



Anti-predation Behavior in Bearded Anoles (Dactyloidae: *Anolis*, Clade *Chamaeleolis*): A Review

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Bearded anoles — anoles in the clade *Chamaeleolis* (Poe et al. 2017) — are chameleon-like lizards endemic to Cuba that are widely distributed on the island (Rodríguez-Schettino 1999; Rodríguez Schettino et al. 2013). They have heads with a distinctive casque-like structure, relatively short limbs, and semi-prehensile tails. Most of the pertinent literature addresses Linnean alpha taxonomy, new distribution records, and niche modelling, but information concerning natural history is sparse (Henderson and Powell 2009; Rodríguez-Cabrera et al. 2020).

Bearded anoles are among the largest anoles in Cuba (177 mm SVL; Garrido and Schwartz 1968). These lizards, classified as twig-giant ecomorphs (Hass et al. 1993; Mahler et al. 2016), usually inhabit forests (Henderson and Powell 2009), where they perch on small-diameter branches (Garrido 1982; Leal and Losos 2000). Anoles are diurnally active, visually-oriented predators (Losos 2009) and, although no studies address this subject for bearded anoles, their well-developed eyes suggest that they follow the general pattern. Bearded anoles move slowly and feed on slow-moving prey (e.g., certain insects, their larvae, diplopods, and mollusks; Estes and Williams 1984; Díaz et al. 1998; Leal and Losos 2000; Herrel and Holanova 2008; Rodríguez-Cabrera et al. 2020), although they may accept faster prey (e.g., other anoles) in captivity (Fong and Garcés 2001).

Anoles in general are under high predation pressure (Losos 2009; Henderson and Powell 2009); consequently, the lack of speed of bearded anoles must constrain escape abilities, selecting instead for alternative strategies to avoid predation. Predators of bearded anoles probably include other large lizards (e.g., the *Anolis equestris* group), snakes (*Chilabothrus*, *Cubophis*, and *Tropidophis*) and birds, that could prey on either young or adults. Nevertheless, few reports of predation



Fig. 1. An immature Short-bearded Anole (*Anolis chamaeleonides*) from central Cuba with a complex pattern that resembles that of the substrate. Photograph © Raimundo López-Silvero Martínez.

have been published (López 2012; Torres et al. 2014). The paucity of predation records could be attributable to a combination of insufficient fieldwork, effective anti-predation mechanisms, or both. However, if bearded anoles cannot flee rapidly, how do they avoid predation?

Anoles employ multiple anti-predation behaviors, including aggression, immobility (often combined with crypsis), biting, tail autotomy, and efforts to appear larger than they really are (i.e., dewlapping, pushups, lateral body compression, crouching, predator inspection, and lateral face-offs) (Leal and Rodríguez-Robles 1995, 1997a, 1997b). Given that bearded anoles are among the most cryptic anoles, some basic anti-predation mechanisms (concealment combined with camouflage or hiding) would largely go unnoticed. Herein we describe anti-predation strategies used by bearded anoles that we have observed in nature.

Camouflage

In this review we follow the conceptual framework of Stevens and Merilaita (2011), focusing on the anti-predation component of camouflage instead of its evolution as a strategy to avoid detection by potential prey. Thus, we consider visual camouflage as an anti-predation mechanism for evading visual predators and examine all forms of concealment, including strategies that diminish the probability of being detected (crypsis) and those that reduce the likelihood of being recognized (e.g., masquerade).

Crypsis by background matching.—Background matching occurs when the coloration of an animal resembles that of its surroundings, diminishing the risk of being detected by a predator. During the day, when active, bearded anoles maintain a complex coloration (Fig. 1), whereas at night their coloration is lighter and more uniform (Fig. 2). This change



Fig. 2. An adult female Short-bearded Anole (*Anolis chamaeleonides*) from central Cuba in the typical light phase while sleeping at night. Photograph © T.M. Rodríguez-Cabrera.



Fig. 3. An immature Short-bearded Anole (*Anolis chamaeleonides*) (same individual illustrated in Fig. 1) changed its color in less than a minute while trying to adjust more closely to the background after the detection of potential predators (human observers). Photograph © Raimundo López-Silvero Martínez.



Fig. 4. An adult female Western Bearded Anole (*Anolis barbatus*) a minute after collection and being moved to an irregular twig thinner than her body. She conformed immediately to the shape of the new perch in the presence of potential predators (human observers). Body and limb configuration and possession of a semi-prehensile tail appear to be adaptations to a life on twigs. Photograph © Raimundo López-Silvero Martínez.

probably occurs because the maintenance of a complex pattern is more energetically demanding and unnecessary at night (but see Horowitz 1958).

Diurnal coloration in bearded anoles is a complex of green, brown, and gray tones with dark yellow or orange spots that resemble the pattern and coloration of twigs and trunks (Fig. 1). These anoles could be considered structural habitat specialists because they live mainly on trunks and twigs (Leal and Losos 2000) that have a predominantly brown background. Nevertheless, a certain level of heterogeneity exists in that environment. This includes randomly dispersed

contrasting markings produced by shade or by lichens and mosses.

The capacity of background-matching in such diverse situations is called the compromise strategy (Stevens and Merilaita 2011). Within a specific habitat these lizards employ this strategy by actively adjusting to differences in a given background by, for example, creating lichen-like markings on the body (Figs. 1 & 3).

Masquerade.—Masquerade is a type of camouflage that diminishes the probability of being recognized by a predator by mimicking an uninteresting object (Skelhorn et



Fig. 5. A neonatal Escambray Bearded Anole (*Anolis guamuhaya*) with typical nocturnal coloration sleeping on a narrow perch. Photograph © Raimundo López-Silvero Martínez.



Fig. 6. Short-bearded Anoles (*Anolis chamaeleonides*) from central Cuba exhibiting hiding behavior. An adult female (top) has “squirreled,” which is typical of anoles, and an immature individual (bottom) is keeping an eye on potential predators (human observers). Photographs © Raimundo López-Silvero Martínez.

al. 2010; Stevens and Merilaita 2011). One example of this kind of camouflage is known in the Round-tailed Horned Lizard (*Phrynosoma modestum*), which can imitate a rock (Cooper and Sherbrooke 2012). Bearded anoles have a limb configuration that allows them to grasp thin branches tightly, and behaviors that let them conform to the shape of a given perch when they are active (Fig. 4) or sleeping (Figs. 2 & 5).

Motion camouflage.—Motion camouflage involves two strategies that reduce the probability of being detected while moving (Stevens and Merilaita 2011). “Motion Signal Minimization” functions when movement is so slow that progress is very difficult to detect, whereas “Optic Flow Mimicry” occurs when an individual moves forward and backward while on a perch being moved by wind (or water). The latter strategy, described as “rocking walking,” has been documented in Western Bearded Anoles (*Anolis barbatus*) and Oriente Bearded Anoles (*A. porcus*) (Leal and Losos 2000), as well as in other lizards (chameleons; Butler 2005), colubrid snakes (Fleishman 1985), and a number of invertebrates (e.g., O’Dea 1991; Stevens and Merilaita 2011).

Hiding

We treat hiding separately from camouflage, as it is not an intrinsic trait that facilitates concealment. It is instead a behavior in which potential prey avoids a predator’s visual field, with camouflage playing a secondary role in reducing the risk of predation.

Squirreling.—This hiding behavior, which is common in anoles, consists of moving to the other side of a perch when they detect a disturbance (sound, vibration, or visual stimulus) that might indicate the presence of a predator (Fig. 6A) (Schneider et al. 2000; Cooper 2006). When the stimulus is visual, bearded anoles can even keep an eye on the potential predator (Fig. 6B). If the predator approaches too closely, they either flee, adjust their position on the perch, or remain immobile while relying on camouflage (typically background-matching crypsis).

Compression with tail- and limb-elevation.—This could be considered a more elaborate form of squirreling. It is elicited when a bearded anole detects a predator and its perch is too narrow to properly hide the entire body. When this happens the lizard compresses its body laterally, elevates the tail over the hindlimbs, the heels of which touch one another, and grasps the perch only with the digits (tarsals and metatarsals are not in contact with the perch) (Fig. 7). We have not found evidence of this behavior in the literature for any lizard, with the most similar strategy that of a chameleon moving to the opposite side of a branch and laterally compressing its body when the branch is too thin to hide it (Stuart-Fox et al. 2006).

Perch Selection

Bearded anoles have body and limb configurations that allow them to grasp very thin branches. Lacking caudal autotomy



Fig. 7. An adult female Escambray Bearded Anole (*Anolis guamuhaya*) engaged in enhanced “squirreling” behavior, which involves elevation of the tail to accommodate the hindlimbs in order to present the narrowest possible profile while hiding behind a small-diameter perch. Photograph © T.M. Rodríguez-Cabrera.

(common in most anoles), they instead have semi-prehensile tails that are used when moving along narrow branches (Garrido et al. 1991; Losos 2009; Fig. 4). They thus can reach and remain on branches thinner than their own bodies (Garrido 1982; Leal and Losos 2000) and often sleep on these kinds of perches (Rodríguez-Cabrera et al. 2020). The smaller the individual, the smaller the branch they can use as a perch (Figs. 2 & 5). Such resting places are likely unreachable by most potential predators.

Aggression

Aggression usually is the last resort of prey trying to survive a predator's attack (Wittenberger 1981). It is energetically demanding and the risk of being wounded or killed is higher than when using other anti-predation strategy (Sansom et al. 2009). Bearded anoles initially exhibit aggression by inflating their bodies and erecting their dorsal crests, giving them a larger appearance (Leal and Losos 2000). The aggressive state in these lizards includes gaping with tongue extension (tongue darker in most species; Holáňová et al. 2012), body compression, dorsal crest erection, lung inflation and hissing by rapid lung deflation, and changes in coloration. Aggressive-state colors are brighter and more conspicuous (Fig. 8) than normal coloration (Fig. 2). Such displays can end with biting. These lizards have large, massive, bony heads, and the posterior teeth are modified for crushing hard prey (e.g., beetles and mollusk shells), which allows them to inflict strong and painful bites (Herrel and Holanová 2008).

Anolis lizards are prey of other reptiles (including other anoles), birds, and even invertebrates (Henderson and Powell 2009; Fonseca and Rodríguez-Cabrera 2014; Dahn and

Sharpe 2017). Many species can flee rapidly but nevertheless are frequently captured (Losos 2009). Although certainly an underestimate, we found only one report of actual predation (López 2012) and one of a predation attempt (Torres et al. 2014) on a bearded anole, while predation of other anoles has been documented frequently. The anti-predation strategies used by bearded anoles to minimize detection appear to be quite efficient.

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Fig. 8. An adult female Short-bearded Anole (*Anolis chamaeleonides*) (same individual illustrated in Fig. 2) in an aggressive posture. Notice the differences in color, shape, and attitude compared to the sleeping mode in Fig. 2. Photograph © T.M. Rodríguez-Cabrera.

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