

## The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*)

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The zebra-tailed lizard (*Callisaurus draconoides*) is a small, sit-and-wait predator, which itself is subject to predation by a variety of animals, including other larger lizards. It lives in relatively open, flat habitats, and is well camouflaged. Nevertheless, it has a distinctive black and white banded tail that it exposes by curling and wagging. We demonstrate that tail-wagging is a response to the approach of a potential predator (here, humans). We tested alternative hypotheses regarding the function of this behavior. Our results support the pursuit deterrent hypothesis, namely, that the conspicuous behavior of the lizards is aimed at their predators to communicate the signaler's state of alertness and its relative escape ability, and functions to reduce the likelihood of further pursuit. Alternative hypotheses tested here are not supported. We suggest that such interspecific signals are common in nature.

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Le lézard *Callisaurus draconoides* est un prédateur qui utilise l'affût et il sert lui-même de proie à plusieurs animaux, y compris d'autres lézards plus grands. Ce lézard vit dans les habitats relativement découverts, plats, et est bien camouflé. Il possède cependant une queue rayée blanc et noir caractéristique qu'il brandit en la recourbant et en la remuant. Nous démontrons ici que les mouvements de la queue sont une réaction à l'approche d'un prédateur potentiel (ici, un humain). Nous avons envisagé d'autres hypothèses sur le rôle de ce comportement. Nos résultats corroborent l'hypothèse du détournement de l'ennemi qui veut que ce comportement ostentatoire des lézards serve à faire connaître aux prédateurs l'état d'alerte du « signaleur » et sa capacité relative de fuite et réduise ainsi la probabilité que la poursuite se continue. Les autres hypothèses n'ont pas été confirmées par les résultats. Nous croyons que les signaux interspécifiques tels celui-ci sont communs en nature.

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### Introduction

Frequently, when animals are approached by a predator, they neither escape nor hide, but instead expose themselves to the predator. The zebra-tailed lizard, *Callisaurus draconoides*, often curls its tail up and wags it in response to the approach of humans (Stebbins 1966; Tanner and Krogh 1975; Vitt and Ohmart 1977). The tail-wagging behavior of this lizard, when combined with its "trademark," a banded black and white tail (Fig. 1), is so striking that in Mexico the lizard is called "perrito" (Spanish for "little dog"). Several hypotheses may explain the behavior. Here, we present the results of an experiment designed to distinguish among some of the hypotheses.

We consider four hypotheses that are relevant to this study. The logical weakness of the pursuit invitation hypothesis (Smythe 1970) has been discussed thoroughly elsewhere (Coblentz 1980; Woodland et al. 1980) and is not considered here.

#### Flash concealment hypothesis

The sudden disappearance of a conspicuous "flash" may confuse the predator when the camouflaged prey takes cover and conceals its conspicuous parts (Hailman 1977; Bildstein 1983).

#### Distraction-autotomy hypothesis

Directing the predator's attack to a conspicuous but elusive

tail, assisted by tail autotomy, may preserve the vital anatomy of the lizard (e.g., Vitt and Ohmart 1977).

#### Warning signal hypothesis

Animals may warn others, usually conspecifics, of an approaching predator, although they often expose themselves to the predator by doing so. This interpretation usually assumes risk to the signaler and benefit to others, and is almost always explained by kin selection theory (Maynard Smith 1965; Wilson 1975; but see Trivers 1971).

#### Pursuit deterrent hypothesis

Prey may advertise their alertness and defense potential to deter pursuit by predators (escape is considered here as a defensive strategy). This hypothesis has been recently and independently advanced by Zahavi (1977), Baker and Parker (1979; following Hingston 1933), and Woodland et al. (1980). Because the first two hypotheses can be dismissed by relatively simple tests, and because the third hypothesis is not supported by available data, the rest of the Introduction focuses on the pursuit deterrent hypothesis and formulates the basis for new, detailed predictions.

The probability that a predator will successfully catch its prey decreases after the predator is detected by the prey. Therefore, once detected, the predator should increase its tendency to seek other prey rather than pursue (Baker and Parker 1979). Consequently, prey can take advantage of the predator strategy of abandoning alerted prey more frequently than unaware prey, and inform the predator that it has been detected. Zahavi (1977) and Woodland et al. (1980) further suggested that prey may exploit yet another predator strategy, that of avoiding the best escapers, by advertising their relative escape ability (REA).

For the predator to be selected to respond to its potential

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prey's signals, the signals must reliably inform the predator of either the signaler's alertness or its REA, or both. The nature of signals should differ, however, depending upon whether information conveyed pertains to escaping ability or alertness.

Alertness can be reliably advertised at relatively low cost, especially if delivered audibly when the prey is safely in or near cover (birds in canopy, mice in burrows, etc.). In contrast to auditory signals, visual signals increase cost to the prey because, by definition, to be effective such signals must indicate to the predator the exact location of the prey. Nevertheless, if visual signals are delivered at a sufficient distance from the predator, their cost may still be low.

If predators respond to signals of alertness, then one can argue that prey should be selected to cheat by signalling continuously, even if they do not detect a predator (and because cheating has a negative effect on the evolution of the predator's response, it would, in turn, destabilize the system). However, cheating would be too costly for the following reason: if predator response is not unconditional but, instead, depends also on the assessment of other factors (e.g. the probability of successfully catching an alerted prey), the prey would usually not benefit by exposing itself to predators unless predator location was known.

Cheating would be even more dangerous to prey if predators could recognize prey signals that reliably advertise that the predator is indeed being watched. This would enable the predators to discriminate between cheaters (unalerted signalers) and noncheaters (alerted signalers). A. Zahavi's observations (Department of Zoology, Tel Aviv, Israel; personal communication) on the Arabian babblers, *Turdoides squamiceps*, elegantly show how such signals are possible. Zahavi noticed that when the babblers mob a predator, they call sharply and sometimes make quick movements whenever the predator makes a move. Based on his observations, Zahavi suggests that a precise timing of deliberate exposure to predators reliably informs the predator that it has been detected; this can be verified by the predator when it moves. A similar reaction of the little owl *Athene noctua* to a human observer was described by Daanje (1951), although he classified the reaction as an intention movement.

REA may be advertised reliably by a different set of signals; unlike signals of alertness, many of them must confer cost. We define REA as the relative probability of escape if the predator initiates a pursuit. REA is a function of the immediate physical condition of both prey and predator and of their distance from each other and from the prey's refuge; it is relative to the probability of the prey's escape during other encounters with the same predator. The components of REA can be conveyed reliably by using costly signals that are, because of their risk, differentially distributed among the prey population (Zahavi 1977). In other words, a weaker or slower individual, or one in an exposed site, is expected to take a smaller risk (for details, see Nur and Hasson 1984).

Nur and Hasson (1984) show that a nonzero optimal predation risk is possible only if there exist (i) a very high probability of surviving a pursuit when the signal is given with low volume or intensity, and (ii) exponentially decreasing probability of surviving a pursuit with linearly increasing signal intensity. Because distance from the predator is the type of risk that creates such a convex survivorship curve, optimization of risk (distance) and benefit (predator deterrence) is possible. Thus a predator can use its distance from the signaling prey to

assess how the prey estimates its own REA when it exposes itself to the predator by giving the signal.

The pursuit deterrent hypothesis is supported by an increasing number of field studies (Woodland et al. 1980; Tilson and Norton 1981; Bildstein 1983; Randall and Stevens 1987; and especially Caro 1986). An additional study (Dial 1986) has also proposed that tail display of another iguanid lizard is aimed at its predators. That study, however, assumed that alarm signals, whether they function as pursuit deterrent or as warning signals, can only be expressed by tail display. Because the study tested the hypothesis that tail-wagging is aimed at the predator only by correlating the frequency of tail-wagging of two species of iguanid lizards (one of them does not tail-wag at all) with their population density, it depends crucially on this underlying assumption. Yet other sorts of signals (e.g., head-bobbing) are conceivable. Its conclusion is, therefore, unreliable.

To previous studies on pursuit deterrent signals we add here the distinction between signals of alertness and signals of REA; this allows us to make additional new predictions.

## Materials and methods

### The study site

Most of the study was conducted in the Central Gulf Coast subdivision of the Sonoran Desert (Shreve 1951) at Punta la Ona (29°07'N, 110°08'W), approximately 20 km north of Bahia Kino, Sonora, Mexico, March 14–17, 1984. The area is flat, the soil is beach quartz sand, and vegetation is sparse with approximately 30–35% cover. During daytime observations (between 9:00 a.m. and 4:00 p.m.), air temperatures recorded at approximately 3 cm above the surface fluctuated between 22 and 32°C. Soil temperatures measured at the surface fluctuated between 28 and 47°C. Additional observations were conducted by one of us (O.H.) just south of Puerto Peñasco, Sonora, on September 5, 1987. The habitat in Puerto Peñasco consists of low sand dunes with vegetation distributed similarly to that of Punta la Ona. The lizards' behavior toward the human observer seemed also to be roughly the same in the two locations. The latter observations were used mostly in the test of the flash concealment hypothesis.

### Animals

*Callisaurus draconoides* is a small (40–90 mm snout to vent), fast lizard. Its optimal body temperature is 38.1–39.1°C (Pianka and Parker 1972), and during the observations at Punta la Ona it was active during the warmer part of the day. It has keen vision and uses a sit-and-wait feeding strategy to capture arthropods and occasionally small lizards (Pianka and Parker 1972; Tanner and Krogh 1975; Vitt and Ohmart 1977). The zebra-tailed lizard is solitary and highly territorial, and rarely leaves its home range (Pianka and Parker 1972; Tanner and Krogh 1975).

Scan sampling transects of 400 × 10 m indicated an average density of 5.0 lizards per transect ( $n = 5$  transects,  $SD = 2.55$ ) at midday (50 individuals/h). This density is far greater than those reported by Pianka and Parker (1972; 0.52/h) and by Tanner and Krogh (1975; 12.5–15.5/h). It is not exceptional, however, for the Sonoran Gulf populations (C. H. Lowe, Department of Ecology and Evolutionary Biology, The University of Arizona, Tucson, personal communication).

The general color pattern of the zebra-tailed lizard is cryptic, except for striking black bars across a white background on the underside of the tail (the black bars extend to the dorsal surface of the tail in older adult males) and the black and blue-green pattern on the lateroventral side behind the front legs of older individuals (especially of males) (Fig. 1). The lizard can conceal most of these conspicuous markings behaviorally.

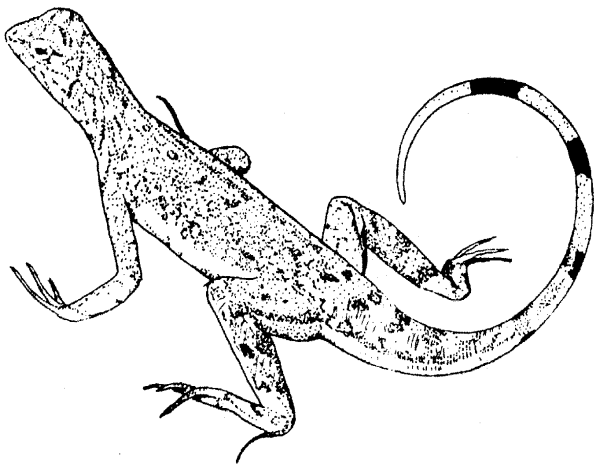


FIG. 1. The zebra-tailed lizard, showing the conspicuous upraised tail which is wagged laterally. (Drawing prepared by D. Thompson, based on photographs by G. Ceballos.)

Walking in the study site, we were perceived by the lizards as a potential danger, and our approaches were followed by their retreats. Their behavior toward us was qualitatively similar to their behavior toward natural predators, especially the leopard lizard, *Gambelia wislizeni* (R.H., personal observations).

#### Methods

To test the different hypotheses, we walked in the study area and recorded lizard behavior in different contexts. These contexts are explained below in the procedure description of each test.

To decrease the lizards' tendency to flee before we could observe their behavior, we moved slowly through the study area until we detected a lizard. We then usually approached or retreated slowly and, if possible, alternated approaches and retreats (we could rarely do this more than three times before the lizard fled). Our slow movements minimized the occurrence of uncontrolled quick movements which might have caused the lizards to flee. Consequently, behavior was mostly a response to distance from the observer rather than to observer behavior. Other types of approaches are explained below. In all instances, we recorded the type of our approach and the response of the lizard.

By considering area covered and lizard density, we estimate that we recorded the behavior of 60–100 lizards. Many lizards were probably recorded more than once. If so, then observations may not always have been independent. Although a bias could not be entirely avoided without marking the lizards, we minimized the chances of resampling individuals by moving continuously throughout the study site. Therefore, it is unlikely that any lizard was recorded more than once in tests that included only a small number of observations. We therefore feel confident that our qualitative conclusions remain unaffected.

After the description of each test we present the specific prediction of the hypothesis it examines. For statistical analyses we followed procedures of Zar (1984).

## Results

### The context of tail-wagging

#### Test 1

To test whether tail-wagging was performed in response to our approach, we compared the proportion of tail-wagging during our approaches to that during our retreats.

**Prediction**—If the context of tail-wagging was other than our approach, we would expect its frequency to be equal between approaches and retreats (the average durations of retreats and approaches were approximately the same).

**Result**—Lizards wagged their tails 119 out of 198 times

when we approached (0.60). For this calculation, we considered each approach within a sequence of approaches as a single entry (a comparison of the frequencies of tail-wagging during first and second approaches showed no significant difference,  $p = 0.23$ , two-tailed Fisher exact test). In contrast, lizards wagged their tails only 6 out of 49 times when we retreated (0.12). Therefore, the context of tail-wagging was clearly in response to the approach of humans ( $p \ll 0.001$ , two-tailed Fisher exact test).

### Flash concealment hypothesis

#### Test 2

Because of a lack of quantitative data from Punta la Ona, this test was conducted later near Puerto Peñasco. The observer walked in a large zigzag path so that no lizard was observed more than once. Only lizards that were observed wagging their tail were counted. Tail-wagging was divided into the following two categories: those that were performed only while running and those that were performed while the lizard was stationary, either before or after it ran, regardless of its behavior during the run.

**Prediction**—If tail-wagging functions to cause predators to lose eye contact with their prey, tail disappearance should be quick and unexpected. Thus the flash concealment hypothesis predicts that the lizards do not tail-wag while they are stationary, but do when they escape (or immediately before escaping).

**Result**—Twelve lizards wagged their tails while remaining stationary, and only 1 wagged its tail only while running. The ratio of 12:1 is significantly different from the expected, 0:13 ( $p \ll 0.01$ , Fisher exact test). This result is consistent with our observations at Punta la Ona. On many occasions the lizards exposed their tail pattern while remaining stationary, moved their tails up and down very slowly, or wagged their tails immediately after they had stopped running. Furthermore, older males wagged their tails although the dorsal surface of their tails were almost as brightly colored as the abdominal surface, and hence not effectively concealed. All of these behavioral patterns conflict with the flash concealment hypothesis.

### Distraction—autotomy hypothesis

The field test of the distraction—autotomy hypothesis is based on the following argument: if tail-wagging functions to lure the predators' attack to the tail rather than to the head, it should be conducted more frequently when the risk of capture is high. We were not able to create a high risk of capture by chasing the lizards rapidly (because of their quickness and the investigators' slowness). We therefore created a dangerous situation to which the lizards could respond, as follows.

#### Test 3

After slowly approaching an alerted lizard, we suddenly and rapidly threw an object (usually a short stick) at the lizard, aiming very close to it. This created a quickly approaching danger.

**Prediction**—Because the lizards responded by running faster and directly to the nearest cover rather than around it (as they did in response to our standard approach), we assume that the lizards perceived the quickly approaching object (or us, in this context) as conferring higher risk. Consequently, if the lizards use tail-wagging to divert the predator's attack to the tail, their tendency to wag their tail should increase. Therefore we pre-

dicted a higher proportion of tail-wagging than the average proportion, 0.60 (see test 1).

**Result**—All lizards in this test responded by fleeing rapidly while holding their tails down ( $n = 15$ ). The proportion of tail-wagging was significantly lower than the average proportion ( $\chi^2 = 9.01, p < 0.005$ ). It should be noted that 13 out of 15 lizards in this test wagged their tails before or after (upon reemergence from cover in our presence) this particular test, and so normally perform tail-wagging. Although the method used was rather crude and the objects were not standardized by shape or size, the uniformity of the results is highly suggestive. Three more lizards that were treated similarly in Puerto Peñasco followed exactly the same pattern.

#### Warning signals

This hypothesis is substantially different from all other hypotheses in that it suggests that the signaler's behavior decreases its own individual fitness (while increasing that of others; i.e., it is an "altruistic" behavior). All of the alternative interpretations suggest that individuals benefit by their own behavior, though others may benefit incidentally as well.

We could not directly test this clearly dichotomous prediction. However, we can use our data on the proportions of tail-wagging to make a testable prediction.

#### Test 4

We compared the proportions of tail-wagging in two contexts: (i) all observations and (ii) observations in which at least two lizards were within line of sight and the behaviors of both were known.

**Prediction**—The relationship between the probability of having recipients within range of warning signals and the expected proportion of predator-prey encounters in which prey should give warning signals is nonmonotonic and rather complicated (O. Hasson<sup>4</sup>). Nevertheless, when the probability of detecting potential recipients (if present within a warning signal range) is high, the proportion of warning signals is expected to be a positive function of the probability of having recipients present (Hasson, see footnote 4). Because the zebra-tailed lizard's eyesight is extremely good, we can use this procedure here. For this test we computed a different average proportion of tail-wagging than used above. We based the average proportion on the entire sequence of approaches rather than on individual approaches. We did so because if signals are directed toward related conspecifics, then the additional benefit of a second signal may not exceed its additional cost, and may not be given. The proportion of at least one signal being given during a sequence was 0.65. Therefore, the probability that at least one lizard would signal when two occurred together was 0.88. If zebra-tailed lizards use tail-wagging to warn conspecifics, we expected to find a proportion  $>0.88$ .

**Result**—At least one of the two lizards present wagged its tail in 9 of 14 such observations, or  $p = 0.64$ . The 95% confidence limits for this proportion (using  $F$  statistics) were 0.35–0.87, below the expected values. Thus, it appears that the lizards do not tail-wag more often in the presence of conspecifics, and may even signal less frequently. However, if instead of 0.65 we use our standard average proportion, 0.60 (and the relevant proportion can be somewhere between the

two), the probability that at least one lizard should signal becomes  $>0.84$ , which is within the confidence limits (i.e., the parametric proportion of tail-wagging may be above the expectation). Therefore, although our result suggests that tail-wagging is not aimed at conspecifics, it is not conclusive: the statistical conclusion depends on our initial assumption. Nevertheless, the conclusion of test 4, that tail-wagging is probably not important as an intraspecific warning signal, is further supported by the following arguments. (i) The average probability of having two lizards in visual contact (i.e., within a bare patch) was between 0.042 and 0.183 (the first was calculated by measuring lizard density and the average patch size, and computing this probability by assuming a Poisson distribution of lizards among patches; the second is the observed proportion, which could have been artificially higher because the lizards escaped from one clearing to another as a result of our approach). Therefore, the proportion of recipients within sight is low. (ii) The occurrence of tail wagging of the zebra-tailed lizard is a function of risk (see tests of pursuit deterrent function below), and is, therefore, probably not cost-free. (iii) In spite of the first two arguments, the proportion of signaling was high (between 0.60 and 0.65), implying that tail-wagging has evolved for reasons other than to warn conspecifics. This can be illustrated with a numerical example: if the probability of having a recipient within a warning signal range is about 0.20 (which is probably an overestimate), and the probability of detecting a potential recipient that is found there is about 0.80 (which is probably an underestimate), a proportion of signaling as high as 0.60 would be achieved only if the inclusive fitness benefits (taking into account relatedness, probability of receiving given warning signals, and net benefit to recipients) exceed costs in 54% of all encounters of prey with predators (using equations in Hasson, see footnote 4). Because tests of the pursuit deterrent hypothesis suggest that the perceived cost is not exceptionally low, this seems unlikely.

#### Pursuit deterrent

The assumption that pursuit deterrent signals are divided into signals of REA (that include a component of risk) and signals of alertness enables us to produce useful predictions. Here we tested some of them.

#### Test 5

**Prediction**—Although the zebra-tailed lizard is very fast, some of its predators may be faster. In addition, being an ectotherm, it probably cannot long outrun a bird (e.g., a roadrunner) or a mammal (e.g., a coyote), and therefore uses its high burst speed to reach a hiding place. Our observations confirmed that the lizards seek refuge in or behind the vegetation rather than in the open. Therefore, assuming that risk of capture is a positive function of distance from cover, we predict that the proportion of signaling is negatively correlated with distance from cover.

**Result**—When the distance between prey and cover exceeded 2–2.5 m, the proportion of tail-wagging decreased considerably (Fig. 2). The detailed pattern, however, appears to be more complex. A dramatic decline in the proportion of signaling appeared also at distances less than 50 cm from cover. This pattern fits the RIA's risk-optimizing hypothesis and is discussed further below.

#### Test 6

**Prediction**—Assuming that a positive correlation exists between body temperature of the zebra-tailed lizard and

<sup>4</sup>Hasson, O. The effect of uncertainty on the relationship between the frequency of warning signals and prey density. Manuscript submitted for publication.

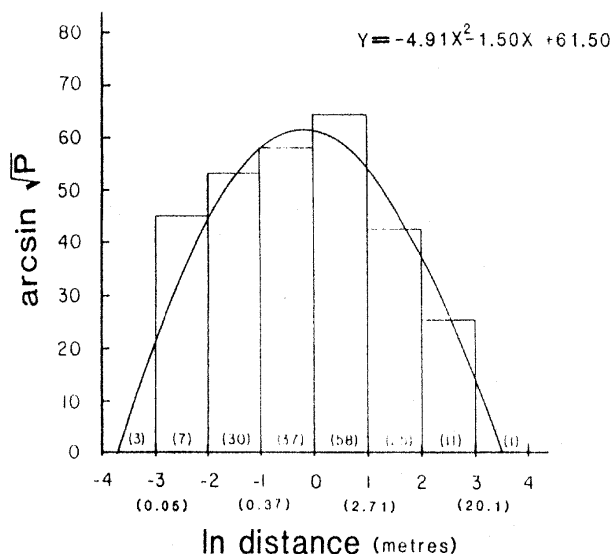


FIG. 2. The arc sine square root transformation of the proportion of tail-wagging ( $P$ ) plotted against the natural logarithm of distance from cover. SPSS multiregression test was used to fit the curve. See discussion in text for explanation. The numbers of observations are given in parentheses above the horizontal axis, and the distances in metres that correspond to the logarithmic scale are found in parentheses below.

ground surface temperature (throughout the study, the air temperature was lower than the lizard's optimal body temperature), and assuming further that running performance is positively correlated with body temperature (as long as body temperature is lower than optimal body temperature; for references, see Huey 1982), we expect that a lizard's escape ability improves with increasing ground temperature. This association between ground temperature and a lizard's performance can be supported by the general activity pattern of the lizards. Walking transects of  $400 \times 10$  m (the same observer walked through the same transect at a constant traveling rate every 30 min) showed a positive correlation between the number of lizards observed and ground temperature ( $n = 16$ ,  $r = 0.8465$ ,  $p < 0.001$ ). Because high ground temperatures increased the lizards' general activity (probably by increasing their body temperature), and is likely to improve their REA as well, we predict that lizards tail-wag more often as the ground temperature increases. The procedure of this test, however, created the following bias: on occasion, particularly in the early morning (i.e., at lower temperatures), when we first observed a lizard, it was already fleeing. In such cases we did not know the preflight behavior, and these observations were not recorded. While running the diurnal activity transects we observed that significantly more lizards fled when ground temperature was below  $38^\circ\text{C}$  (27 out of 33) than when it was above  $40^\circ\text{C}$  (49 out of 87) ( $p = 0.016$ , two-tailed Fisher exact test), demonstrating this bias. The bias, however, should weaken our test because the proportion of signalers would be artificially increased at lower temperatures (as we were more likely to record stationary lizards than fleeing lizards).

**Result**—The proportion of tail-wagging significantly increased with ground temperature (Table 1).

*Test 7*

**Prediction**—In situations of high predatory risk, REA becomes, by definition, low. As a result, the optimal risk at which prey should display decreases, and prey become less

TABLE 1. The proportion of tail-wagging of the zebra-tailed lizard in relation to ground temperature

Temperature range ( $^\circ\text{C}$ )	Proportion of lizards signalling
25–30	0.5 (2)
30–35	0.25 (16)
35–40	0.47 (59)
40–45	0.82 (17)
45–50	0.83 (6)

NOTE: The number of observations for each temperature range is given in parentheses. The first two rows were pooled for the statistical test because of small sample sizes. There was a significant difference in the proportion of tail-wagging as a result of the changing temperature ( $\chi^2 = 12.47$ ,  $0.025 > p > 0.01$  ( $df = 3$ )).

prone to signal their REA. Throwing objects at the lizards appeared to increase the lizards' perceived risk (see procedure of test 3). Here, the procedure of test 3 produced a prediction opposite to that of test 3: according to the pursuit deterrent hypothesis, the proportion of signaling should be lower than the average proportion of tail-wagging when objects are thrown at the lizards.

**Result**—All of the lizards ( $n = 15$ ) held their tail down while escaping under conditions of increased risk; this proportion of signalling was significantly lower than the average proportion of tail-wagging, 0.60 ( $p \ll 0.001$ , one-tailed Fisher exact test). Thirteen lizards of the 15 tested did raise their tail before the treatment.

*Test 8*

**Prediction**—When a camouflaged prey estimates that it may not have been detected by the predator, and that the predator may soon leave if it does not detect any prey, it should stay motionless as long as the risk and the cost of waiting are low (see also Ydenberg and Dill 1986). When it moves it should signal to demonstrate its alertness, since its movement increases the probability of being detected by the predator. The prediction is that a lizard should remain motionless for a while, and then signal and move (or move and signal).

**Procedure**—Once a resting lizard was spotted at close range (i.e., when we appeared from behind a shrub or a mound of sand; in such cases the lizards always spotted us at approximately the same time as we spotted them), we waited motionless until it moved.

**Result**—On six occasions, when the observer stood still a few metres away from the lizard, the lizard waited motionless for a while (mean 3 min, 12 s, range 16 s to 5 min, 36 s) before it moved, and invariably, signaled. Three more observations in which the observer stood still after prior treatment also ended with signaling, resulting in a proportion of 1.0 ( $n = 9$ ), significantly higher than the average proportion, 0.60 ( $p = 0.028$ , one-tailed Fisher exact test). The behavior of an additional lizard observed in Puerto Peñasco was similar, as it waited nearly 5 min before it moved and signaled.

**Discussion**

Our results strongly support predictions of the pursuit deterrent hypothesis for tail-wagging in the zebra-tailed lizard. In contrast, none of the alternatives tested here were supported.

Furthermore, some observed patterns could not be explained by any of the alternative hypotheses but are consistent with the pursuit deterrent hypothesis.

A greater tendency to display a pursuit deterrent signal at intermediate distances from cover (Fig. 2) is not unique to the zebra-tailed lizard. A similar pattern is exhibited by the eastern swamphen, *Porphyrio porphyrio*. Close to cover, it tends to take refuge there rather than signal (Woodland et al. 1980). Similarly, the flight distance (i.e., the distance of the prey from the predator at the initiation of flight) of the grey squirrel, *Sciurus carolinensis*, when approached by a stuffed motorized cat, was shorter at intermediate distances from cover. The squirrel's alertness was demonstrated by its standing and staring (i.e., directing its facial symmetry) at the approaching cat (Dill and Houtman 1989). The delayed flight observed at intermediate distances from cover can be a consequence of this pursuit deterrent signal.

In favor of the warning signal hypothesis, benefit to recipients could decrease when the signaler is close to cover, because either the probability of seeing recipients or the probability that recipients will see signals is lower. This explanation may not apply to the gray squirrel because it did not produce any conspicuous warning signal (but nevertheless demonstrated alertness). Similarly, we doubt that this effect was significant in our system. Most of the open spaces between shrubs are completely visible even to lizards close to plant cover; perhaps more importantly, the cost of signaling probably decreases even faster than the probability that the signal will be visible to conspecifics. In contrast, the pursuit deterrent hypothesis provides an explanation that is inherent in the risk-optimizing nature of advertising REA (Nur and Hasson 1984). Close to cover, the distance between prey and predator must be shorter for prey to signal high REA because high REA is displayed by relatively high apparent risk. Consequently, as the average benefit of deterring predators decreases when the risk of signaling is low, prey should decrease their tendency to signal when they are close to cover (for the mathematical details of the optimization process, see the additive model of Nur and Hasson (1984) when the deterrence curve, as a function of distance from the predator, is shifted to the right, and therefore the tendency to display at a lower risk should decline; for a related verbal discussion see Zahavi's "model of inflation" in Zahavi (1981)).

The importance of the risk component in determining the occurrence of signals strongly supports the hypothesis that the lizards do advertise REA. Furthermore, alertness can be reliably advertised even when the animals are close to cover. If signaling frequency nevertheless decreases, it is probably a result of decreasing importance of REA only. Therefore, Fig. 2 strongly suggests that displaying REA is a major component in pursuit deterrent signals of the zebra-tailed lizard.

Nevertheless, our observations qualitatively suggest that the zebra-tailed lizard also advertises alertness as an independent signal, in the reliable, noncostly way of prey movement as a reaction to predator movement. We observed this kind of behavior after we threw objects at the lizards. In doing so we were probably assessed as faster, more dangerous predators. After fleeing, the lizard reemerged from the shrub, signaling intensively and, upon our first movement, fled back to the shrub and then reemerged again (it was interesting to notice that upon reemergence from cover, the lizards ignored the object thrown and focused their attention on the observer only).

A third behavioral pattern that is difficult to interpret by the other hypotheses but is readily understood in terms of prey-predator signals, is the way lizards delayed tail-wagging when we suddenly appeared at close quarters to the lizards but remained motionless thereafter. During these observations we did not make any movement to suggest that lizard location was known to us. Therefore, their tail-wagging immediately before or after their own movement revealed them to the "predator's" eyes, supporting the hypothesis that the relevant interaction is signaler to predator rather than signaler to conspecifics.

Interestingly, populations of the zebra-tailed lizard on some small islands in the Gulf of California, where predation pressure is much relaxed, do not wag their tails (C. H. Lowe, Department of Ecology and Evolutionary Biology, The University of Arizona, Tucson, personal communication). In contrast, casual observations at the Santa Rita Experimental Station, at Saguaro National Monument in Arizona, and at Death Valley National Monument in California suggest that tail-wagging is much more frequent than it was at our study area (even though lizard densities are significantly lower). Since flight distance in those areas is significantly greater, these observations also suggest that predation pressure is an important factor in the evolution of this behavior.

Although sample sizes were sufficient for the statistical conclusions, some of them were relatively small. Nevertheless, because various aspects of the pursuit deterrent hypothesis are supported, and most are very specific, the general conclusion of the study is robust. The conspicuous tail-wagging of the zebra-tailed lizard in the presence of predators seems to have evolved to deter predator pursuit by advertising both alertness and REA.

Daanje (1951) includes under the label of "intention movements" many nonextravagant movements (at least in the predator-prey context) which, as a result, have been otherwise overlooked by behaviorists, and no other interpretation was assigned to them. We suspect that many of these behavioral patterns, extravagant or discreet, are actually part of prey-predator communication, and that pursuit deterrent signals are common. Further study is required, however, especially on the response of natural predators (e.g., Caro 1986).

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