

- FEENER, D. H., JR. AND B. V. BROWN. 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae), in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Ann. Entomol. Soc. Amer.* 85: 80–84.
- KERR, W. E., R. ZUCCHI, J. T. NAKADAI, AND J. E. BUTOLO. 1962. Reproduction in the social bees (Hymenoptera: Apidae). *J. New York Entomol. Soc.* 70: 265–276.
- ROUBIK, D. W. 1989. *Ecology and natural history of tropical bees*. Cambridge University Press, New York, New York.
- . 1990. Mate location and mate competition in males of stingless bees (Hymenoptera: Apidae: Meliponinae). *Entomol. Gener.* 15: 115–120.
- SAKAGAMI, S. 1982. Stingless bees. In H. R. Hermann (Ed.). *Social Insects*, pp. 360–423. Academic Press, New York & London.
- SCHWARZ, H. F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. *Bull. Am. Mus. Nat. Hist.* 90: 1–546.
- SIMÕES, D., L. R. BEGO, R. ZUCCHI, AND S. F. SAKAGAMI. 1980. *Melaloncha sinistra* Borgmeier, an endoparasitic phorid fly attacking *Nannotrigona* (*Scaptotrigona*) *postica* Latreille (Hymenoptera, Meliponinae). *Rev. Bras. Entomol.* 24: 137–142.
- SOMMEIJER, M. J. AND L. L. M. DE BRUIJN. 1995. Drone congregations apart from the nest in *Melipona favosa*. *Insectes Sociaux* 42: 123–127.
- THORNHILL, R. AND J. ALCOCK. 1983. *The evolution of insect mating systems*. Harvard University Press, Cambridge & London.

Brian V. Brown

Entomology Section
Natural History Museum of Los Angeles County
900 Exposition Boulevard
Los Angeles, California 90007, U.S.A.

BIOTROPICA 29(3): 372–375 1997

Antipredator Responses of the Puerto Rican Giant Anole, *Anolis cuvieri* (Squamata: Polychrotidae)¹

Key words: *Alsophis portoricensis*, *Anolis cuvieri*, antipredator responses, behavior, predator-prey interaction.

ANOLIS LIZARDS ARE THE most conspicuous, abundant, and diverse vertebrates inhabiting terrestrial ecosystems on islands of the West Indies (Williams 1969, 1983). Although considerable research has been conducted on the biology of *Anolis*, particularly on Caribbean islands (Schwartz & Henderson 1991, Losos 1994, Roughgarden 1995, and references therein), most aspects of the ecology and behavior of the giant species (>100 mm snout-vent length [SVL]; Williams 1983) are poorly known, including observations on signals transmitted between anoles and their predators. The only published report on predation on the infrequently encountered Puerto Rican giant anole, *Anolis cuvieri* Merrem, is that by Rand & Andrews (1975), who commented on the color pattern of juvenile lizards and its possible function in avoiding intraspecific predation by adults, but Gorman (1977) refuted this explanation and suggested that the dimorphism in color pattern of juvenile and adult *A. cuvieri* serves to avoid detection by visually-oriented predators in their respective habitats (juvenile *A. cuvieri* are largely terrestrial, but adults are mostly arboreal).

On Puerto Rico, snakes (Henderson & Crother 1989, Schwartz & Henderson 1991) and birds (Waide & Reagan 1983, Pérez-Rivera 1985, Santana & Temple 1988) are probably the principal natural vertebrate predators of *Anolis*. Although there are no reports of the colubrid snake *Alsophis portoricensis* preying upon *A. cuvieri*, the observations that *Alsophis* feeds on several species of *Anolis* (Rodríguez-Robles & Leal 1993) and that both juvenile and adult *A. cuvieri* forage on the ground (Gorman 1977, Pérez-Rivera 1985; M. Leal, pers. obs.) and are sympatric with *Alsophis portoricensis* suggest that *Alsophis* is a likely natural predator of *A. cuvieri*.

In June 1995, we induced predator-prey encounters between an *Alsophis portoricensis* stimulus and five adult *Anolis cuvieri* at the Cambalache Forest Reserve, Barrio Garrochales, Arecibo, Puerto Rico, a

¹ Received 28 July 1995; revision accepted 10 January 1996.

site where both species occur sympatrically. Each episode consisted of presenting a single, previously untested and undisturbed lizard with an intact, stuffed skin of an *Alsophis portoricensis* collected at Cam-balache. Several studies (e.g., Magurran & Girling 1986, Yasukawa *et al.* 1992, Moore 1994, Götmark 1995) have shown that model predators are effective in eliciting a response from prey species. Anoles have an excellent high-acuity, optical system very sensitive to motion and they rely on visual cues almost exclusively for detection of predators (Underwood 1970, Fleishman 1992).

The snake model (SVL=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 portoricensis*. 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 behavioral acts performed by the lizard 5 min before ("control period") and 5 min after ("experimental period") we started moving the snake model towards the anole. We positioned the model 4–8 m (depending on the physiography of the surrounding area) from the base of the lizard's perch 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, the senior author, from behind the tree where the lizard was perching and using the transparent fishing line attached to the Plexiglas stand, pulled the snake model by hand toward the anole at approximately 7 cm/sec 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, the junior author 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 sec, in an attempt to mimic the foraging behavior of *Alsophis portoricensis*. We followed the behavioral descriptions of Jenssen (1977, 1978) and Greene (1988) to categorize the behavior of *A. cuvieri*. After each episode, we measured (SVL $\pm$ 1 mm) and weighed (body mass [BM] $\pm$ 0.5 g) the subject and recorded its perch height (PH) and diameter (PD) to the nearest cm. We marked the animals with Pentel correction liquid to avoid testing the same individual repeatedly.

Anolis cuvieri performed five behavioral acts during predatory encounters with the *Alsophis portoricensis* model: positioning of the body perpendicularly to the snake model (lateral face-off), extension and contraction of the throat fan (dewlap) in a vertical axis (dewlapping), body movements up and down in a vertical plane (pushups), movement at least 30 cm away (*i.e.*, up the tree) from the snake model (flight), and flattening of the body against the substrate (crouching). None of the *A. cuvieri* showed any signaling displays (*i.e.*, lateral face-off, dewlapping, pushups) during the control period. During the experimental period, *A. cuvieri* performed pushups after the model reached the base of the perch, but not before. The following behavioral patterns were performed by *A. cuvieri* during the experimental period, and thus all reported times are after we started moving the snake model toward the anole.

A male *A. cuvieri* (SVL 120 mm; BM 41.8 g) that was perching head-down (PH 50 cm; PD 14.8 cm) was presented with the *Alsophis* model. At 43 sec the lizard turned its head toward the approaching snake and at 60 sec the anole positioned its body perpendicularly to the model and extended its dewlap twice. At 262 sec the snake reached the base of the anole's perch and the anole fully extended its two front legs, lifting the anterior portion of its body while keeping its head oriented toward the model. The lizard retained this position until the end of the trial (*i.e.*, at 300 sec).

We observed a male (SVL 128 mm; BM 47.3 g) that was also perching head-down (PH 38 cm; PD 7.5 cm). The *A. cuvieri* turned its head toward the snake model at 48 sec. The snake reached the base of the lizard's perch at 115 sec and the anole fled up the tree approximately 140 cm, where it stopped and remained head-up. At 163 sec the lizard oriented head-down (looking at the snake) and lifted its head and trunk from the perch by fully extending its forelimbs. The anole moved approximately 15 cm toward the model at 186 sec and performed pushups at 204 sec while still looking at the snake. After partially flexing its front legs at 241 sec, the lizard continued looking at the snake until the trial ended.

A male *A. cuvieri* (SVL 126 mm; BM 44.5 g) that was perching head-down (PH 160 cm; PD 9.7 cm) was presented with the *Alsophis* model. This anole remained immobile and did not show any display behavior during the experimental period.

A female *A. cuvieri* (SVL 118 mm; BM 34.0 g) that was also perching head-down (PH 114 cm; PD

8.3 cm) was presented with the snake model. At 8 sec the lizard positioned head-up and turned its head toward the snake. The model reached the base of the anole's perch at 114 sec. At 121 sec the lizard initiated pushups while looking at the snake; it finished this display at 151 sec after performing three pushups. At 247 sec the anole crouched and remained in that position until the end of the trial.

A male *A. cuvieri* (SVL 128 mm; BM 45.0 g) that was perching head-up (PH 81 cm; PD 6.1 cm) was presented with the model. The lizard oriented its head toward the snake at 40 sec and the model reached the base of the anole's perch at 68 sec. During the entire experimental period the anole kept looking at the snake and remained immobile until 227 sec, when it oriented its body perpendicularly to the model. The lizard remained in that position until the trial ended.

During the experimental period, three of the five *A. cuvieri* showed conspicuous signaling displays that we classify as pursuit-deterrent signals. Pursuit-deterrent signals are behavioral patterns that communicate to the predator that it has been detected, and because the chances of the predator successfully attacking the prey decrease when the prey is aware of the incoming predator, these behavioral acts presumably discourage the predator's attack (Hasson 1991). Antipredator responses used by *A. cuvieri* that belong to this category are pushups, lateral face-off, and dewlapping. Combined use of these three displays is also performed by *A. cristatellus* and *A. pulchellus* during staged predatory encounters with living *Alsophis portoricensis* (Leal & Rodríguez-Robles 1995; M. Leal, unpublished data). The first reaction of *Alsophis* when the anoles performed these behavioral patterns was to stop its motion toward the lizards, and the snake would only continue its approach after the anoles stopped dewlapping. In four of the five episodes in which *A. cristatellus* showed dewlapping combined with lateral face-off, *Alsophis* did not reattack the lizard (Leal & Rodríguez-Robles 1995). Signaling to an incoming predator has also been reported for the lizards *Cophosaurus texanus* (Dial 1986) and *Callisaurus draconoides* (Hasson et al. 1989).

When approached by the *Alsophis portoricensis* model, an *A. cuvieri* positioned its body perpendicularly to the snake and extended its dewlap, which resulted in an apparent increase in size. Combined use of lateral face-off and dewlap extension is also shown by *A. cristatellus* and by the lizard *Corytophanes cristatus* during encounters with a predatory snake (Davis 1953; Leal & Rodríguez-Robles 1995). In one episode, an *A. cuvieri* used crouching, perhaps to look less conspicuous to the snake. Crouching is also performed by *A. cristatellus* before being attacked by *Alsophis portoricensis* (Leal & Rodríguez-Robles 1995).

Lateral face-off, dewlapping, and pushups are widely used by various species of *Anolis* in species recognition, female attraction, and agonistic interactions at the intra- or inter-specific level (Jenssen 1977, 1978; Losos 1985). Our observations show that these behavioral acts are used as well by *Anolis cuvieri* as defensive responses, and therefore are multipurpose behavioral acts (behavioral patterns used for defense and other functions [Endler 1986]), which have also been documented for *A. cristatellus* (Leal & Rodríguez-Robles 1995). Furthermore, the dual function of these behavioral acts suggests that both intra- and inter-specific communication (*i.e.*, sexual selection) and predation pressure were important selective forces in the evolution of signaling behaviors in *Anolis* (Leal & Rodríguez-Robles 1995).

We thank H. W. Greene, T. A. Jenssen, J. B. Losos, M. J. Mahoney, and R. Thomas for critical comments on earlier versions of this manuscript, and R. Thomas for providing laboratory facilities. This study was partially supported by grants from the Department of Integrative Biology, University of California, Berkeley to JAR and from NSF (RII-8903827) to the University of Puerto Rico.

DAVIS, D. D. 1953. Behavior of the lizard *Corytophanes cristatus*. *Fieldiana Zool.* 35: 1–8.

DIAL, B. E. 1986. Tail display in two species of iguanid lizards: a test of the "predator signal" hypothesis. *Am. Nat.* 127: 103–111.

ENDLER, J. A. 1986. Defense against predators. In M. E. Feder and G. V. Lauder (Eds.). *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*, pp. 109–134. University of Chicago Press, Chicago, Illinois.

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: S36–S61.

GORMAN, G. C. 1977. Comments on ontogenetic color change in *Anolis cuvieri* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* 11: 221.

GOTMARK, 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 C. Gans and R. B. Huey (Eds.). *Biology of the Reptilia*, Vol. 16, Ecology B, Defense and life history, pp. 1–152. Alan R. Liss, New York, New York.

HASSON, O. 1991. Pursuit-deterrent signals: communication between prey and predator. *Trends Ecol. Evol.* 6: 325–329.

- , R. HIBBARD, AND G. CEBALLOS. 1989. The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.* 67: 1205–1209.
- HENDERSON, R. W., AND B. I. CROTHER. 1989. Biogeographic patterns of predation in West Indian colubrid snakes. In C. A. Woods (Ed.), *Biogeography of the West Indies: past, present, and future*, pp. 479–517. Sandhill Crane Press, Gainesville, Florida.
- JENSSEN, T. A. 1977. Evolution of anoline display behavior. *Am. Zool.* 17: 203–215.
- . 1978. Display diversity in anoline lizards and problems of interpretation. In N. Greenberg and P. D. MacLean (Eds.), *Behavior and neurology of lizards*, pp. 269–285. National Institute of Mental Health, Rockville, Maryland.
- LEAL, M., AND J. A. RODRÍGUEZ-ROBLES. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* 1995: 155–161.
- LOSOS, J. B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. *Copeia* 1985: 905–910.
- . 1994. Integrative studies of evolutionary ecology: Caribbean *Anolis* lizards as a model system. *Annu. Rev. Ecol. Syst.* 25: 467–493.
- MAGURRAN, A. E., AND S. L. GIRLING. 1986. Predator model recognition and response habituation in shoaling minnows. *Anim. Behav.* 34: 510–518.
- MOORE, F. R. 1994. Resumption of feeding under risk of predation: effect of migratory condition. *Anim. Behav.* 48: 975–977.
- PÉREZ-RIVERA, R. A. 1985. Nota sobre el hábitat, los hábitos alimentarios y los depredadores del lagarto *Anolis cuvieri* (Lacerta: Iguanidae) de Puerto Rico. *Caribb. J. Sci.* 21: 101–103.
- RAND, A. S., AND R. ANDREWS. 1975. Adult color dimorphism and juvenile pattern in *Anolis cuvieri*. *J. Herpetol.* 9: 257–260.
- RODRÍGUEZ-ROBLES, J. A., AND M. LEAL. 1993. Natural history notes: *Alsophis portoricensis* (Puerto Rican racer). *Diet. Herpetol. Rev.* 24: 150–151.
- ROUGHGARDEN, J. 1995. *Anolis* lizards of the Caribbean: ecology, evolution, and plate tectonics. Oxford University Press, New York, New York.
- SANTANA C. E., AND S. A. TEMPLE. 1988. Breeding biology and diet of red-tailed hawks in Puerto Rico. *Biotropica* 20: 151–160.
- SCHWARTZ, A., AND R. W. HENDERSON. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. University Florida Press, Gainesville, Florida.
- UNDERWOOD, G. 1970. The eye. In C. Gans and T. S. Parsons (Eds.), *Biology of the Reptilia*, Vol. 2, Morphology B, pp. 1–97. Academic Press, New York, New York.
- WAIDE, R. B., AND D. P. REAGAN. 1983. Competition between West Indian anoles and birds. *Amer. Nat.* 121: 133–138.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* 44: 345–389.
- . 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), *Lizard ecology: studies of a model organism*, pp. 326–370. Harvard University Press, Cambridge, Massachusetts.
- YASUKAWA, K., L. K. WHITTENBERGER, AND T. A. NIELSEN. 1992. Anti-predator vigilance in the red-winged blackbird, *Agelaius phoeniceus*: do males act as sentinels? *Anim. Behav.* 43: 961–969.

Manuel Leal²

Department of Biology
PO Box 23360
University of Puerto Rico
San Juan, Puerto Rico 00931-3360, U.S.A.

and

Javier A. Rodríguez-Robles

Museum of Vertebrate Zoology and
Department of Integrative Biology
University of California
Berkeley, California 94720-3160, U.S.A.

² Present address: Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130-4899, U.S.A.
