

Signalling displays during predator–prey interactions in a Puerto Rican anole, *Anolis cristatellus*

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Abstract. We examined conspicuous signalling displays in the context of predator–prey interactions. To determine in which context Puerto Rican crested anoles, *Anolis cristatellus*, perform conspicuous signals, we exposed wild lizards to a model of a natural snake predator. The lizards gave six behavioural responses to the model: immobility, predator inspection, flight, lateral face-off, dewlapping and push-ups. They displayed significantly more push-ups and push-up bouts in the presence of the snake model. Alternative theories regarding the function of conspicuous signals in *A. cristatellus*, the flash concealment and predator deterrent hypotheses, were also tested. The flash concealment hypothesis proposes that the sudden display exhibition of signalling behaviour followed by the flight of the animal may confuse the predator about the position of the prey, thus causing the predator to abort the attack. The pursuit deterrent hypothesis contends that because the chances of the predator successfully attacking its prey decrease when the prey is aware of the incoming predator, prey have evolved signalling behaviours that communicate to the predator that it has been detected, therefore discouraging the attack. Results supported the use of push-ups, dewlapping, lateral face-off and predator inspection as predator deterrent signals. During the recognition phase of a predatory encounter, *A. cristatellus* may rely more on behavioural signals than on flight to avoid predation. Because the predator deterrent signals are the same as the signals used in social interactions, it is suggested that predation pressure may have reinforced the effects of sexual selection in the evolution of *Anolis* signalling displays.

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A signal is an organismal attribute that transmits information from one individual to another at the intra- or interspecific level (Zahavi 1987). Scenarios to explain the evolution of conspicuous signalling displays by males typically involve processes in which the signals are used during social interactions, thus usually implying the action of sexual selection (Ryan 1994). None the less, mounting evidence supports the alternative hypothesis that conspicuous signals can also evolve for communication between predators and their prey (Hasson 1991; Caro 1995).

During any encounter between a predator and its prey, information is necessarily transferred

between them in the form of signals (e.g. visual, auditory, chemical), which ultimately alters the probabilities of their respective actions (Hasson 1991) and consequently the outcome of the encounter. Two main hypotheses may explain the evolution of conspicuous signals due to predator–prey interactions (Hasson et al. 1989). The flash concealment hypothesis proposes that the sudden display of signalling behaviour followed by the flight of the animal may confuse the predator about the position of the prey, therefore causing the predator to abort the attack. The pursuit deterrent hypothesis contends that because the chances of the predator successfully attacking its prey decrease when the prey is aware of the incoming predator, prey have evolved signalling behaviours that communicate to the predator that it has been detected, therefore discouraging the attack.

Most examples of the use of conspicuous signals in predator–prey interactions involve

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mammals, particularly ungulates (Caro 1994), but such behaviours have also been reported in fish (Pitcher 1992; Godin & Davis 1995), amphibians (Brodie 1977, 1978) and reptiles (Dial 1986; Hasson et al. 1989), including birds (Kruuk 1976; Curio 1978; Götmark 1992, 1995). Two basic approaches have been used to investigate the evolution of signalling displays. The first and most frequent kind of data show that conspicuous signals are given in the presence of a potential predator (in most cases an approaching human), and that these signals are not directed toward conspecifics (Caro 1995). Although these studies are informative, prey exposed to non-natural predators may respond by displaying behaviours not commonly given during predatory encounters (Hirsch & Bolles 1980; Greene 1988; Lima & Dill 1990; Caro 1995). Furthermore, when the potential predator is a species that is not encountered in nature, such studies cannot address the response of an actual predator to the display. Even when unrealistic models of natural predators are used, variation in the prey's behavioural responses can occur depending on subtle differences in cues, such as the presence or absence of predator's eyes (Burghardt & Greene 1988) or the size of the predator's eyes (Burger et al. 1991). The second and preferred type of evidence shows how animals display toward natural predators. Such observations are rare and so far are available only for fish (Godin & Davis 1995) and mammals (Caro 1986; FitzGibbon & Fanshawe 1988; Holley 1993).

Anolis comprises a diverse group of neotropical, polychrotid iguanian lizards that are behaviourally characterized by complex display repertoires. These behaviours consist mainly of visual signals that can be divided into two main categories, according to the degree of movement along the Y-axis of the part(s) of the lizard's body involved in producing the display: low-amplitude and high-amplitude signals (Jenssen 1978; Fleishman 1988). During social interactions in anoles and other iguanians, head-bobbing (head movements up and down in a vertical plane) is the dominant low-amplitude display, and push-ups (body movements up and down in a vertical plane, performed by flexion and extension of the legs) and dewlapping (extension and contraction of the throat fan, dewlap, in a vertical axis) are the most commonly observed high-amplitude signals (Jenssen 1977; Carpenter 1978; Martins 1993).

Anoles rely almost exclusively on visual cues for social communication and the detection of potential predators (Underwood 1970; Fleishman 1992). Although social interactions have been considered the main selective force in the evolution of signals in *Anolis* (Crews 1975; Jenssen 1977), some anoles give conspicuous displays in the presence of a predator when conspecifics are absent (Leal & Rodríguez-Robles 1995, in press), implying that predation pressure may have also contributed to the evolution of these signals.

The flash concealment hypothesis predicts that an anole should not perform any signalling display while it is motionless, but should do so while it flees (or immediately before fleeing) from a predator. The pursuit deterrent hypothesis predicts the opposite: that an anole should perform signalling displays while stationary, but should not do so while it flees (or immediately before fleeing) from a predator. Based on these predictions, our goal was to examine the context in which wild Puerto Rican crested anoles, *A. cristatellus*, give conspicuous signals while being approached by a model of their natural snake predator, *Alsophis portoricensis* (Rodríguez-Robles & Leal 1993). We also compared the displays elicited by the snake model to those given by *A. cristatellus* when facing living *Alsophis* in laboratory enclosures (Leal & Rodríguez-Robles 1995).

METHODS

We induced predator-prey encounters between a model *Alsophis portoricensis* and 35 adult male *A. cristatellus* at the Cambalache Forest Reserve, Barrio Garrochales, Arecibo, Puerto Rico, where both species occur sympatrically. *Anolis cristatellus* is a medium-large (snout-vent length=56–76 mm), grey-brown, sexually dimorphic, tree trunk and ground anole (Rand 1964a; Williams 1983) that occurs in mesic-xeric areas. On Puerto Rico, it is common in open forests and fields from sea level to mid-elevation. The *A. cristatellus* used in this study had a mean \pm SE snout-vent length of 50.5 ± 0.9 mm (range=42–60 mm, $N=28$) and a body mass of 4.4 ± 0.3 g (range=2.6–7.8 g, $N=28$). Anole body mass was linearly related to snout-vent length ($r^2=0.91$, $t_{26}=16.1$, $P<0.0001$). The colubrid *Alsophis portoricensis* (maximum snout-vent length=923 mm) is largely a ground-dwelling, diurnal, active forager (Henderson &

Sajdak 1986) that preys primarily on reptiles, mostly anoles (Rodríguez-Robles & Leal 1993; Henderson & Sajdak 1996).

We conducted trials from 6 to 19 June 1995 during the daytime (1000–1500 hours), when both *A. cristatellus* and *Alsophis* are active. Only lizards perching in the normal, alert, head-down posture within 1.3 m of the ground were tested. Each episode consisted of presenting a single, previously untested and undisturbed lizard with an intact, stuffed skin of an *A. portoricensis* collected at Cambalache. Models of natural predators are effective in eliciting responses from prey species (e.g. Mueller & Parker 1980; Magurran & Girling 1986; Jennions & Backwell 1992; Yasukawa et al. 1992; Moore 1994). The snake model (snout–vent length=64 cm, tail length=27 cm) was fashioned such that its anterior end (11 cm) was raised 9 cm off the ground to simulate the foraging pose of *Alsophis*. We used transparent fishing line to fasten the anterior 18 cm of the stuffed snake to a 15.2 × 16.2 cm Plexiglas stand. The posterior 73 cm of the model had a sinuous shape that remained in contact with the ground.

Using a stop-watch and an audio tape recorder, we recorded all behavioural acts performed by the lizard 5 min before ('control period') and 5 min after ('experimental period') we started moving the snake model toward the anole. We positioned the model 4–8 m from the base of the lizard's perch (depending on the physiography of the surrounding area) and in such a way that it was unlikely that the anole could see it before we began moving it. To account for any disturbance that we may have caused to the anole while setting up the snake model, we started the control observations after we had positioned the model and ourselves in relation to the subject lizard. During the experimental period, one of us (M.L.), from behind the tree where the lizard was perching and using a transparent fishing line attached to the Plexiglas stand, pulled the snake model by hand toward the anole at approximately 7 cm/s until it reached the base of the tree where the *A. cristatellus* was perched, where the model was left until the end of the trial. Meanwhile, J.A.R.-R. watched the anole from a partially concealed (by the surrounding vegetation) position 4–5 m in front of the lizard's perch. Once during each trial we stopped pulling the snake toward the base of the anole's perch for up to 5 s, in an attempt to mimic the foraging behaviour of

Alsophis portoricensis. We deleted from the study anoles whose behaviour during the control or experimental periods was apparently affected by the presence of neighbouring lizards. In preliminary trials ($N=5$) in which we pulled the Plexiglas stand without the snake model toward anoles, the lizards did not show any behaviour that was apparently directed at the stand.

We followed the behavioural descriptions of Jenssen (1977, 1978) and Greene (1988) to categorize the behavioural acts exhibited by *A. cristatellus*. We recorded the duration and number of iterations of each lizard's behaviour. We considered displays of identical behaviour patterns (i.e. dewlapping, push-ups) separated by 30 s or more as belonging to different bouts (L. J. Fleishman, personal communication). Whenever possible (28 of 35 times), we caught the subject after the trial to measure (snout–vent length \pm 1 mm), weigh (\pm 0.2 g) and mark it (with Pentel correction liquid) to avoid repeated testing of the same individual. To minimize the chances of retesting subjects that escaped capture, we used only anoles that were at least 150 m apart and changed localities within the forest each day. Except when otherwise indicated, significance probabilities are one-tailed because our a priori prediction was that the frequency of signalling behaviour of *Anolis* would increase after exposing the lizard to the snake model.

RESULTS

Anolis cristatellus displayed six behaviours during the experimental period: remaining still for at least 120 s while looking toward the snake model (immobility), movement toward the predator (predator inspection), movement at least 30 cm away (e.g. up the tree) from the snake model (flight), positioning of the body perpendicularly to the predator (lateral face-off), dewlapping and push-ups. Anoles flexed either two (two-legged push-ups) or four (four-legged push-ups) legs during the push-up displays.

The behavioural responses of *Anolis cristatellus* during the experimental period can be grouped into three main classes: non-signalling displays (immobility, flight), conspicuous signalling displays (push-ups, dewlapping, lateral face-off), and predator inspection. Before the snake model reached the base of the lizard's perch, the most

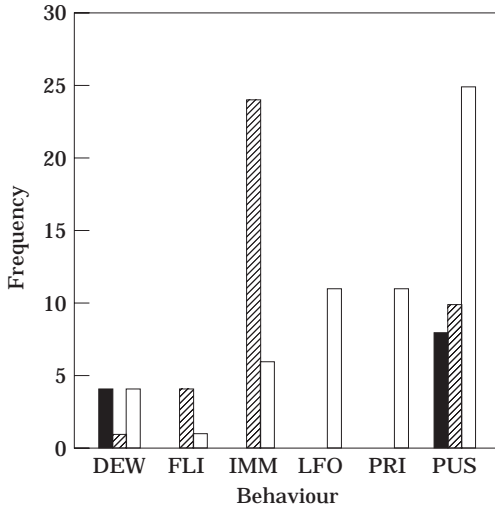


Figure 1. Frequency of *Anolis cristatellus* that gave behaviour patterns during control (■) and experimental periods [before (▨) and after (□) the snake model reached the base of the *Anolis*' perch]. Because the display of the different behavioural patterns is not exclusive, frequencies do not have to add up to 100. DEW: dewlapping; FLI: flight; IMM: immobility; LFO: lateral face-off; PRI: predator inspection; PUS: push-ups.

common behaviour presented by *A. cristatellus* was immobility. The anoles usually turned their head toward the approaching snake while remaining in the same position until the model reached the base of their perch. The anoles then showed either one or a combination of flight, immobility, dewlapping, lateral face-off, push-ups and predator inspection (Fig. 1). In 11 of 35 (31%) of the trials in this study, *A. cristatellus* approached the snake using a series of short, 'jerky' jumps that were interrupted by dewlapping or push-up displays.

Anoles performed significantly more push-ups during the experimental than during the control period (Wilcoxon's signed-ranks test: $T=4.34$, $N=27$, $P<0.0001$), but there was no difference in the frequency of dewlapping between the two periods ($T=0.42$, $N=8$, $P=0.32$). The number of push-up bouts was significantly higher during the experimental than during the control period ($T=4.52$, $N=26$, $P<0.0001$), but the number of dewlapping bouts was not ($T=0.21$, $N=8$, $P=0.42$). During the experimental period, push-up bouts were more frequent after the snake

model reached the base of *A. cristatellus*' perch than during the time the snake was approaching it ($T=3.14$, $N=17$, $P=0.0008$).

Only one lizard fled immediately (within 2 s) after performing push-ups, but 25 performed push-ups while remaining stationary. The ratio of 1:25 is not significantly different from the predicted 0:26 by the pursuit deterrent hypothesis (two-tailed Fisher's exact test of independence: $P=1.0$), suggesting that push-ups that were performed during the experimental period served as a pursuit deterrent signal. Four lizards dewlapped while remaining immobile and none dewlapped while fleeing. The ratio of 4:0 is identical to that predicted by the pursuit deterrent hypothesis, indicating that when dewlapping was performed during the experimental period, it served as a pursuit deterrent signal in *A. cristatellus*. Similarly, one lizard fled after displaying lateral face-off and 10 remained still. The ratio of 1:10 is not statistically different from the theoretical 0:11 (two-tailed Fisher's exact test of independence: $P=1.0$), suggesting that lateral face-off is also a pursuit deterrent signal of *A. cristatellus*.

DISCUSSION

The results of our field study support the prediction of the predator deterrent hypothesis: *Anolis cristatellus* performed push-ups, dewlapping and lateral face-off while remaining stationary or, in the case of push-ups and dewlapping, in combination with predator inspection. Except for lateral face-off, all the predator deterrent signals given by *A. cristatellus* during the experimental period were high-amplitude displays. The absence of low-amplitude displays (i.e. head-bobbing) indicates that *A. cristatellus* is only using a subset of its display repertoire as predator deterrent signals. High-amplitude displays may be more efficient than low-amplitude displays in eliciting the predator's attention. If true, predation pressure may have selected for the preferential use of high-amplitude displays during predator-prey communication.

Some differences between the responses of *A. cristatellus* during the experimental period of this study and those observed during laboratory predatory trials of another study (Leal & Rodríguez-Robles 1995) need to be addressed.

First, *A. cristatellus* had a greater diversity of anti-predator behaviours in the field than before being attacked by living *Alsophis portoricensis* in the laboratory, where anoles showed only immobility, dewlapping and crouching (body is flattened against the substrate). During laboratory trials, anoles were never more than 50 cm away from the snakes, but in the field this distance was never less than 1 m. The distance to the predator can limit the prey's use of predator deterrent signals (Hasson 1991). Thus, the anoles' limited behavioural diversity in the laboratory before being attacked by the snakes may have been a consequence of conducting these trials in relatively small cages. Second, anoles never showed predator inspection behaviour during laboratory trials, but in the field, predator inspection was one of the three most common signalling displays performed. The absence of predator inspection in the laboratory perhaps was related to the unavailability of vertical perches for the anoles in the bare cages where the trials were carried out.

During our laboratory studies of anti-predator responses of *A. cristatellus* (Leal & Rodríguez-Robles 1995), we interpreted push-ups, dewlapping and lateral face-off as bluffing behaviour. Bluffing displays are performed by prey to intimidate potential predators, but they do not result in injury to predators that attack the prey (Greene 1988). None the less, results of our field trials imply that these behaviours may serve both as bluffs and as predator deterrent signals. Whether push-ups, dewlapping and lateral face-off behaviour are used as bluffs or as signalling displays, their function seems to be the same; prevention of predatory attacks.

Immobility was the most common behaviour displayed by *A. cristatellus* before the snake model reached the base of the lizard's perch. By staying immobile, anoles may be able to escape detection by *Alsophis*. This is suggested by the cryptic coloration of *A. cristatellus* (Heatwole 1968) and the fact that *Alsophis portoricensis* relies mainly on visual stimuli to localize its prey (Leal & Thomas 1994), and thus usually does not attack anoles until they move (Rodríguez-Robles 1992).

Anolis cristatellus performed significantly more push-up displays after being exposed to the snake model than during control observations, which suggests that push-ups were given in response to the presence of the snake. Push-ups may function as a signal that indicates to the

predator that it has been detected, therefore eliminating the surprise factor of the attack (Smythe 1970). In this sense, push-ups are analogous to tail-display behaviour in the phrynosomatid lizards *Cophosaurus texanus* and *Holbrookia propinqua*, which also use tail-display for signalling to a predator (Dial 1986; Hasson et al. 1989). *Anolis cristatellus* performed two different push-up displays, distinguished by the number of legs flexed and extended. During control observations, anoles mostly used only their front legs during the display, but in the presence of the snake model, lizards usually used all four legs. In social interactions in polychrotid and phrynosomatid lizards, this difference in the structural pattern of push-ups is related to the intensity or aggressiveness of the interaction (Jenssen 1977; Martins 1993), with anoles using four-legged push-ups during highly aggressive inter-male encounters (Ortiz & Jenssen 1982; Losos 1985). Because a predator can infer that it has been detected by the degree of alertness shown by the prey (Hasson 1991), four-legged push-ups may be more effective than two-legged push-ups in communicating to the snake that it has been detected.

Push-up bouts were significantly more frequent after the model reached the base of the anole's perch than during the time the snake was approaching it. The distance at which the prey starts signalling to a predator is related to the prey's escape ability; the better the escaping abilities of the prey, the shorter this distance is (Woodland et al. 1980; Caro 1986; Hasson 1991). *Anolis cristatellus* is a scansorial lizard with morphological adaptations for effective locomotion on tree trunks (i.e. the subdigital adhesive pads; Collette 1961; Irschick et al. 1996); *Alsophis portoricensis* is a heavier and largely ground-dwelling species (Henderson & Sajdak 1986). This difference in body mass and habitat use suggests that *Anolis* is probably able to escape up a tree faster than *Alsophis* can climb it, which, when the anole is perching on tree trunks, should select for signalling to an approaching predator at shorter distances.

Approaching the predator is an effective predator deterrent signal in fish (Pitcher 1992; Godin & Davis 1995), and it is thought to be used by some mammals and birds as well (Kruuk 1976; Hirsch & Bolles 1980). Eleven *A. cristatellus* approached the snake model using a series of

jerky jumps. Displays performed in a jerky fashion are designed to exaggerate the amplitude of the display, which enables the prey to elicit the predator's attention faster and in a more effective way (Fleishman 1992). Moving toward the snake in a jerky pattern while performing dewlapping or push-ups supports the use of dewlapping and push-ups as predator deterrent signals. In addition to communicating to the snake that it has been detected, predator inspection may also enable *A. cristatellus* to assess the risk of being attacked by *Alsophis*.

Field studies of anti-predator responses in *Anolis* have emphasized the study of flight as the main escape tactic of anoles (Rand 1964b; Heatwole 1968; Losos & Irschick 1996). In all of these studies (as in almost all studies of anti-predator behaviour in reptiles; Greene 1988), the responses to an approaching human predator were extrapolated to a natural predator. Our findings indicate that, at least in *A. cristatellus*, flight is only rarely used as an anti-predator response during the recognition phase of a predatory encounter (i.e. before the predator's attack), but that push-ups, dewlapping and lateral face-off are effective in delaying or even preventing further capture attempts by living *Alsophis portoricensis* in both the laboratory (Leal & Rodríguez-Robles 1995) and in the wild. If the anti-predator responses of *A. cristatellus*, which are similar to those of *A. cuvieri* (Leal & Rodríguez-Robles, in press), are also given by other species of anoles, *Anolis* may rely more on behavioural signals than on flight to avoid predation.

Studies on *Anolis* and other reptiles have focused on social interactions as the main selective force in the evolution of conspicuous signals (Crews 1975; Jenssen 1977), but the results of the present study and of recent laboratory and field observations (Leal & Rodríguez-Robles 1995, in press) demonstrate that *Anolis* uses conspicuous signals as anti-predator mechanisms. Because anoles use push-ups, dewlapping and lateral face-off to deter predators as well as in courtship (Jenssen 1977; Leal & Rodríguez-Robles 1995), we propose that predation pressure may have reinforced the effects of sexual selection in the evolution of these signalling displays. If this suggestion is correct, the theoretical models (Crews 1975; Jenssen 1977) for the evolution of conspicuous signals in *Anolis* should be revised.

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REFERENCES

- Brodie, E. D., Jr. 1977. Salamander antipredator postures. *Copeia*, **1977**, 523–535.
- Brodie, E. D., Jr. 1978. Biting and vocalization as antipredator mechanisms in terrestrial salamanders. *Copeia*, **1978**, 127–129.
- Burger, J., Gochfeld, M. & Murray, B. G., Jr. 1991. Role of a predator's eye size in risk perception by basking black iguana, *Ctenosaura similis*. *Anim. Behav.*, **42**, 471–476.
- Burghardt, G. C. & Greene, H. W. 1988. Predator simulation and duration of death feigning in neonate hognose snakes. *Anim. Behav.*, **36**, 1842–1843.
- Caro, T. M. 1986. The functions of stotting in Thomson's gazelles: some tests of the prediction. *Anim. Behav.*, **34**, 663–684.
- Caro, T. M. 1994. Ungulate antipredator behaviour: preliminary and comparative data from African bovines. *Behaviour*, **128**, 189–228.
- Caro, T. M. 1995. Pursuit-deterrence revisited. *Trends Ecol. Evol.*, **10**, 500–503.
- Carpenter, C. C. 1978. Ritualistic social behavior in lizards. In: *Behavior and Neurology of Lizards* (Ed. by N. Greenberg & P. D. MacLean), pp. 253–267. Maryland: National Institute of Mental Health.
- Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bull. Mus. comp. Zool.*, **125**, 137–162.
- Crews, D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. *Anim. Behav.*, **23**, 349–356.
- Curio, E. B. 1978. The adaptive significance of avian mobbing. *Z. Tierpsychol.*, **48**, 175–183.
- Dial, B. E. 1986. Tail display in two species of iguanid lizards: a test of the 'predator signal' hypothesis. *Am. Nat.*, **127**, 103–111.
- FitzGibbon, C. D. & Fanshawe, J. H. 1988. Stotting in Thomson's gazelles: an honest signal of condition. *Behav. Ecol. Sociobiol.*, **23**, 69–74.
- Fleishman, L. J. 1988. Sensory influences on physical design of a visual display. *Anim. Behav.*, **36**, 1420–1424.

- Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.*, **139**, 36–61.
- Godin, J.-G. J. & Davis, S. A. 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proc. R. Soc. Lond. Ser. B*, **259**, 193–200.
- Götmark, F. 1992. Anti-predator effect of conspicuous plumage in a male bird. *Anim. Behav.*, **44**, 51–55.
- Götmark, F. 1995. Black-and-white plumage in male pied flycatchers (*Ficedula hypoleuca*) reduces the risk of predation from sparrowhawks (*Accipiter nisus*) during the breeding season. *Behav. Ecol.*, **6**, 22–26.
- Greene, H. W. 1988. Antipredator mechanisms in reptiles. In: *Biology of the Reptilia, Vol. 16, Ecology B, Defense and Life History* (Ed. by C. Gans & R. B. Huey), pp. 1–152. New York: Alan R. Liss.
- Hasson, O. 1991. Pursuit-deterrent signals: communication between prey and predator. *Trends Ecol. Evol.*, **6**, 325–329.
- Hasson, O., Hibbard, R. & Ceballos, G. 1989. The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.*, **67**, 1205–1209.
- Heatwole, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. *Copeia*, **1968**, 109–113.
- Henderson, R. W. & Sajdak, R. A. 1986. West Indian racers: a disappearing act or a second chance? *Lore*, **36**, 13–18.
- Henderson, R. W. & Sajdak, R. A. 1996. Diets of West Indian racers (Colubridae: Alsophis): composition and biogeographic implications. In: *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz, Contributions to Herpetology, Vol. 12* (Ed. by R. Powell & R. W. Henderson), pp. 327–338. Ithaca, New York: Society for the Study of Amphibians and Reptiles.
- Hirsch, S. M. & Bolles, R. C. 1980. On the ability of prey to recognize predators. *Z. Tierpsychol.*, **54**, 71–84.
- Holley, A. J. 1993. Do brown hares signal to foxes? *Ethology*, **94**, 21–30.
- Irschick, D. J., Austin, C. C., Petren, K., Fisher, R. N., Losos, J. B. & Ellers, O. 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.*, **59**, 21–35.
- Jennions, M. D. & Backwell, P. R. Y. 1992. Chorus size influences on the anti-predator response of a Neotropical frog. *Anim. Behav.*, **44**, 990–992.
- Jenssen, T. A. 1977. Evolution of anoline display behavior. *Am. Zool.*, **17**, 203–215.
- Jenssen, T. A. 1978. Display diversity in anoline lizards and problems of interpretation. In: *Behavior and Neurology of Lizards* (Ed. by N. Greenberg & P. D. MacLean), pp. 269–285. Maryland: National Institute of Mental Health.
- Kruuk, H. 1976. The biological function of gulls' attraction towards predators. *Anim. Behav.*, **24**, 146–153.
- Leal, M. & Rodríguez-Robles, J. A. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia*, **1995**, 155–161.
- Leal, M. & Rodríguez-Robles, J. A. In press. Antipredator responses of the Puerto Rican giant anole, *Anolis cuvieri* (Squamata: Polychrotidae). *Biotropica*.
- Leal, M. & Thomas, R. 1994. Notes on the feeding behavior and caudal luring by juvenile *Alsophis portoricensis* (Serpentes: Colubridae). *J. Herpetol.*, **28**, 126–128.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**, 619–640.
- Losos, J. B. 1985. Male aggressive behavior in a pair of sympatric sibling species. *Breviora*, **484**, 1–30.
- Losos, J. B. & Irschick, D. J. 1996. The effect of perch diameter on escape behaviour of *Anolis lizards*: laboratory predictions and field tests. *Anim. Behav.*, **51**, 593–602.
- Magurran, A. E. & Girling, S. L. 1986. Predator model recognition and response habituation in shoaling minnows. *Anim. Behav.*, **34**, 510–518.
- Martins, E. P. 1993. Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Anim. Behav.*, **45**, 25–36.
- Moore, F. R. 1994. Resumption of feeding under risk of predation: effect of migratory condition. *Anim. Behav.*, **48**, 975–977.
- Mueller, H. C. & Parker, P. G. 1980. Naive ducklings show different cardiac response to hawk than to goose models. *Behaviour*, **74**, 101–113.
- Ortiz, P. R. & Jenssen, T. A. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Z. Tierpsychol.*, **60**, 227–238.
- Pitcher, T. 1992. Who dares wins: the function and evolution of predator inspection behaviour in shoaling fish. *Netherlands J. Zool.*, **42**, 371–391.
- Rand, A. S. 1964a. Ecological distribution in anoline lizards of Puerto Rico. *Ecology*, **45**, 745–752.
- Rand, A. S. 1964b. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology*, **45**, 863–864.
- Rodríguez-Robles, J. A. 1992. Notes on the feeding behavior of the Puerto Rican racer, *Alsophis portoricensis* (Serpentes: Colubridae). *J. Herpetol.*, **26**, 100–102.
- Rodríguez-Robles, J. A. & Leal, M. 1993. Natural history notes: *Alsophis portoricensis* (Puerto Rican Racer). Diet. *Herpetol. Rev.*, **24**, 150–151.
- Ryan, M. J. 1994. Mechanisms underlying sexual selection. In: *Behavioral Mechanisms in Evolutionary Ecology* (Ed. by L. A. Real), pp. 190–215. Chicago: The University of Chicago Press.
- Smythe, N. 1970. On the existence of 'pursuit invitation' signals in mammals. *Am. Nat.*, **104**, 491–494.
- Underwood, G. 1970. The eye. In: *Biology of the Reptilia, Vol. 2, Morphology B* (Ed. by C. Gans & T. S. Parsons), pp. 1–97. New York: Academic Press.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In: *Lizard Ecology: Studies of a Model Organism* (Ed. by R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 326–370. Cambridge, Massachusetts: Harvard University Press.
- Woodland, D. J., Jaafar, Z. & Knight, M.-L. 1980. The 'pursuit deterrent' function of alarm signals. *Am. Nat.*, **115**, 748–753.

- Yasukawa, K., Whittenberger, L. K. & Nielsen, T. A. 1992. Anti-predator vigilance in the red-winged black-bird, *Agelaius phoeniceus*: do males act as sentinels? *Anim. Behav.*, **43**, 961–969.
- Zahavi, A. 1987. The theory of signal selection and some of its implications. In: *Proceedings of the International Symposium of Biological Evolution* (Ed. by V. P. Delfino), pp. 305–327. Bari: Adriatica Editrice.