

## Behavior and Ecology of the Cuban "Chipojos Bobos" *Chamaeleolis barbatus* and *C. porcus*

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Morphologically, the five recognized species of *Chamaeleolis* (*C. agueroi*, *C. barbatus*, *C. chamaeleontides*, *C. guamuhaya*, and *C. porcus*), all endemic to Cuba, are among the most bizarre West Indian lizards. *Chamaeleolis* is characterized by a prominent bony head casque, relatively large body size (snout–vent length [SVL] of up to 177 mm), proportionately short limbs, cryptic coloration, the ability to move its eyes independently, and lack of tail autotomy (Wilson, 1957; Garrido and Schwartz, 1968; Williams and Rand, 1969). Based on these features, *Chamaeleolis* traditionally has been considered to be an early offshoot of the anoline lizard radiation that diverged prior to the evolution of *Anolis* (Etheridge, 1960; Williams, 1969). However, recent molecular systematic studies indicate that *Chamaeleolis* evolved within *Anolis* (Hass et al., 1993; Jackman et al., 1999), suggesting that the unusual morphology of *Chamaeleolis* indicates relatively rapid evolution, rather than antiquity of the lineage (and also suggests that the generic name *Chamaeleolis* might be subsumed within *Anolis* [Hass et al., 1993; Jackman et al., 1999]).

Few published reports exist on the ecology and behavior of *Chamaeleolis*. Wilson (1957, 1994) commented on the sluggish behavior of a captive *C. porcus* named Methuselah, noting that it would remain in the same spot for hours or even days without changing position. Gorman et al. (1969) mentioned that captive *C. porcus* actively moved between perches, jumped toward prey (crickets, grasshoppers, and mealworms), and displayed to each other by extending their dewlaps, opening their mouths and protruding their tongues. Garrido (1982) suggested that the simple courtship display repertoire in *C. barbatus*, which consists only of head-bobs displays, supported the idea that *Chamaeleolis* diverged early in the anole radiation. All previous observations on *Chamaeleolis* have been conducted on captive animals. During the course of field work on the community ecology of Cuban anoles in 1997 and 1999, we had the opportunity to study the behavior and ecology of this lizard under natural conditions. Here we report data on the habitat use, locomotion, display, and foraging behavior of *C. barbatus* and *C. porcus*.

Observations on *C. barbatus* were conducted at Soroa, which is located in the eastern part of La Sierra del Rosario mountain range in the province of Pinar del Río, Cuba. The habitat at Soroa can be categorized as a mesic secondary forest that has a closed canopy at 15–25 m, many understory trees and shrubs, and only sparse vegetation on the forest floor. Eleven spe-

cies of anoles occur sympatrically at Soroa, which constitutes one of the highest levels of anole species richness recorded for any locality in the West Indies. Focal observations were taken between 21 May and 6 June 1997, during daytime hours (700–1500 h). Observations on *C. porcus* were conducted at La Gran Piedra, which is located in the western part of La Sierra Maestra mountain range in the province of Oriente, Cuba. The habitat at La Gran Piedra can be categorized as montane rain forest, characterized by a mixture of pine, tree-ferns, and broadleaf vegetation. Focal observations were taken between 2–4 June 1999, during daytime (930–1700 h). Using binoculars we watched each lizard from a distance of 5–15 m. Using an audio tape recorder and a stopwatch, we recorded for each individual the amount of time spent moving, feeding, and displaying, as well as any other pertinent observations. All movements were noted as walks, runs, or jumps. Displays were categorized following the descriptions by Jenssen (1977, 1979). Perch height and diameter were estimated for all substrates used during the observations. Whenever possible, we caught the lizard after the observation to measure SVL. We took cloacal body temperature ( $T_b$ ) with an Omega Model HH21 Type T thermocouple thermometer on four of the focal animals. Body temperatures were taken immediately after catching the lizards.

Focal observations were taken on seven undisturbed individuals of *C. barbatus*: three males, three females, and one juvenile; and two individuals of *C. porcus*: one adult, and one juvenile (Table 1). Individuals of *C. barbatus* spent 63.3% of their time stationary, 31.2% moving around the habitat and 5.5% displaying. Individuals of *C. porcus* exhibited a similar pattern (Table 1). Cloacal body temperature was only taken on *C. barbatus*. Lizard  $T_b$ s were: 27.1 (at 1030 h), 27.3 (at 1000 h), 27.5 (at 17:00 h), and 32.5 C (at 14:25 h). The lizard with a  $T_b$  of 32.5 C was perching completely exposed to the sun, whereas the other lizards were active in shaded or semi-shaded areas.

Individuals of both species were mostly found in closed canopy forest in areas in which the vegetation was aggregated in tangles or bundles. The tangles usually consisted of small diameter branches occurring in close proximity to each other; lianas and vines also wound through the branches. Lizards were observed perching on small diameter surfaces at different heights (Table 2). During searches at night, we located individuals of both species sleeping on small diameter perches, especially leafless twigs. Garrido (1982) reported similar observations for *C. barbatus*.

Five individuals of *C. barbatus* (three males and two females) performed a total of 17 display bouts (defined as displays of identical behavior patterns [e.g., dewlapping, head-bobbing] separated by at least 30 sec [L. J. Fleishman, pers. comm.]). While the lizards were signalling, we did not detect the presence of another lizard, suggesting that signals were given as assertion displays (Carpenter, 1967; Jenssen, 1977; but see Decourcy and Jenssen, 1994). *Chamaeleolis porcus* did not display during our focal observations.

*Chamaeleolis barbatus* performed two distinctive patterns of dewlap displays: basic dewlap displays and dewlap rolls. In both displays, the lizard's dewlap, which is white with a pinkish to peach edge, was very conspicuous against the background vegetation. Both

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TABLE 1. Summary of focal observations for each individual of *Chamaeleolis barbatus* and *C. porcus*. The % of each activity is the time that a lizard spent in each category divided by total observation time. The % of type of walking is the total time that the lizard spent in each type of walking divided by the total walking time. <sup>1</sup> These individuals were not captured, but clearly exceeded 100 mm SVL. <sup>2</sup> The categories do not add up to 100% because this lizard spent some time feeding. <sup>3</sup> This individual displayed, but we were unable to quantify the duration of the display. <sup>4</sup> This individual was not captured, but clearly did not exceed 100 mm SVL.

Individual	Time (min:sec)	% of activity			% type of walking	
		Stationary	Moving	Displaying	Rocking	Normal
<i>C. barbatus</i>						
Male SVL = 83 mm	174:00	60.6	31.4	8.0	61.2	38.8
Female SVL = 100+ <sup>1</sup> mm	15:44	18.1	81.9	0.0	100.0	0.0
Male SVL = 119 mm	40:00	94.7	5.3	— <sup>3</sup>	0.0	100.0
Female SVL = 140 mm	196:15	86.3	11.0	2.7	89.3	10.7
Female SVL = 122 mm <sup>2</sup>	56:55	29.9	49.9	15.0	66.0	34.0
Juvenile SVL = 59 mm	35:58	76.3	23.7	0.0	100.0	0.0
Male SVL = 100+ <sup>1</sup> mm	257:00	77.2	15.4	7.5	89.0	11.0
Mean		63.3	31.2	5.5	72.2	27.8
Standard Error		11.0	10.1	2.4	13.4	13.4
<i>C. porcus</i>						
Juvenile SVL = 100- <sup>4</sup> mm	96:07	87.6	12.4	0.0	75.9	24.1
Adult SVL = 100+ <sup>1</sup> mm <sup>2</sup>	155:20	83.7	9.3	0.0	64.0	36.0
Mean		85.7	10.9		70.0	30.1
Standard Error		2.0	1.6		6.0	6.0

displays began with the same movement of the forelimbs and head, but differed in the movement of the head once the dewlap was extended. In the basic dewlap display, the forelimbs as well as the neck elevated the lizard's head to a point at which the neck and back were in a straight line. Once this position was achieved, the dewlap was slowly extended. The dewlap was not pulsed repeatedly during a display; instead, in four bouts, after the initial extension, the dewlap was slowly partially retracted and then extended back to its original position. In the three other bouts, the dewlap was initially completely extended and kept extended until it was retracted. The spines that are present at the edge of the dewlap, on both male and females, were very conspicuous when the

dewlap was fully extended. Basic dewlap displays were performed by three males and one female.

In the other dewlap display, the lizard kept the dewlap fully extended and used the neck to slowly rotate its head and dewlap, a display that we term a "dewlap roll." In a dewlap roll, the lizard used its neck to slowly rotate its head around its long axis; the head is slowly tilted to one side (e.g., left), then returned to its original position, and then the head is tilted to the other side (e.g., right). The whole time, the dewlap is extended; the head movements have the effect of repeatedly tilting the dewlap outward to one side and then the other. Bouts of dewlap rolls lasted 37–307 sec. Dewlap rolls were performed by two males.

TABLE 2. Summary of habitat use and distance travelled during focal observations for each individual of *Chamaeleolis barbatus* and *C. porcus*. Perch diameter data are provided for each distinct substrate used (including portions of the same branch that differed in diameter). Total distance is an estimate of the distance that an individual moved during the focal observations. The focal observation times are the same as reported in Table 1.

Individual	Perch diameter (cm) X ± SE (range; N)	Perch height (m) minimal-maximal	Total distance moved (m)
<i>C. barbatus</i>			
Male SVL = 83 mm	1.4 ± 0.3 (0.5–4.0; 18)	1.5–4.0	6.5
Female SVL = 100+ <sup>1</sup> mm	7.5 ± 1.5 (6.0–19.0; 2)	4.0–4.0	2.5
Male SVL = 119 mm	4.0 (4.0; 1)	3.0–3.5	0.5
Female SVL = 140 mm	0.8 ± 0.2 (0.3–1.5; 5)	1.25–1.75	1.8
Female SVL = 122	1.8 ± 0.4 (0.3–6.0; 20)	0.0–7.5	10.0
Juvenile SVL = 59 mm	0.6 ± 0.1 (0.5–0.75; 3)	2.0–2.0	1.0
Male SVL = 100+ <sup>1</sup> mm	2.1 ± 0.3 (1.0–3.5; 8)	7.0–12.0	11.5
<i>C. porcus</i>			
Juvenile SVL = 100- <sup>4</sup>	1.5 ± 0.4 (0.5–4.0; 11)	2.5–4	4.0
Adult SVL = 100+ <sup>1</sup> mm	4.3 ± 0.6 (2.0–8.0; 9)	2.0–4.5	12.0

Head-bobs were given by a male and a female. The lizard used its forelimbs to elevate its head. Once the forelimbs were extended, the lizard used its neck muscles to move the head up and down in a series of rapid head-bobs. Two patterns were observed: low amplitude head-bobs, in which only the lizard's head moved, and high amplitude head-bobs, in which the lizard also flexed its forelimbs in synchrony with the head-bobs. Only the male lizard gave high amplitude head-bobs.

Two static display modifiers (*sensu* Jenssen, 1977, 1979) were performed in association with dewlap and head-bob displays: change in color pattern and erection of dorsal and nuchal crests. These modifiers were performed slowly and simultaneously. While displaying, the lizard's body color slowly became lighter from an initial dark-gray or brown. At the same time, conspicuous vertical dark stripes appeared on the body and limbs of the lizard and the crest was raised from the top of the neck to the base of the tail, resulting in an apparent increase in body size.

The most common type of locomotion employed by both species was walking, which was used in 89% of all movements and was performed in two different patterns: rocking and non-rocking (Table 1). Walking in a non-rocking pattern was observed to be slow and deliberate. When using the rocking pattern of walking, a lizard would slowly rock back and forth while slowly advancing forward. The amount of rocking per walking cycle was variable; in some episodes, the body rocked forward and backward as many as 20 times per complete cycle of limb movements. Frequently, the lizard's body was rocking even when the lizard was not moving forward. The distance that lizards traveled in a rocking pattern without stopping was variable, but usually covered 10–30 cm. Nevertheless, some of the lizards were able to travel long distances during our focal observations by stopping and resuming walking repeatedly (Table 2).

Two instances of running were observed in *C. barbatus*: one individual ran 175 cm up a vine 3 cm in diameter whereas the other ran 30 cm down a vine of 2.5 cm in diameter. While running, the lizards lifted their entire body from the perch and undulated their torsos as their legs moved alternately. Another lizard ran immediately upon release, on the forest floor for a distance of 200 cm, undulating its torso as it ran. Undulation of the body was never observed while lizards were walking.

Jumping was employed by both species to move from one perch to another. Jumping was employed on 15 occasions by *C. barbatus* and on two occasions by *C. porcus*. To jump, a lizard turned its body perpendicular to the stem on which it was perching and hunched its body into a preparatory position (see fig. 1 in Bels and Theys, 1989) before launching itself to the other stem. The distance of jumps was relatively short for both *C. barbatus* ( $\bar{x} \pm SE = 11.8 \pm 1.0$  cm; Range = 10–20 cm; N = 11) and *C. porcus* ( $\bar{x} \pm SE = 17.5 \pm 2.5$  cm; Range = 15–20 cm; N = 2).

Only one individual of each species was observed feeding. Because these are the first notes on feeding behavior of these species under natural conditions, we provide extensive details. One female *C. barbatus* (SVL = 122) was initially observed perched 7 m high on a liana. It then slowly moved down until it was perched

approximately 30 cm from the ground. While walking down, the lizard stopped repeatedly, lifted its head from the substrate by completely extending the forelimbs and scanned the ground in a typical anole search position (Scott et al., 1976; Stamps, 1977). While perching 30 cm from the ground, the lizard jumped to the ground, walked a short distance, and caught what appeared to be a snail. Then the lizard jumped to another stem approximately 10 cm above the ground and used its mouth to manipulate the food item, moving it up and down and from side to side in its mouth for a period of approximately 60 sec. At the end of this period, a crunching sound could be heard and then the lizard swallowed the prey item. After swallowing the prey item, the lizard moved around the habitat, mainly by walking in a rocking fashion, stopping periodically to scan the leaf litter. After moving for a period of 47:30 (min:sec), and while perching 50 cm above the ground, the lizard jumped to the ground, walked a short distance over the leaf litter and caught what appeared to be a slug. The prey item was fairly big and gooey. While standing in the leaf litter, the lizard manipulated the item for a period of 98 sec before swallowing it. The lizard then jumped to a stem and moved around the habitat in the same fashion described above for a period of 21:15 before jumping back to the ground and catching another prey item. The prey, a red cylindrical object with ridges running transversely, may have been a beetle pupae. The lizard crushed the item and manipulated it in its mouth for a period of 75 sec before swallowing it. Once the lizard finished, it jumped back to a stem.

An adult *C. porcus* was initially observed perched approximately 2 m high among a group of branches. During the first 22:34 the lizard moved a distance of 2 m, mainly by walking in a rocking fashion and stopping repeatedly, at which time it appeared to scan the area. At 22:39 of the observation period, the lizard jumped to a new perch and walked a distance of approximately 5 m to capture what appeared to be a cockroach. After capturing the cockroach, the lizard moved approximately 10 cm with the insect in its mouth to a shaded spot. The lizard then manipulated the cockroach in its mouth and oriented it head-first and chewed on it repeatedly for a period 9:53 before swallowing it. After swallowing the prey, the lizard remained on the same perch actively scanning the area for a period of 32:05.

Our observations on the display, locomotor, and foraging behavior of these two *Chamaeleolis* species indicate both extreme differences and some similarities to the ethoecology of other species of anoles. Below, we compare each aspect of *Chamaeleolis* ethoecology to what is known about anoles and discuss some aspects of *Chamaeleolis* natural history that might be responsible for these differences and similarities.

The displays of *C. barbatus* exhibited some similarities, as well as some marked differences, from the general pattern of displays exhibited by most anoles. *Chamaeleolis barbatus* is similar to other anoles in using head-bobs and dewlap displays as the main signals (Jenssen, 1977; Fleishman, 1992); it is also similar to other anoles in using static display modifiers in association with dewlap and head-bob displays (Jenssen, 1979; Ortiz and Jenssen, 1982). In contrast, the

assertion displays of *C. barbatus* did not combine either of the two dewlap displays with head-bob displays, which is a common characteristic of the assertion displays of many species of *Anolis* (Ruibal, 1967; Jenssen, 1977; Fleishman, 1992; but see Jenssen and Feely [1991] on the anole *Chamaelinorops barbouri*).

Dewlap roll displays have never been reported for any other anole species. The long duration and exaggerated movement of dewlap rolls might facilitate long distance transmission (Fleishman, 1988, 1992), which would make dewlap rolls analogous to the high amplitude head bob displays given by most anoles as part of their assertion displays to advertise their position (Stamps and Barlow, 1973; Jenssen, 1977; Fleishman 1992). Furthermore, at least to the human eye, movement of the fully extended dewlap during dewlap rolls was very conspicuous. Dewlap rolls might be analogous to head rolls given by *Iguana iguana* and other iguanines as assertion displays (Dugan, 1982). However, head rolls are performed in a rapid sequence of head movements and are given in combination with head-bob displays (Dugan, 1982), whereas dewlap rolls were performed in a slow sequence and were not combined with head-bob displays.

Our observations suggest that *Chamaeleolis barbatus* and *C. porcus* primarily use small diameter perches. In the West Indies, this structural habitat is also exploited by "twig-anoles" (e.g., Thomas, 1965; Rand, 1967; Williams and Rand, 1969; Hicks and Trivers, 1983; Thomas and Hedges, 1991). "Twig-anoles" are characterized by possession of a slender body, short tail, and short limbs, all of which have been interpreted as adaptations for moving slowly and carefully on narrow surfaces (Williams, 1983; Beuttell and Losos, 1999). Although *C. barbatus* and *C. porcus* are at least twice the SVL of the largest twig-anole (*A. valencienni*) and at least ten times the mass, they are in other respects fairly similar to twig anoles. Hence, in many respects, *C. barbatus* and *C. porcus* appear to be giant twig anoles, as Hass et al. (1993) suggested.

The locomotor behavior of *C. barbatus* and *C. porcus* may be a consequence of their use of relatively narrow surfaces. Like twig anoles (Hicks and Trivers, 1983; Losos, 1990; Irschick and Losos, 1996), both species move primarily by walking. Because small diameter perches may limit the lizard's ability to balance, slow walking allows the lizard to effectively move on small perches (Losos and Sinervo, 1989; Losos, 1990). Individuals of both species were never observed using their tails in a prehensile fashion while walking on narrow surfaces.

The rocking pattern exhibited by *C. barbatus* and *C. porcus* while walking has not been previously observed in any West Indian anole. One possible function of this behavior is to blend the lizard's movements with those of the surrounding vegetation, thus rendering the lizard difficult to detect (Fleishman, 1985). The efficacy of this locomotor pattern was evident during focal observations, when we often lost sight of a lizard, only to relocate it shortly thereafter on the same perch a short distance away. Walking in a rocking fashion is also exhibited by the lizard *Polychrus guttuosus* (T. A. Jenssen, pers. comm.) and lizards of the genus *Chamaeleo* (Gans, 1967), presumably for the same reason; a similar behavior is exhibited by the vine snake *Oxybelis aeneus* (Fleishman, 1985).

In summary, our field observations suggest that the unusual ethoecology of *C. barbatus* and *C. porcus* may have evolved to avoid predator detection. For three reasons, both species may be particularly vulnerable to predation. First, due to their relatively large size, *C. barbatus* and *C. porcus* may be conspicuous to visually oriented predators while perching on small diameter perches. However, cryptic coloration and behavior may allow *C. barbatus* and *C. porcus* to minimize the likelihood of predator detection while perching on twigs. Other anoles and related species that also use small diameter perches as perching sites also exhibit cryptic coloration and behavior (Vitt and Lacher, 1981; Hicks and Trivers, 1983; Irschick and Losos, 1996).

Second, the short limbs exhibited by twig anoles allow these lizards to move without difficulty on narrow surfaces, but come at the cost of limiting the maximum sprint speed that can be attained (Losos and Sinervo, 1989; Losos, 1990; Irschick and Losos, 1998). Thus, by adapting to use narrow perches, *C. barbatus* and *C. porcus* may have compromised their abilities to escape by rapid locomotion and thus may have to rely on avoiding detection. Finally, *Chamaeleolis* exhibits unusual dental morphology that suggests specialization for feeding on slugs and snails (Estes and Williams, 1984), a hypothesis which is in accord with our foraging observations on *C. barbatus*. Slugs have been also reported as part of the diet of *C. agueroi* (Díaz et al. 1998), and of *C. barbatus* in captivity (Garrido, 1982). Because snails and slugs are less active than insects, the prey items most commonly exploited by anoles (Wolcott, 1923; Waide and Reagan, 1983), *C. barbatus* may be forced to actively move around their habitat and thereby expose themselves more often to predation (Huey and Pianka, 1981). In the case of *C. porcus* our observations suggest that the diet is not limited to snails and slugs; nevertheless our observations suggest that *C. porcus* actively move around in search of prey. Therefore, *Chamaeleolis* may have evolved a cryptic locomotion pattern to avoid detection by predators while actively foraging.

Clearly, our data only provide a limited and preliminary view of the ethoecology of these remarkable anoles. Further work on all aspects of the natural history of this species is needed. Of particular interest is how the ecology and behavior of other species of *Chamaeleolis* compares to that of *C. barbatus* and *C. porcus*. In Cuba, *Chamaeleolis* lizards are commonly called "Chipujo Bobo" (i.e., big dumb lizard) due to their sluggish behavior; however, our observations suggest that *C. barbatus* and *C. porcus* are active, but extremely cryptic, anoles with a deceiving name.

*Acknowledgments.*—We thank L. Rodríguez-Schettino, A. R. Chamizo-Lara, V. Rivalta, and the other members of the 1997 and 1999 herpetological expeditions for their assistance in the field, the Cuban Institute of Ecology and Systematics, Cuban Academy of Sciences for essential logistical support and the National Geographic Society and the National Science Foundation (NSF DEB-9318642 and IBN-9902323) for support.

#### LITERATURE CITED

- BELS, V. L., AND J. P. THEYS. 1989. Mechanical analysis of hind limb of *Anolis carolinensis* (Reptilia: Iguanidae) in jumping. *Fortschr. Zool.* 35:608–612.
- BEUTTELL, K., AND J. B. LOSOS. 1999. Ecological mor-

- phology of Caribbean anoles. *Herpetol. Monogr.* 13:1-28.
- CARPENTER, C. C. 1967. Aggression and social structure in iguanid lizards. In W. W. Milstead (ed.), *Lizard Ecology, a Symposium*, pp. 87-105. Univ. Missouri Press, Columbia.
- DECOURCY, K. R., AND T. A. JENSSSEN. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* 47:251-262.
- DÍAZ, L. M., N. NAVARRO, AND O. H. GARRIDO. 1998. Nueva especie de *Chamaeleolis* (Sauria: Iguanidae) de la Meseta de Cabo Cruz, Granma, Cuba. *Avicennia* 8/9:27-34.
- DUGAN, B. 1982. A field study of the headbob displays of male green iguanas (*Iguana iguana*): variation in form and context. *Anim. Behav.* 30:327-338.
- ESTES, R., AND E. E. WILLIAMS. 1984. Ontogenetic variation in the molariform teeth of lizards. *J. Vert. Paleont.* 4:96-107.
- ETHERIDGE, R. 1960. The relationships of the anoles (Reptilia, Sauria, Iguanidae): An interpretation based on skeletal morphology. Unpubl. Ph.D. Diss., Univ. Michigan, Ann Arbor.
- FLEISHMAN, L. J. 1985. Cryptic movement in the vine snake *Oxybelis aeneus*. *Copeia* 1985:242-245.
- . 1988. Sensory influences on physical design of a visual display. *Anim. Behav.* 36:1420-1424.
- . 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Amer. Natur.* 139:36-61.
- GANS, C. 1967. The chameleon. *Nat. Hist.* 76(4):53-59.
- GARRIDO, O. H. 1982. Descripción de una nueva especie cubana de *Chamaeleolis* (Lacertilia: Iguanidae), con notas sobre su comportamiento. *Poeyana* 236:1-25.
- , AND A. SCHWARTZ. 1968. Cuban lizards of the genus *Chamaeleolis*. *Q. J. Florida Acad. Sci.* 30:197-220.
- GORMAN, G. C., R. B. HUEY, AND E. E. WILLIAMS. 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides*, and *Phenacosaurus*, with behavioral notes. *Breviora* 316:1-17.
- HASS, C. A., S. B. HEDGES, AND L. R. MAXSON. 1993. Molecular insights into the relationships and biogeography of West Indian anoline lizards. *Biochem. Syst. Ecol.* 21:97-114.
- HICKS, R. A., AND R. L. TRIVERS. 1983. The social behavior of *Anolis valencienni*. In A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*, pp. 570-595. *Mus Comp. Zool.*, Cambridge, Massachusetts.
- HUEY, R. B., AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. *Ecology* 62:991-999.
- IRSCHICK, D. J., AND J. B. LOSOS. 1996. Morphology, ecology, and behavior of the twig anole, *Anolis angusticeps*. In R. Powell and R. W. Henderson (eds.), *Contributions to West Indian Herpetology: A tribute to Albert Schwartz, Contributions to Herpetology*, Vol. 12, pp. 291-301. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- , AND ———. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219-226.
- JACKMAN, T. R., A. LARSON, K. DE QUEIROZ, AND J. B. LOSOS. 1999. Phylogenetic relationships and the tempo of early diversification in *Anolis* lizards. *Syst. Biol.* 48:254-285.
- JENSSSEN, T. A. 1977. Evolution of anoline lizard display behavior. *Amer. Zool.* 17:203-215.
- . 1979. Display modifiers on *Anolis opalinus* (Lacertilia: Iguanidae). *Herpetologica* 35:21-30.
- , AND P. C. FEELY. 1991. Social behavior of the male anoline lizard *Chamaelinorops barbouri*, with a comparison to *Anolis*. *J. Herpetol.* 24:454-462.
- LOSOS, J. B. 1990. Concordant evolution of locomotor behaviour, display rate, and morphology in *Anolis* lizards. *Anim. Behav.* 39:879-890.
- , AND B. SINERVO. 1989. The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* 145:23-30.
- ORTIZ, P. R., AND T. A. JENSSSEN. 1982. Interspecific aggression between lizard competitors, *Anolis cooki* and *Anolis cristatellus*. *Z. Tierpsychol.* 60:227-238.
- RAND, S. A. 1967. The ecological distribution of the anoline lizards around Kingston, Jamaica. *Breviora* 272:1-18.
- RUIBAL, R. 1967. Evolution and behavior in West Indian anoles. In W. W. Milstead (ed.), *Lizard Ecology, a Symposium*, pp. 116-140. Univ. Missouri Press, Columbia.
- SCOTT, N. J., JR., D. E. WILSON, C. JONES, AND R. M. ANDREWS. 1976. The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* 10:75-84.
- STAMPS, J. A. 1977. The function of the survey posture in *Anolis* lizards. *Copeia* 1977:756-758.
- , AND G. W. BARLOW. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). *Behaviour* 47:67-94.
- THOMAS, R. 1965. A new anole (Sauria Iguanidae) from Puerto Rico. Part II. Field observations on *Anolis occultus* Williams and Rivero. *Breviora* 231:10-18.
- , AND S. B. HEDGES. 1991. Rediscovery and description of the Hispaniolan lizards *Anolis darlingtoni* (Sauria: Iguanidae). *Carib. J. Sci.* 27:90-93.
- VITT, L. J., AND T. E. LACHER, JR. 1981. Behavior, habitat, diet, and reproduction of the iguanid lizard *Polychrus acutirostris* in the Caatinga of northeastern Brazil. *Herpetologica* 37:53-63.
- WAIDE, R. B., AND D. P. REAGAN. 1983. Competition between West Indian anoles and birds. *Amer. Natur.* 121:133-138.
- WILSON, E. O. 1957. Behavior of the Cuban lizard *Chamaeleolis chamaeleontides* (Duméril and Bibron) in captivity. *Copeia* 1957:145.
- . 1994. *Naturalist*. Island Press, New York.
- 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 Univ. Press, Cambridge, Massachusetts.
- , AND S. A. RAND. 1969. *Anolis insolitus*, a new dwarf anole of zoogeographic importance from the mountains of the Dominican Republic. *Breviora* 326:1-21.
- WOLCOTT, G. N. 1923. The food of Porto Rican Lizards. *J. Dept. Agric. Porto Rico* 7:5-43.