

Ecological Correlates of Population and Individual Variation in Antipredator Behavior of Two Species of Desert Lizards

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Antipredator behavior was measured in four populations of zebra-tailed lizards (*Callisaurus draconoides*) and two populations of greater earless lizards (*Cophosaurus texanus*). Lizards were approached in the field, and five measures of wariness were recorded. *Callisaurus* had significantly greater approach distance and greater final distance than did *Cophosaurus*. Among populations of *Callisaurus*, lizards were wariest at the site with the least plant cover. Within populations, air temperature, the directness of the observer's approach, and the lizard's distance to nearest cover when first sighted had significant direct effects on flight behavior based on path analysis. Windiness and time of day had significant direct effects and indirect effects through their relationships with air temperature and distance to cover. Path analysis indicated no one variable with great overall influence on antipredator behavior in these lizards but rather a combined influence of several environmental factors.

The magnitude of threat imposed on an animal by an approaching predator is expected to vary with conditions surrounding the encounter (Ydenberg and Dill, 1986; Helfman, 1989). Threat is determined by the animal's behavioral options, morphological attributes, and physiological capacities, in relation to the type and behavior of the predator, as well as environmental characteristics such as substrate, availability of cover, and temperature (Heatwole, 1968). Running away is a common antipredator behavior, but it may incur certain costs. For example, the animal may vacate a territory (Walther, 1969; Shallenberger, 1970), attract attention to itself (Heatwole, 1968; Lawler, 1989; Luke, 1989), or disrupt its thermoregulatory behavior (Losos, 1988). Therefore, the prey's response to the approach of a predator is predicted to balance the magnitude of the threat with the costs associated with the response (Ydenberg and Dill, 1986; Helfman, 1989).

Lizards employ a wide range of antipredator tactics, but the most common initial tactic is escape by running (Greene, 1988). Lizards may be more vulnerable to predation under conditions which reduce running ability or when located far from refuge. Low temperature, for example, decreases locomotor ability in lizards (Bennett, 1980; van Berkum, 1986; Mautz et al., 1992). Also at low body temperatures, some lizards alter their antipredator tactic by fleeing sooner (Rand, 1964); other lizards and snakes switch to stationary defensive displays (Hertz et al., 1982; Crowley and Pietruszka, 1983; Arnold and Bennett, 1984). Several studies have

demonstrated an influence of distance to refuge on antipredator behavior in lizards (Snell et al., 1988), squirrels (Dill and Houtman, 1989), and fish (Grant and Noakes, 1987; McLean and Godin, 1989; Dill, 1990). Finally, lizards (Burger and Gochfeld, 1990), nesting gulls (Burger and Gochfeld, 1981), and gazelles (Walther, 1969) flee sooner when approached directly, presumably because a directly approaching predator is more likely to encounter hidden prey or may have detected it already.

In this study, I compare the flight behavior (escape by running) of several populations of two species of lizards to examine simultaneously the effects of multiple environmental factors. *Callisaurus draconoides*, the zebra-tailed lizard, and *Cophosaurus texanus*, the greater earless lizard, are closely related members of the Iguanidae (Clarke, 1965; Etheridge and de Queiroz, 1988) and are similar in body size (SVL *Callisaurus* 61-94 mm; *Cophosaurus* 60-77 mm; Smith et al., 1987), body temperature (mean field active body temperatures: *Callisaurus* 38.2 C, *Cophosaurus* 38.5 C; Smith et al., 1987), coloration, and general ecology (Clarke, 1965; Pianka and Parker, 1972; Vitt and Ohmart, 1977). Both species inhabit flat, open areas and use running as their main antipredator tactic.

Although *Callisaurus* and *Cophosaurus* are similar in ecology, preliminary data suggest that *Callisaurus* may be faster (T. Garland, Jr., pers. comm.). Sympatric populations differ in microhabitat preference; *Callisaurus* prefer open, sandy areas and *Cophosaurus* prefer areas containing rocks and boulders (Smith et al., 1987). Therefore, these species might be expected to

differ in their species-typical responses to the approach of a predator, such as how soon to run as the predator approaches and whether to run to cover. A multipopulation approach is useful because differences in habitat structure (Snell et al., 1988) or predator pressure (Pianka and Parker, 1972) may correlate with variation in antipredator behavior. Most studies of within-population variation have examined variability in only one aspect of antipredator behavior and have considered the influence of only one ecological factor (e.g., temperature) on antipredator behavior (e.g., Rand, 1964; Dill, 1990). In contrast, I examined simultaneously the influence of several ecological variables on several aspects of flight behavior. Including many factors at once increases explanatory power, and path analysis allows examination of the influence of several factors together that are related in a complex, hierarchical fashion (Arnold, 1972; Li, 1975; Sokal and Rohlf, 1981).

I tested for species and population differences in wariness as indicated by approach distance, distance moved, angle of flight relative to the predator's path, and running to cover. I predicted that lizards inhabiting more open areas would be warier; a wary lizard may remain closer to cover, but in a sparsely vegetated habitat, the lizard may respond to a predator by running sooner or further.

In addition, I tested the effects of directness of approach, air temperature, windiness, time of day, and distance to nearest cover on the distance of the run and the closeness of approach to individual lizards. Figure 1 outlines the hypothesized relationships among the variables which were examined using path analysis (Arnold, 1972; Li, 1975; Sokal and Rohlf, 1981). This path diagram illustrates the expected causal relationships between particular environmental variables and components of flight behavior. Constraints imposed on lizards by environmental conditions (Porter et al., 1973) provide a basis for predictions of the direction of these relationships. Because lizards with a lower body temperature have an impaired ability to run (Bennett, 1980; Hertz et al., 1982; Mautz et al., 1992), I predicted that lizards would be warier in conditions that tend to lower body temperature, such as low air temperature, high wind speed, and low sun early or late in the day (Porter et al., 1973); a negative relationship is expected between temperature and the variables indicating wariness, approach distance and flight distance (Rand, 1964). I also predicted that a lizard would be warier when approached while it is further from cover (Dill and Houtman, 1989; Dill, 1990) or when approached di-

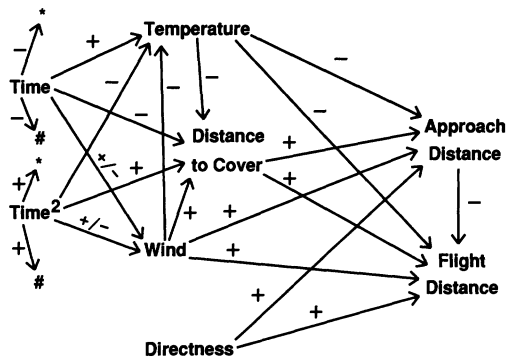


Fig. 1. Path diagram illustrating the hypothesized causal relationships between intensity of threat (directness, distance to cover, air temperature, wind, time) and wariness (approach distance and flight distance). * = points to approach distance; # = points to flight distance. Predicted directions of relationships are indicated with "+" or "-" Time² is the square of the z-score of time (see text).

rectly such that the potential predator would intercept or pass close to the lizard (Walther, 1969; Burger and Gochfeld, 1990). I expected direct effects of each of the environmental variables on approach distance and flight distance, as well as indirect effects through their interrelationships. For example, at higher temperatures (or low wind or at midday), lizards are expected to be closer to cover for shade (Porter et al., 1973) and would then be less wary. I also predicted compensation between approach distance and flight distance; a lizard that runs far can be lax in other aspects of antipredator behavior and run at a short approach distance.

METHODS

Study sites.—I made observations at three sites in southern California from 31 May to 9 July 1989 (*Callisaurus* only) and two sites in Hidalgo County, New Mexico, from 17 July to 18 Aug. 1989 and from 29 May to 6 June 1990 (*Callisaurus* and *Cophosaurus*). All observations were made between 0830 h and 1830 h, Pacific Daylight Time. *Callisaurus* were observed near Whitewater and Desert Center in Riverside County, California; the Desert Tortoise Preserve near California City, Kern County, California; and at San Simon Cienagas, off Federal Highway 80 in Hidalgo County, New Mexico. *Cophosaurus* were observed near State Route 9, Hidalgo County, New Mexico, and sympatrically with *Callisaurus* at San Simon Cienagas.

At each site, vegetation transects were taken following Hafner (1977) to estimate relative

TABLE 1. PERCENT COVER PROVIDED BY VEGETATION AT EACH SITE.

Site (species)	Percent cover	Shrub height (m)			Mean intershrub distance (m)
		Mean	Min	Max	
California					
Whitewater	4.1	0.42	0.05	0.7	10.1
Desert Center	27.5	1.97	0.35	6.0	8.1
Tortoise Preserve*	11.3	0.92	0.3	2.4	8.6
New Mexico					
San Simon*	50.1	1.11	0.2	3.5	1.5
Route 9*	35.2	0.59	0.2	1.4	2.1

* Lizards found in washes at these sites; the transect excluded the washes.

cover. At the Desert Tortoise Preserve and the two sites in New Mexico, the lizards were found in washes, which were devoid of vegetation. At these sites, therefore, relative cover was estimated for the areas surrounding the washes. Two 100-m transects were laid at right angles to each other and crossing in the middle. The amount of each line that was covered by shrubs was recorded, and the height and width of each shrub were measured to the nearest 0.1 m (Table 1).

The Whitewater site is flat, sparsely vegetated (4.1% cover) and bordered by highways, minor roads, and houses at the edge of Palm Springs. The vegetation consisted of sparse, scattered creosote (*Larrea tridentata*), smaller patches of dead or dry shrubs, sticks, and clumps of grass. The ground ranged from a hard surface with occasional rocks to accretion dunes. This site was also characterized by particularly strong and perpetual wind.

The Desert Center site is flat with no rocks and sandy to hard surface. The dominant vegetation is large (> 1 m height) creosote, ironwood trees (*Olneya tesota*), cholla (*Opuntia* sp.), and a few species of grasses in small, scattered clumps. Anderson and Karasov (1981) described this site. The area occupied by lizards at the Desert Tortoise Preserve was a sandy, open wash surrounded by diverse vegetation including cheesebush (*Hymenoclea salsola*), Cooper's thornbush (*Lycium cooperi*), Anderson's thornbush (*L. andersoni*), goldenhead (*Acamptopappus spherocephalus*), paper-bag bush (*Salazaria mexicana*), Thurber's sandpaper bush (*Patalonyx thurberi*), *Grayia spinosa*, and *Tetradymia stenolepis*.

Both sites in New Mexico were characterized by open, sandy washes with desert willow (*Chilopsis linearis*) and creosote covering most of the area surrounding the washes. The wash adjacent to Route 9 was scattered with rocks.

Data collection.—To collect data on flight behavior, I walked through each site and recorded the behavior of all *Callisaurus* and *Cophosaurus* that I encountered. *Callisaurus* and *Cophosaurus* run readily from humans; and by approaching lizards myself, I could minimize the variation among approaches. At the Whitewater and Desert Center sites (those without washes), I walked straight lines (> 200 m), traversing back and forth such that each subsequent line was parallel to and approximately 60 m from the previous line. *Callisaurus* occupy home ranges varying in size from 0.35–0.50 ha, with one as large as 0.60 ha (Tanner and Krogh, 1975). My path across the area minimized the likelihood of encountering the same animal twice because the distance between paths was greater than the diameter of a circular, 0.5-ha home range. At the Desert Tortoise Preserve, San Simon Cienagas, and Route 9, I walked along the middle of the wash. To avoid encountering the same individuals more than once, I walked a different section of the wash each day and, in areas that I traversed more than once, included flight behavior data on only unmarked lizards that I subsequently captured and marked.

Both species employ a sit-and-wait foraging strategy (Pianka and Parker, 1972; Vitt and Ohmart, 1977) and are territorial (Clarke, 1965), so all lizards encountered initiated running from a stationary position. To standardize my speed (approximately 0.84 m/s), I walked to the pace of a taperecording of a metronome played on a Sony "Walkman." All positions and distances measured are illustrated in Figure 2. When I spotted a lizard, I changed direction and walked directly toward it. When the lizard ran, I stopped and dropped a flag at the point at which I was standing (observer). Flags were subsequently dropped at the place the lizard was located before running from me (lizard's origin) and at the place the lizard stopped running (li-

zard's destination). I attempted to capture the lizard by noosing and, if successful, measured cloacal temperature using a Miller and Weber quick-reading mercury thermometer. SVL, total length (nose to tip of the tail), hind-limb span, and forelimb span were measured to the nearest mm using a plastic ruler. Limbs were stretched perpendicularly to the body, and limb spans were measured from toe tip to toe tip, excluding the claws (Garland, 1985). A Pesola scale was used to weigh the animal to the nearest 0.1 g. Sex was noted, and females were palpated to determine reproductive condition. To distinguish individuals, lizards were marked with a small drop of red, blue, and/or yellow fingernail polish on the dorsal side of the neck, mid-back, lower back, or the base of the tail and were then released at the site of capture.

Shaded air temperature (1 cm above the ground) at lizard's origin (Fig. 2) was measured to the nearest 0.1 C using a Miller and Weber quick-reading mercury thermometer. The distance from my position (observer) to lizard's origin (approach distance) and the distance from lizard's origin to lizard's destination (flight distance) were measured to the nearest 0.1 m. The angles between my projected path and approach distance and flight distance were estimated visually to the nearest 5°. The angle of flight was labeled FD angle. The distance to nearest cover (distance to cover) was measured to the nearest 0.1 m as the distance from lizard's origin to the crown of the closest shrub. If the shrub was small and thin and did not seem to provide adequate cover, the distance to the nearest larger shrub from lizard's origin (distance to big shrub) was also recorded. The former variable is the more objective measure of nearby cover. Microhabitats at the origin and destination of the lizard's run were recorded in five categories: open (0); on the far side of but not under a shrub (1); under shrub edge (2); concealed and fully under a shrub (3); down a hole or under the sand (4). Each day, cloud cover was recorded as clear (0), partly cloudy (1), or fully cloudy (2); and windiness was estimated on a scale of 0–4: no wind (0) to strong enough to bend trees (4; approximately 50–65 km/h).

Calculations.—Using the above measurements, I calculated the final distance between myself and the lizard after the lizard ran (Fig. 2). The angle of the observer's approach is a measure of directness. However, the angle between the observer's path and approach distance is geometrically correlated with approach distance, i.e., as approach distance decreases, the angle

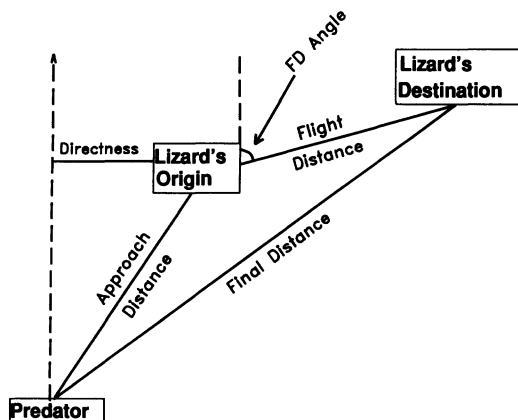


Fig. 2. Positions of the observer and the lizard at the time of the encounter and the distances measured.

necessarily increases. To avoid this confounding correlation in the analyses, I calculated the length of the line from the lizard's original position to its perpendicular intersection with my projected forward path. This distance served as a measure of the directness of the observer's approach, and the variable is called directness.

Because some variables (e.g., temperature) are not expected to vary linearly with time, both time and the square of standardized time were used as potential predictors in the path analysis. Standardized time for each individual was calculated as the z-score of time with respect to its population by subtracting the population mean from the individual score and dividing by the standard deviation (Sokal and Rohlf, 1981).

Statistics.—I used analysis of variance (ANOVA) run on SPSS/PC+ (Norusis, 1989) to test for differences among populations and between species. Residual analysis was used to determine the necessity of transforming data. A Kruskal-Wallis nonparametric ANOVA was performed when transformations failed to achieve approximate normality. To avoid the effects of differences among sites in interspecific comparisons, I compared species only at San Simon Cienagas where they occurred in sympatry.

Relative limb lengths were compared using analysis of covariance (ANCOVA) of log-transformed limb span on log SVL. SVL was used instead of mass because mass is confounded with reproductive condition, since gravid females are heavier. Because lizards have continuous growth, size comparisons are biased by age structure. Therefore, I used only the largest 20% of lizards in each group to compare SVL between species and among populations (Case, 1979).

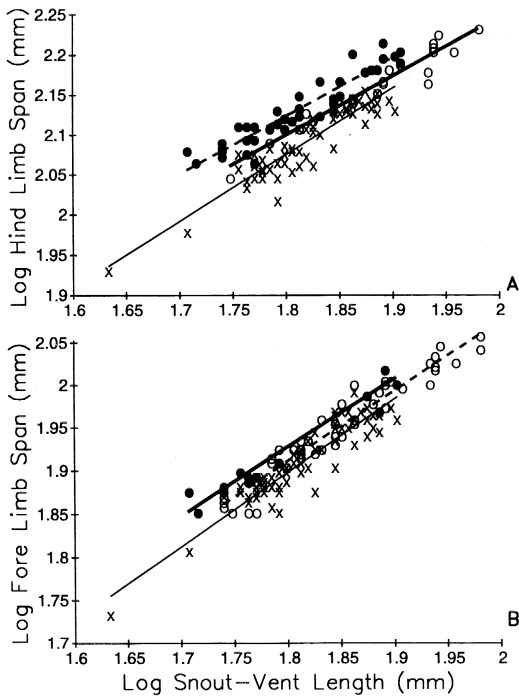


Fig. 3. Plot of log limb lengths vs log snout-vent length for all populations except Whitewater (see text). (A) Hind-limb span: open circles and the heavy, solid line represent *Callisaurus* at San Simon Cienagas; closed circles and the dashed line are *Callisaurus* at Desert Center and the Desert Tortoise Preserve; and Xs and the light, solid line are both populations of *Cophosaurus*. (B) Forelimb span: open circles and the dashed line represent *Callisaurus* at Desert Center and San Simon Cienagas; closed circles and the heavy, solid line are *Callisaurus* at the Desert Tortoise Preserve; and Xs and the light, solid line are both populations of *Cophosaurus*.

Path analysis was performed for each species using Lisrel (Joreskog and Sorbom, 1989) for all variables depicted in Figure 1. This type of analysis allows examination of the relative importance of the response variables to several predictor variables based on the a priori assumed causal relationships among the variables (Arnold, 1972; Li, 1975; Sokal and Rohlf, 1981). Prior to path analysis, data were standardized to account for population differences by calculating the standardized residuals from the regressions of each variable on dummy variables for population. Distance to big shrub was used instead of distance to cover in path analysis because distance to big shrub generally had higher correlations with the other variables than did distance to cover. Approach distance and flight distance were log-transformed, and the square root was taken of distance to cover (big shrub)

and directness to normalize the distribution of the data. All predicted paths (Fig. 1) were entered in the original model, and a final model was reached by backward elimination of paths with a coefficient < 0.1 . Because some variables (e.g., temperature and wind) were not expected to vary linearly with time, the square of the z-score of time was excepted from this restriction if time remained in the model. Significance of the overall model was tested using the χ^2 statistic as a measure of the goodness of fit; small χ^2 value corresponds to a good fit for the model. The coefficient of determination for all structural equations is a measure of the strength of several relationships jointly (Joreskog and Sorbom, 1989).

RESULTS

I captured 35% of *Callisaurus* and 86% of *Cophosaurus* observed, and few of either species were caught within three minutes of sighting. Therefore, reliable body temperatures were not available for most animals. The correlation between body and ground temperature is loose for lizards (Packard and Packard, 1970); however, small lizards such as *Callisaurus* and *Cophosaurus* are tightly coupled to the convective environment (Muth, 1977; see also Packard and Packard, 1970). Therefore, air temperature at 1 cm (recorded for all individuals in the analysis) was a more reasonable substitute for cloacal temperature.

Because not all individuals were captured, the data for sex and SVL are incomplete. In analyses on lizards for which sex and SVL were available, sex and SVL were never significant predictors of flight behavior. Therefore, these variables were excluded from the path analyses.

Species comparisons.—Size: The largest 20% of all captured lizards (60 *Callisaurus* and 64 *Cophosaurus*) were included in this analysis. *Callisaurus* were larger in SVL (Kruskal-Wallis $\chi^2 = 18.56$, $df = 1$, $P < 0.0001$; *Callisaurus*: $n = 13$; *Cophosaurus*: $n = 13$), hind-limb span (ANCOVA: $F = 127.15$, $df = 1, 122$, $P < 0.0001$), and forelimb span (ANCOVA: $F = 25.49$, $df = 1, 121$, $P < 0.0001$) than were *Cophosaurus* (Fig. 3). For hind-limb span only, the interaction term between SVL and hind-limb span was also significant, indicating different slopes for the two species.

Flight behavior: Descriptive statistics for all components of flight behavior are listed in Table 2. At the site in New Mexico where *Callisaurus* and *Cophosaurus* occur together, *Calli-*

saurus ($n = 65$) ran at a greater approach distance, ($F = 23.16$, $df = 1$, 81 , $P < 0.0001$) and to a greater final distance ($F = 28.37$, $df = 1$, 81 , $P < 0.0001$) than did *Cophosaurus* ($n = 18$).

Population comparisons.—Size: Measures of body size and limb proportions differed among the populations of *Callisaurus* (Fig. 3). SVL (Kruskal-Wallis $\chi^2 = 7.02$, $df = 1$, $P = 0.03$; Desert Center: $n = 5$; Desert Tortoise Preserve: $n = 2$; San Simon Cienagas: $n = 4$), relative hind-limb span (ANCOVA: $F = 26.14$, $df = 2$, 57 , $P < 0.0001$; Desert Center: $n = 26$; Desert Tortoise Preserve: $n = 12$; San Simon Cienagas: $n = 22$), and relative forelimb span (ANCOVA: $F = 8.64$, $df = 2$, 57 , $P = 0.0005$) were significantly different among populations. (Because only four of the 60 individuals observed at Whitewater were captured, this population was excluded from this analysis). The lizards at San Simon Cienagas were the largest of the three populations, whereas the lizards at Desert Center were smallest. Relative hind-limb span was shorter in the San Simon Cienagas lizards, and relative forelimb span was longest in the Desert Tortoise Preserve lizards. The two populations of *Cophosaurus* did not differ in SVL (Kruskal-Wallis $\chi^2 = 0.18$, $df = 1$, $P = 0.6674$; San Simon Cienagas: $n = 2$; Route 9: $n = 10$), hind-limb span (ANCOVA: $F = 0.89$, $df = 1$, 62 , $P = 0.3484$; San Simon Cienagas: $n = 16$; Route 9: $n = 48$), nor forelimb span (ANCOVA: $F = 0.08$, $df = 1$, 61 , $P = 0.7836$; San Simon Cienagas: $n = 16$; Route 9: $n = 47$). Interactions between population and SVL were insignificant in all cases.

Flight behavior in Callisaurus draconoides: The four *Callisaurus* populations differed significantly in flight behavior (Table 2). The Whitewater lizards fled at greater approach distances (Kruskal-Wallis $\chi^2 = 20.93$, $df = 3$, $P = 0.0001$), ran significantly greater flight distances ($F = 9.22$, $df = 3$, 189 , $P < 0.0001$), and ran to greater final distances ($F = 10.26$, $df = 3$, 189 , $P < 0.0001$) than did the other populations. The *Callisaurus* at San Simon Cienagas also had greater approach distances and final distances than did the Desert Center lizards. The populations also differed in the proportion of lizards that ran to the open rather than to cover (Kruskal-Wallis $\chi^2 = 9.88$, $df = 3$, $P = 0.0196$); Whitewater lizards ran to the open most frequently.

Flight behavior in Cophosaurus texanus: The two *Cophosaurus* populations did not differ significantly in any of the flight variables; however, San Simon Cienagas *Cophosaurus* were initially

significantly further from cover (distance to cover) than were those at Route 9 ($F = 5.52$, $df = 1$, 73 , $P = 0.0215$).

Individual variation.—Sex differences: I also compared the sexes at the three populations of *Callisaurus* using two-way ANOVA. (The Whitewater population was excluded from this analysis). The effect of population was significant for approach distance ($F = 4.83$, $df = 2$, 57 , $P = 0.012$). However, neither sex nor the sex \times population interaction were significant for either approach distance (sex: $F = 3.08$, $df = 1$, 57 , $P = 0.085$; interaction: $F = 0.67$, $df = 2$, 57 , $P = 0.514$) or final distance (sex: $F = 2.30$, $df = 1$, 57 , $P = 0.135$; interaction: $F = 0.18$, $df = 2$, 57 , $P = 0.836$). On the other hand, mean approach distance and final distance were higher in males in all three populations of *Callisaurus* and both populations of *Cophosaurus*. A two-tailed sign test for this difference was not significant ($P = 0.0625$).

In one-way ANOVAs, the only site at which males and females differed significantly in flight behavior was at the Desert Tortoise Preserve (Table 3). At the Desert Tortoise Preserve, males ran at significantly greater approach distances ($F = 6.86$, $df = 1$, 10 , $P = 0.0257$) and ran to greater final distance ($F = 6.17$, $df = 1$, 10 , $P = 0.0323$) than did females. Five of the seven females at this site were gravid. When males and gravid females were compared, approach distance was still significantly different ($F = 6.91$, $df = 1$, 8 , $P = 0.0302$), but final distance was not ($F = 3.56$, $df = 1$, 8 , $P = 0.0960$). Furthermore, when nongravid females only and males were compared at the other sites, the sex differences were insignificant. Based on all of these analyses, sex per se had little effect on flight behavior in these populations.

Correlates of individual variation within populations: Residual values after removal of population differences for all lizards (*Callisaurus*: $n = 193$; *Cophosaurus*: $n = 75$) were used in this analysis. The analysis excluded SVL and sex (see Methods). The final path models for each species with insignificant paths constrained to zero and deleted from the diagram are illustrated in Figure 4. Goodness of fit of both models was acceptable; neither differed significantly from expectation (*Callisaurus*: $\chi^2 = 8.30$, $df = 13$, $P = 0.823$; *Cophosaurus*: $\chi^2 = 17.11$, $df = 13$, $P = 0.194$). Path coefficients in Figure 4 are the partial correlation between the variables at each end of the arrows. The coefficient of determination (r^2) for the overall path model for *Callisaurus* was 0.31, and that for *Cophosaurus* was 0.37. The magnitude of most of the path

TABLE 2. DESCRIPTIVE STATISTICS FOR POPULATIONS.*

	Approach distance (m)	Flight distance (m)	Final distance (m)	FD angle	Distance to cover (m)	Big shrub (m)	Temperature (C)	Destination (% to open)	Origin (% in open)
<i>Callisaurus draconoides</i>									
Whitewater (n = 60)	8.8 ± 0.57	9.2 ± 0.94	15.9 ± 0.99	50 ± 4.9	1.41 ± 0.16	3.7 ± 0.56	39.8 ± 0.42	73.3	85.0
Desert Center (n = 45)	5.6 ± 0.39	6.0 ± 0.88	10.3 ± 0.98	55 ± 6.0	1.44 ± 0.21	2.0 ± 0.26	40.2 ± 0.54	48.9	75.6
Tortoise Preserve (n = 23)	6.5 ± 0.66	4.6 ± 0.67	9.7 ± 0.74	44 ± 6.7	1.19 ± 0.26	1.3 ± 0.31	41.5 ± 0.72	52.2	65.2
San Simon (n = 65)	8.8 ± 0.62	4.1 ± 0.34	11.7 ± 0.69	56 ± 3.8	1.92 ± 0.20	2.1 ± 0.2	36.8 ± 0.37	54.0	88.9
<i>Cophosaurus texanus</i>									
San Simon (n = 18)	3.6 ± 0.52	3.2 ± 0.45	6.2 ± 0.77	51 ± 9.0	2.2 ± 0.47	2.3 ± 0.46	35.4 ± 0.68	61.1	88.9
Route 9 (n = 59)	5.0 ± 0.46	3.0 ± 0.27	6.9 ± 0.55	61 ± 5.4	1.42 ± 0.13	1.8 ± 0.16	34.9 ± 0.32	55.9	98.3

* Mean ± SEM.

coefficients was between 0.10 and 0.30. The proportion of unexplained variation in approach distance and flight distance exceeded 0.75 for *Cophosaurus* and 0.90 for *Callisaurus*.

Positive direct effects were significant in both species between temperature and flight distance, directness and approach distance, and between distance to cover and both approach distance and flight distance. Wind correlated negatively with approach distance for *Callisaurus* and positively with flight distance for *Cophosaurus*. Thus, in windy conditions, *Callisaurus* ran later, which suggests decreased wariness, and *Cophosaurus* ran further, indicating increased wariness. The relationship between approach distance and flight distance was significant for *Cophosaurus* but not for *Callisaurus*. *Cophosaurus* that ran at a large approach distance also ran far.

Wind, time, and standardized time² had direct and indirect significant effects on flight behavior. Flight distance in *Callisaurus* and approach distance in *Cophosaurus* decreased with time at the beginning of the day and increased later in the day, suggesting that wariness was highest early and late in the day and was lowest in the middle of the day. Wind, time, and standardized time² had indirect effects on flight behavior through their effects on temperature. For observations of both lizard species, air temperature rose early in the day and decreased later in the day and was negatively related to wind. In addition for *Callisaurus*, time and standardized time² had an indirect effect through distance to cover; lizards decreased their distance from shrubs early in the day and later slightly increased the distance. The value of an indirect path is calculated as the sum of the products of all possible paths between two variables (excluding the direct path; Li, 1975; Sokal and Rohlf, 1981). For example, the indirect effect of time on flight distance in the final model for *Callisaurus* (Fig. 4A) equals the product of

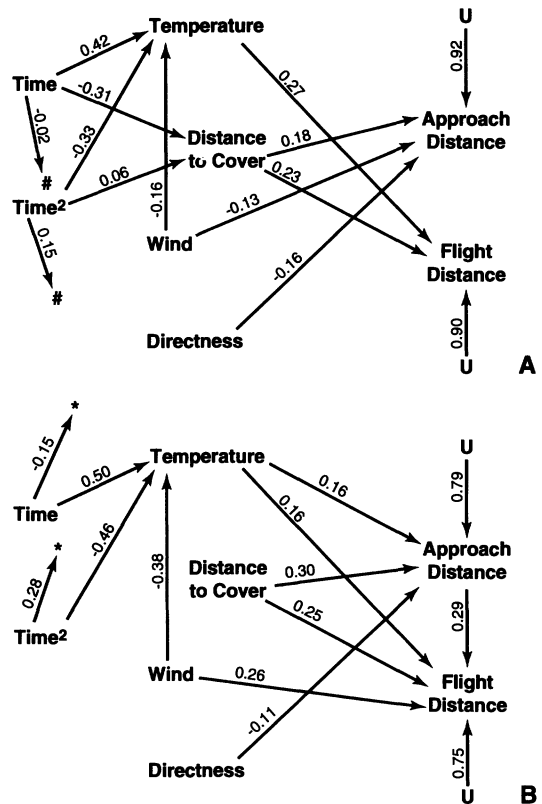


Fig. 4. Path diagrams for each species. Path coefficients are indicated above the arrows for each significant path. * = points to approach distance; # = points to flight distance. "U" indicates proportion of unexplained variation. (A) *Callisaurus draconoides*. (B) *Cophosaurus texanus*.

the direct paths from time to temperature and temperature to flight distance (0.42×0.27) plus the product of the paths from time to distance to cover and distance to cover to flight distance (-0.31×0.23). Therefore, the value associated with the indirect path from time to flight distance is 0.04. All indirect paths between wariness

TABLE 3. DESCRIPTIVE STATISTICS BY SEX.^a

Population	Number ^b		Approach distance (m)		Final distance (m)	
	Males	Females	Males	Females	Males	Females
<i>Callisaurus draconoides</i>						
Desert Center	17	11 (0)	5.4 ± 0.75	4.7 ± 0.51	9.0 ± 1.36	7.6 ± 1.04
Tortoise Preserve	5	7 (5)	7.0 ± 1.26	3.7 ± 0.57	9.9 ± 0.89	6.6 ± 0.94
San Simon	13	10 (1)	8.3 ± 1.26	6.9 ± 1.08	10.6 ± 1.78	9.0 ± 1.20
<i>Cophosaurus texanus</i>						
San Simon	12	5 (2)	3.7 ± 0.59	2.3 ± 0.39	5.9 ± 0.88	5.4 ± 0.95
Route 9	26	23 (5)	5.0 ± 0.82	3.9 ± 0.30	6.8 ± 0.94	5.4 ± 0.39

^a Mean ± SE are given for approach distance and final distance by sex for each population.
^b The number of gravid females included in the total is in parentheses.

ness and time, standardized time², and wind had values less than or equal to 0.10.

DISCUSSION

Species comparisons.—*Callisaurus* are larger lizards than are *Cophosaurus* with longer relative hind-limb and forelimb spans and may also be faster runners. Relative limb length is expected to correlate with sprint speed, although this has rarely been documented (Garland, 1985; Snell et al., 1988; Tsuji et al., 1989). T. Garland, Jr. (pers. comm.) has measured mean maximal sprint running speeds on a high-speed treadmill of 17.7 km/h (SD = 4.44, min = 13.2, max = 22.7) for five *Callisaurus* and 16.7 km/h (SD = 3.14, min = 13.2, max = 20.0) for three *Cophosaurus*. Punzo (1982) reported laboratory running speeds ranging from 3.6–6.8 km/h for *Cophosaurus*, and Belkin (1961) measured *Callisaurus* running in the field as fast as 29 km/h. Based on the potentially greater ability of *Callisaurus* to escape by running, I had expected these lizards to be less wary than were *Cophosaurus*. Comparison of the two species at one site suggests that *Callisaurus* are warier than are *Cophosaurus*; *Callisaurus* ran sooner and ran to a further distance from the observer. These results indicating higher wariness of *Callisaurus* is supported by my observation that *Callisaurus* are harder to capture by noosing. Several explanations are possible: (1) Lizards with an especially effective antipredator tactic may tend to use that tactic more readily; *Callisaurus* are swift runners and may be more inclined to run. (2) *Callisaurus*, being larger, may also be more visible to predators and would, therefore, need to be more wary. (3) *Callisaurus* may also be more energetically efficient runners than are *Cophosaurus*, reducing the cost of fleeing at greater approach distances. For example, John-Alder et al. (1986) measured a lower cost of locomotion in *Heloderma suspectum* compared to *Trachydosaurus rugosus*. *Heloderma suspectum* also has a longer hind-limb span as a percent of SVL than does *T. rugosus* (John-Alder et al., 1986). In this study, *Callisaurus* had longer relative hind-limb length than *Cophosaurus* and, therefore, may also have a lower cost of locomotion. (4) Escape behavior diversity among similar, sympatric species may be a tactic to reduce predators' ability to predict the escape behavior of potential prey (Schall and Pianka, 1980). For example, five sympatric species of *Cnemidophorus* in southwestern Texas differed significantly in escape behavior (Schall and Pianka, 1980). Further comparative studies encompassing a

larger number of populations could be used to test these ideas.

Population comparisons.—*Callisaurus* populations differed in wariness. The population at Whitewater was particularly wary; the values for approach distance, flight distance, and final distance were all significantly greater than those of the other populations. The percent cover at Whitewater was considerably lower than at any of the other sites (Table 1), which may explain the high wariness of these lizards. The lizards at Whitewater also remained in the open after running more often than did lizards at the other sites. This also may be explained by the relative dearth of cover at Whitewater. Other studies on *Callisaurus* (Asplund, 1967), Galapagos lava lizards (Snell et al., 1988), and brook trout (Grant and Noakes, 1987) noticed greater wariness in areas with relatively sparse cover.

The *Callisaurus* at San Simon Cienagas were also wary when compared to the lizards at Desert Center and the Desert Tortoise Preserve. The *Callisaurus* captured at San Simon were larger but had relatively shorter hind limbs compared to those at the other two sites and shorter forelimbs compared to the lizards at the Desert Tortoise Preserve (Fig. 3). These differences, however, are difficult to interpret because of several confounding factors. Mean air temperature was not significantly different among the three California sites, but San Simon Cienagas was cooler than the others and differed substantially in sparseness of vegetation. Predation pressure was not examined in this study but could differ among sites. Population variation in antipredator behavior corresponded to differences among sites in predation pressure in lizards (Schall and Pianka, 1980), salamanders (Dowdey and Brodie, 1989), and fish (Magurran and Seghers, 1990). Tail break frequency is often used as an indication of predator pressure on lizard populations (Pianka and Parker, 1972; Schall and Pianka, 1980; but see Schoener, 1979). However, few *Callisaurus* captured in this study had broken tails (Desert Center: two; Desert Tortoise Preserve: two; San Simon Cienagas: four). Interpopulation differences imply that studies of antipredator behavior based on a single population may not be representative of the species (Herzog and Schwartz, 1990).

The two populations of *Cophosaurus* did not differ significantly in their response to an approaching observer. The sites are located only about 16.5 km from each other. Consequently, their habitats are similar, and the populations

may experience considerable gene flow. The difference in distance to cover between the two *Cophosaurus* populations could simply be the result of differences in the widths of the washes at the two sites. The wash at the Route 9 site was narrower, so the lizards at that site may have been unable to be situated as far from shrubs as those in the other population.

Individual variation.—Sex and size differences: Sex differences in flight behavior were significant only for *Callisaurus* at the Desert Tortoise Preserve, perhaps because of the higher proportion of gravid females found at this site. Most of the females caught at this site were gravid, whereas no more than one captured female was gravid at the other sites (Table 3). When the two nongravid females were removed from the analysis of the Desert Tortoise Preserve population, males still ran significantly sooner than did gravid females. This suggests that being gravid, rather than sex per se, influences flight behavior. Several studies have demonstrated that gravid female lizards have reduced maximal sprint speeds in the laboratory (Garland, 1985; van Damme et al., 1989; Cooper et al., 1990). Gravid lizards alter their antipredator behavior in the field by remaining motionless longer (shorter approach distances) and running shorter distances (flight distance) compared to nongravid females and males (Bauwens and Thoen, 1981; Schwarzkopf and Shine, 1992).

SVL was not a significant predictor of wariness, suggesting that neither size nor age affect individual variation in flight behavior in these lizards. Other studies have also failed to find effects of size and age on flight behavior (Heatwole, 1968; Shallenberger, 1970; Daniels and Heatwole, 1990).

Correlates of individual variation in wariness: Based on path analysis (Fig. 4), all of the variables examined in this study influence antipredator behavior in *Callisaurus* and *Cophosaurus*, although not all of the relationships were in the predicted directions. As hypothesized, the presence of nearby cover had direct effects on both approach distance and flight distance in both species (Fig. 4), indicating greater wariness in lizards further from cover. Squirrels (Dill and Houtman, 1989) and fish (Dill, 1990; but see McLean and Godin, 1989) also have positive relationships between cover and approach distance.

Wariness increased with temperature, which is counter to expectations but is consistent with the findings of some other studies. In addition,

individuals of both species ran later (shorter approach distance) when approached directly, contrary to expectations. The threat to a lizard is clearly greater when temperature is lower and when a predator approaches directly. Cold lizards have an impaired ability to run and are, therefore, expected to be more wary (e.g., Rand, 1964; Bennett, 1980; Hertz et al., 1982). Moreover, black iguanas approached by a human (Burger and Gochfeld, 1990) and Thomson's gazelles, in response to a car (Walther, 1969), ran sooner when approached directly. Lizards in the present study, however, ran further at warmer temperatures and fled sooner when approached at an angle. As an alternative hypothesis for these lizards, immobility may be the predominant strategy to perhaps avoid detection when the threat is high, e.g., when the temperature is low or the lizard is approached directly. Warm lizards may also run further because they are more effective (faster) runners at higher temperatures. In addition, movement of the predator may be more detectable during a sidelong approach than a direct approach; a directly approaching predator may not provide enough of a stimulus for a flight reaction from the lizard.

Effect of temperature on wariness in lizards is variable. The positive relationship between temperature and wariness in this study is consistent with the results of Losos (1988) who found that, at high ground temperatures, the military dragon (*Ctenophorus isolepis*) ran further. Earlier in the morning while basking, *Callisaurus* could be approached closely, but they ran far when approached after warming (Tanner and Krogh, 1975). Other studies have found inverse relationships between wariness and temperature in lizards (Rand, 1964; Shallenberger, 1970).

Time and wind had direct effects on flight behavior and indirect effects through their relationships with temperature and distance to cover. Time and wind data for both species showed the expected relationships with air temperature. The direct effects of time and standardized time² on flight behavior suggest an endogenous daily cycle of wariness. Indirect paths through temperature and distance to cover also account for a component of the effects of time, standardized time², and windiness on wariness. For example, under the conditions associated with high temperature, such as being midday or low wind, lizards ran further after being approached. Physical factors were correlated with survival in *Uta stansburiana*; surviving lizards in enclosures were active under clearer skies and at a central time of day compared to nonsurvivors (Fox, 1978). Therefore,

if physical factors influence survival, antipredator behavior should be adjusted to different conditions.

As predicted, approach distance had a direct effect on flight distance in *Cophosaurus* but in the opposite direction expected; individuals that ran early also tended to run far. The relationship between approach distance and flight distance was not significant in *Callisaurus*. The lack of a negative relationship between these two variables in either species indicates that there was no compensation between running soon and running far. Rather, an individual that is wary by one measure (approach distance) is also wary by the other (flight distance).

Flight behavior is highly variable within as well as among populations of desert lizards. All factors measured had significant effects on individual variation in flight behavior. Variation in flight behavior in lizards is also likely to be affected by other factors not measured in this study. For example, locomotor ability decreases after a recent meal in snakes (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986; Herzog and Bailey, 1987) and after tail autotomy in lizards and salamanders (Ballinger et al., 1979; Dowdey and Brodie, 1989; Formanowicz et al., 1990). Few lizards that I encountered had lost their tails (two *Callisaurus*, six *Cophosaurus*), so tail loss was probably not a factor in this study. Future studies might examine the running speeds used by fleeing lizards in the field to determine the relative pertinence of different measures of locomotor abilities (e.g., sprint speed) to flight behavior in free-ranging animals.

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Two New Bathyl *Neobythites* spp. from the Caribbean Sea (Pisces, Ophidiidae)

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Two new bathyl species of the genus *Neobythites* bring the total number of species in the western Atlantic to five. One new species, *N. unicolor*, is characterized by the lack of ocelli and vertical and horizontal stripes on the fins and body. The other new species, *N. elongatus*, has a brownish, marbled pigmentation on the dorsal part of the body but lacks ocelli and stripes on the fins and body.

The ophidiid genus *Neobythites* is known from all tropical waters except for the eastern Atlantic Ocean (Cohen and Nielsen, 1978). The genus is rich in species, with 15 described and about 25 undescribed species (JGN, unpubl.). One of us (JGN) is revising the systematics of the genus. The present material was collected from the Caribbean Sea by the vessel *Oregon* in 1957 and 1959 and by the Marine Biomedical Institute (MBI), Galveston, Texas, in 1976. In addition to the two species described here, the *Neobythites* fauna of the western Atlantic Ocean consists of the following species: *N. gilli* Goode

and Bean, 1886, *N. marginatus* Goode and Bean, 1886, *N. ocellatus* Gunther, 1887, and 1-2 species yet to be described.

MATERIALS AND METHODS

About 250 *Neobythites* specimens from the western North Atlantic Ocean were examined. Of these specimens, the majority were from USNM with smaller numbers from BMNH, FMNH, MCZ, TCWC, and ZMUC. Of the 250 specimens examined, 18 specimens represented the two new species and were obtained from