.3	1.8	100.0

<u>1985</u>												
25 27 29 32 34												
<u>LIZARD NO.</u>	<u>BA</u>		<u>DR</u>		<u>BA</u>		<u>DR</u>		<u>BA</u>		<u>DR</u>	
8b	15	0	15	0	5	101	3	112	1	75		
9b	9	92	15	0	5	119	3	80	4	103		
10b	7	65	6	69	2	94	6	106	3	92		
13	10	38	7	70	2	149	7	65	5	110		
14b	15	0	9	60	1	157	5	131	4	85		
16b	10	52	6	40	1	140	3	121	15	0		
17	13	28	6	108	4	125	7	157	6	138		
18	10	70	11	55	3	138	10	130	2	109		
19	12	62	12	115	15	0	11	89	3	95		
20	7	50	9	78	4	144	6	93	1	145		
Mean (\bar{x})	10.8	45.7	9.6	59.5	4.2	116.7	6.1	108.4	4.4	95.2		

Fig. 17. a) Mean number of bite attempts after simulated predator attack plotted against body temperature for 1984 trials. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.). Although separation procedures showed that temperature differences were not statistically significant, 21.0 C was only marginally indistinguishable from 29.0 C. b) Corresponding data from 1985 predator avoidance experiment. Separation of treatment effects indicated that 25.0 C and 27.0 C were both statistically distinct (greater) from 29.0 C and 34.0 C with respect to bite attempts.

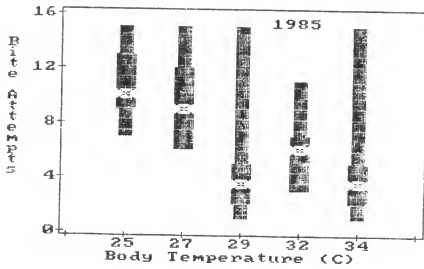
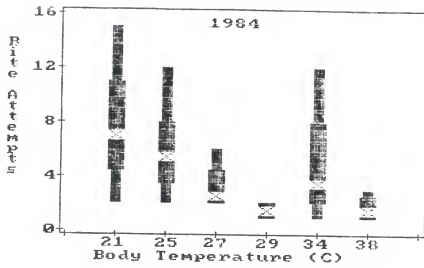
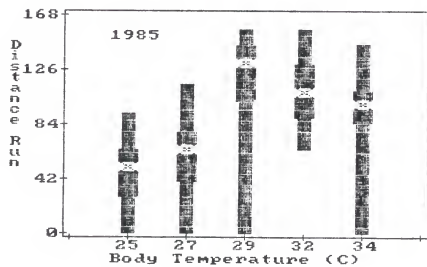
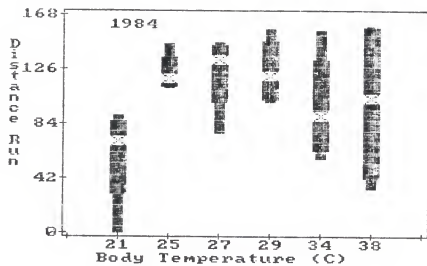


Fig. 18. a) Mean distance run (cm) after simulated predator attack plotted against body temperature for 1984 trials. Bar gradations represent minimum, median, and maximum values, as well as the 25th and 75th percentiles. Shared lower case letters denote statistical similarities (distribution-free multiple comparisons based on Friedman Rank Sums; No diff.). b) Corresponding data for 1985 predator avoidance experiment. Separation procedures revealed that the low values for distance fled at 25.0 C differed statistically from 29.0 C and 32.0 C, and 27.0 C was similarly distinct from 29.0 C.



Lizards fled the farthest and attempted the fewest bites between 29.0 C and 34.0 C. The two behaviors are negatively correlated (1984: $r = -.51$, $P < 0.05$, $n = 24$; 1985: $r = -.75$, $P < 0.01$, $n = 50$; Table 15), indicating that there is a switching of defense behaviors based on body temperature.

Discussion

Territorial Aggression

Territory defense against conspecifics in C. collaris increases markedly in intensity between 27.0 C - 29.0 C, a relatively small portion of the thermal activity range of this species (21.0 C - 45.0 C; Fitch 1956). For each of the four behavioral characteristics that were statistically significant, 29.0 C, 32.0 C, and 34.0 C had higher values than 25.0 C and 27.0 C (Figs. 3, 4, 8, and 11). The three highest temperatures were not statistically distinct from the two lowest temperatures for all measured behaviors, but the overall pattern was consistent, implying a threshold temperature just below 29.0 C where aggressive tendencies by residents increase. As a consequence of the greater energetic requirements associated with activity at low body temperatures, lizards respond less vigorously when their body temperatures are lower than 29.0 C than when they reach this temperature. Once the threshold temperature is reached, the physiological constraints are reduced and lizards are able to raise the level of aggression. The data definitely suggest a temperature range where aggression is greatest (29.0 C - 34.0 C), but a further argument could be made for 29.0 C as being the body temperature for maximum aggression of those tested, since it had higher values than 32.0 C and 34.0 C for all four traits, despite not being statistically distinguishable from the two higher temperatures. Statistical significance should be secondary to biological significance, however, since 29.0 C has the highest mean values for seven of the 10 measured traits (Figs. 2, 3, 4, 8, 9, 10, and 11).

Mention should be made of the drop-off in aggression at 32.0 C and 34.0 C. Initially it might be assumed that residents at this temperature

were heat stressed, and subsequent behaviors were affected. This is known to occur in other iguanids, but only at body temperatures exceeding 40.0 C (Bennett 1980). Field measurements of collared lizards suggest that the preferred body temperature ranges from 36.3 C (Brattson 1965) to 38.0 C (Fitch 1956; actual values may be lower than these since handling probably increases body temperatures), so heat stress may be ruled out as a factor inhibiting aggression at 34.0 C. A more likely explanation is that 34.0 C is not the temperature for C. collaris that provides the most effective territorial defense. A temperature is appropriate only relative to the costs and benefits of the specific behavior in question. In other words, 34.0 C may (or may not) be the most efficient temperature at which to forage, but it does not necessarily follow that territory defense is also effective at this temperature. This study indicates that the net benefits accrued from aggressive territory defense may be maximized at 29.0 C and may be somewhat decreased at higher temperatures, particularly at 34.0 C. The tendency to be most aggressive at 29.0 C represents a maximum for territorial defense, which is just one aspect of C. collaris' overall behavioral repertoire. The maximum temperature for aggression, along with thermal maxima for other behaviors (such as foraging), are influenced by their related costs and benefits such that an optimal temperature for a specific behavior may differ from the temperature at which the behavior is performed most effectively. Thus, an optimal body temperature for a certain behavior is a mosaic of thermal maxima of all conflicting behavioral demands at a particular point in time.

The importance of an optimal temperature or temperature range is exemplified when considering the specific trade-offs involved in territory defense in C. collaris. Costs associated with maintaining a territory

include increased risk of predation and the possibility of injury during combat (Stamps 1977). Males benefit from successful defense by increasing their opportunities to mate, since they control a resource (insects) that is vital to females (Davies 1978). Individuals that are best able to thermoregulate to the optimal temperature and thus balance the conflicting demands related to territory defense will maximize their fitness.

Male collared lizards also exhibited greater aggression when confronted with a large intruder than when interacting with a small one. This pattern is consistent with a study of territorial interactions in the brown anole, Anolis sagrei, which found that large males elicited more aggressive displays from territory holders than did small lizards (Tokarz 1985). Apparently residents recognize large males as a greater threat to displace them from their territories and respond by increasing the intensity of their defense. It may seem to be maladaptive to challenge a potentially dangerous rival, but the ritualistic nature of displays in iguanid lizards serves to deter actual physical combat in most cases, especially when the cost of risking injury is greater than the benefit accrued from winning the contest (Krebs and Davies 1981).

Predator Avoidance Behavior

Christian and Tracy (1981) point out that predator-prey interactions are unique in that the possible outcomes are both distinct and limited from the perspective of the prey; it either escapes and potentially pays a price in terms of lost matings or food acquisition, or is killed. Such strong selective pressure coupled with the fact that reproductive success is dependent on an individual's survival and subsequent contribution to future gene pools, has led to the evolution of a wide array of predator defense mechanisms in animals (Harvey and Greenwood 1978; Alcock 1984).

Collared lizards (and ectotherms in general) are physiologically, and consequently, behaviorally, constrained by body temperature with respect to the effectiveness of different defense strategies. As a result, it would probably not benefit a lizard to attempt to run away from a predator if the lizard's body temperature is below the point where adequate sprint speed is possible. Thus a lizard might be better off holding its ground and fighting when confronted by a predator. The optimal defense strategy at a given body temperature is that which enhances an individual's probability of survival.

Responses to a simulated predator suggest that C. collaris has evolved alternate predator avoidance strategies based on body temperature. At low body temperatures the rate of reaction and speed of movement of lizards is apparently slowed, making them relatively easy prey for their main predators, hawks and snakes (Collins 1982). At low body temperatures the strategy of collared lizards is to respond aggressively to predator attacks, with the inclination to bite inversely related to body temperature (Fig. 17). The adaptive value of aggressive behavior is dependent on the ability of the lizard to dissuade the predator from its attack. These lizards possess a powerful bite, as do other lizard species that exhibit aggressive behavior at low temperatures (Hertz et al. 1982; Crowley and Peitruszka 1983). A contrasting evasive strategy is displayed by the harmless lizard, Anolis lineatopus, which increases flight distance between itself and a potential predator when at a low body temperatures, rather than adopt an aggressive defense (Rand 1964). This tactic serves the same function as the biting tendencies of C. collaris at low body temperatures. The only difference is that the strategy employed by A. lineatopus is necessarily passive because of their inability to deliver a

bite sufficient to discourage a predator.

The fact that lizards fled from simulated predator attacks more frequently at moderate and high temperatures instead of attempting to bite represents a switch in defensive behavior. The data indicate a threshold temperature at which locomotion potential is increased to the extent that escape is more likely. The critical temperature is probably closer to 29.0 C (1985 data) than 25.0 C (1984 data) because of the statistical rigor associated with larger sample sizes. A physiological explanation for this tendency might be the fact that C. collaris has a decreased rate of change in metabolism towards the lower end of its temperature tolerance range, a phenomenon attributable to the high temperatures to which this diurnal species is adapted (Cloudsley-Thompson 1971). Thus, a decrease in the effectiveness of metabolic processes at body temperatures below the threshold should result in defense rather than flight. Conversely, lizard species with relatively high metabolisms at low body temperatures generally rely on rapid escape when threatened by a predator (Bennett 1980). Waldschmidt and Tracy (1983) reported a threshold range of 35.0 - 38.0 C for sprint speed in the side-blotched lizard Uta stansburiana, which is comparable to the results for C. collaris. Additionally, Galapagos land iguanas reduce predation from hawks by choosing to flee only when their body temperatures exceed 32.0 C (Christian and Tracy 1981). The increase in distance run at higher temperatures by C. collaris lends further support to the switching hypothesis if it is assumed that increasing the distance between a prey and predator enhances the lizard's chance of survival. The relationship between the tendency to run, distance run, and sprint speed appears to be linked to the threshold temperature.

The results obtained are consistent with those of other studies. Crowley and Pietruszka (1983) found that aggressive responses to predators increase in both frequency and intensity at low body temperatures in the iguanid Gambelia wislizenii. A shift to flight occurs at a threshold body temperature between 20.0 C and 26.0 C, a range in which running ability increases in this species. Supplementary examples of temperature related defensive behavior are evident in other lizard species (Hertz et al. 1982), and in garter snakes (Heckrotte 1967; Arnold and Bennett 1984).

An effective predator avoidance strategy is one that imparts a selective advantage to the potential prey (Gans and Richmond 1957). Qualitative variations in defensive behavior by C. collaris are adaptive in that they provide a means by which the effect of thermal constraints on locomotion are alleviated. The survival value of an aggressive strategy when at a low body temperature and fleeing when body temperature is adequate for escape is best emphasized when viewed in terms of a trade-off. Collared lizards improve their chances of survival by choosing an aggressive defense against predators when thermal restrictions elevate the costs associated with running, and switching to flight when temperatures are high enough to provide sufficient sprint speed.

Overview

The ecological demands associated with territory defense and predator avoidance are interrelated, as evidenced by increased mortality during reproductive periods in a wide array of taxa (Alcock 1984). A male collared lizard may increase its chance of being eaten by defending a territory, but it also increases its mating opportunities significantly. Lizards that can attract mates to a territory and not be killed by a predator are at a selective advantage. The probability of predator attack coincides with mating behavior in C. collaris, so it is not surprising that the temperature at which the costs and benefits of these two conflicting demands are favorably balanced is the same. The results of the current experiments revealed a threshold temperature between 27.0 C and 29.0 C where territory holders were most aggressive and where the preferred predator avoidance strategy switched from biting to fleeing, thus supporting the notion that associated costs and benefits of a given behavior vary with changing ecological variables, which in this case was body temperature.

Any activity that an animal undertakes has a value, in terms of fitness, that is directly related to the overall physiological state of the animal. Through natural selection, organisms should evolve behavioral strategies that maximize net benefits when subject to specific ecological and/or physiological conditions. Collared lizards, and ectotherms in general, are suitable study animals for analysing temperature dependent behaviors since most aspects of their biology respond to environmental temperature, which is an easily controlled variable. The study of adaptation as an important feature of evolution requires the functional relationships between individuals and the environment (Regal 1983). These

functional relationships are manifested in the behavioral adaptations of C. collaris that allow them to make the appropriate responses to territorial intrusions and predator attack when at different body temperatures.

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TEMPERATURE RELATED AGGRESSION AND PREDATOR AVOIDANCE
IN THE EASTERN COLLARED LIZARD (CROTAPHYTUS COLLARIS)

by

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Abstract

Behavioral means of thermoregulation that alleviate environmental constraints on body temperature have evolved in many ectothermic species. Collared lizards (Crotaphytus collaris) are among those animals that can behaviorally control their body temperatures at levels that allow them to survive in a thermally variable environment. This study is concerned with the relationship between body temperature and behavior in C. collaris. Specifically, experiments were conducted to determine a) if the intensity of territorial aggression in male lizards varies at different body temperatures, and b) if choice of predator avoidance strategies is thermally related.

Results indicated that territorial male collared lizards have elevated aggression against conspecific intruders when residents' body temperatures are between 29.0 C - 34.0 C, with 29.0 C the temperature where the greatest amount of aggression occurred. Less vigorous responses at low body temperatures (25.0 C and 27.0 C) are apparently due to increased physiological constraints. A switching of predator avoidance strategies also occurred between 27.0 C and 29.0. Individuals adopted a biting defense when their body temperatures were at 21.0 C and 25.0 C, and switched to a fleeing strategy between 27.0 C and 29.0 C. The adaptive value of an aggressive response to a predator is dependent on the inability of a lizard to attain sufficient sprint speed to make escape likely.

The conflicting demands of territorial defense and the avoidance of predators occur simultaneously in C. collaris. Thus, it is reasonable to assume that a body temperature at which costs and benefits of the two demands are favorably balanced would be nearly the same. The results of

current experiments revealed a threshold temperature (29.0 C) where territory holders were most aggressive and where the preferred predator avoidance strategy switched from biting to fleeing, supporting the idea that associated costs and benefits of a given behavior vary with changing ecological variables.