



# Coloration and Color Change in the Brown Anole, *Anolis sagrei*

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**Abstract.**—The nonnative Brown anole (*Anolis sagrei*) is the most abundant lizard in peninsular Florida and is a common inhabitant of urban and suburban environments where it competes with native Green anoles (*A. carolinensis*). Brown anoles are largely diurnal and considered a “trunk-ground” ecomorph, typically basking or perching on shrubs and numerous objects near the ground. There is considerable intraspecific variation and plasticity of body colors, but changes of color to match backgrounds in context of crypsis have not been well recorded or understood. Here we discuss the variety of colors exhibited in Brown anoles, and we report observations of color change in lizards that were observed continuously or intermittently for variable periods of time. In contexts generally associated with basking, lizards either lightened or darkened to colors that enhanced camouflage. Moreover, lizards that habitually perched on favored objects were noted to display colors and patterns that were cryptic on respective backgrounds. The observations reported here are consistent with the hypothesis that crypsis is an important function of coloration in Brown anoles, and plasticity of color change as well as postural behaviors enhance camouflage in this species. Our study also emphasizes the importance of continuous or repeated field observations of lizards in their natural habitats.

**Keywords.** Crypsis, Background matching, Green anole, Camouflage, Antipredator, Plasticity

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## Introduction

The family Anolidae includes more than 400 species of anoles, formerly considered to be iguanids and distributed from the southern U.S. to South America. Anoles are primarily arboreal and have expanded toepads, each bearing a claw and lamellar structures for adherence and climbing. A single species is native to the U.S., but nine West Indian species have become established in Florida. Of these, *Anolis sagrei* (Duméril and Bibron 1837, Brown anole) is widely distributed and is often in competition with the native Green anole, *Anolis carolinensis*, with which it also hybridizes (Bock *et al.* 2021). However, behavioral interference and copulation between the two species may not be common (Tokarz and Beck 1987). The Brown anole was first documented in the Florida Keys in 1887 (Garman 1887), and its prevalence as a non-native species is likely attributable to multiple independent introductions, mostly from Cuba (Kolbe *et al.* 2004). The Brown anole is now the most abundant lizard inhabiting peninsular Florida (Campbell 2000).

Densities of native Green anoles have been shown to decline following introduction of Brown anoles, and where the two species interact the Green anole exhibits a shift in usage of habitat to higher perches (Campbell 2000).

The Brown anole introduced to Florida occurs in many habitats and is a familiar lizard in urban and suburban environments. The species is largely diurnal and can be found on trees, shrubs, buildings, rocks and other objects near the ground. It is commonly seen at landscape plantings near buildings or parking lots. The Brown anole is considered a “trunk-ground” ecomorph (Williams 1983) and typically occurs <1 m above the ground (Meshaka *et al.* 2004). The native Green anole has been designated as a “trunk-crown” ecomorph and is typically found in trees and shrubs (Williams 1983; Losos 2009; Poe 2004). In parts of Florida where the native and introduced species of anoles occur together, *Anolis carolinensis* is variably outcompeted and shifts its perch heights to higher parts of the vegetation canopy (Lister 1976; Schoener 1975; Campbell 2000). However,

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there remains overlap of both tree and shrub vegetation whereon both species may co-occur. *Anolis carolinensis* is more often found higher up on the branches of trees and bushes (Oliver 1950), while *A. sagrei* tends to spend more time on the ground and is often found basking in sunny conditions (Rand and Williams 1969).

### Color and Color Lability in Lizards

The colors of skin in lizards and other squamate reptiles are variably adaptive and influenced by multiple factors of environment and mechanisms of change on varying time scales. Lizards have emerged as useful subjects and models for studies of color, and species of anoles are especially noteworthy in context of color change. Changes of color notably serve functions of camouflage, thermoregulation, and intraspecific communication, and they are responsive to stress (Norris and Lowe 1964; Gibbons and Lillywhite 1981; Medvin 1990; Cooper and Greenberg 1992; Stuart-Fox *et al.* 2004; Clusella-Trullas SC *et al.* 2007; Boyer and Swierk 2017; Pellitteri-Rosa *et al.* 2020; Sun *et al.* 2024; Hu *et al.* 2026). Crypsis enhances the fitness of animals and is one of the more important functions of coloration in animals (Stevens and Merilaita 2011).

The colors of lizards are determined both by structural features and pigments. Dark colors depend on the type, density and distribution of melanins. Pathways for synthesis produce two forms of melanin in melanocytes. Eumelanins are responsible for brown to black colors, and pheomelanins produce yellow to red coloration. Attention to changes of color in *Anolis* lizards historically have emphasized transitions from green to brown induced by stimulation of melanophores (Hadley and Goldman 1969; Vaughan 1987). Upward migration of melanophores to surround xanthophores and iridophores blocks light to these cells and produces skin of brown to black color. Alternatively, aggregation of melanin within melanophores reveals a skin of green coloration (Taylor and Hadley 1970). Stimuli from the environment are numerous and interactive in changing the colors of *Anolis* lizards, and the skin itself is sensitive to direct influence of light and temperature (Hadley and Goldman 1969; Vaughan 1987).

### Colors and Changes of Color in *Anolis carolinensis*

The Green anole is known for changing color from green to brown and is sometimes called the American chameleon. Its body coloration changes from bright green to dark brown, and the display of its dewlap is pinkish in color. Color change in Green anoles is hormonally controlled and often occurs in social encounters and during changes of temperature (reviewed in Greenberg 2002, 2003); the causality, context, and physical mechanism of color change is reviewed in Hadley and Goldman (1969) and Cooper and Greenberg

(1992). Several hypotheses to explain the functions of the different body colors have been offered and include crypsis, social signaling, stress, and thermoregulation. Despite much thought, observation, and research on these topics, the role of color and color-change in crypsis remains unclear (Losos 2009; Yabuta and Suzuki-Watanabi 2011). A study by Kiladze (2019) used image analysis to quantitatively assess the effective camouflage of Green anoles relative to color and the conditions of its habitat. Crypsis is clearly demonstrated in this species, but the effectiveness of camouflage depends on the various backgrounds of the chosen habitat.

### Coloration of *Anolis sagrei*

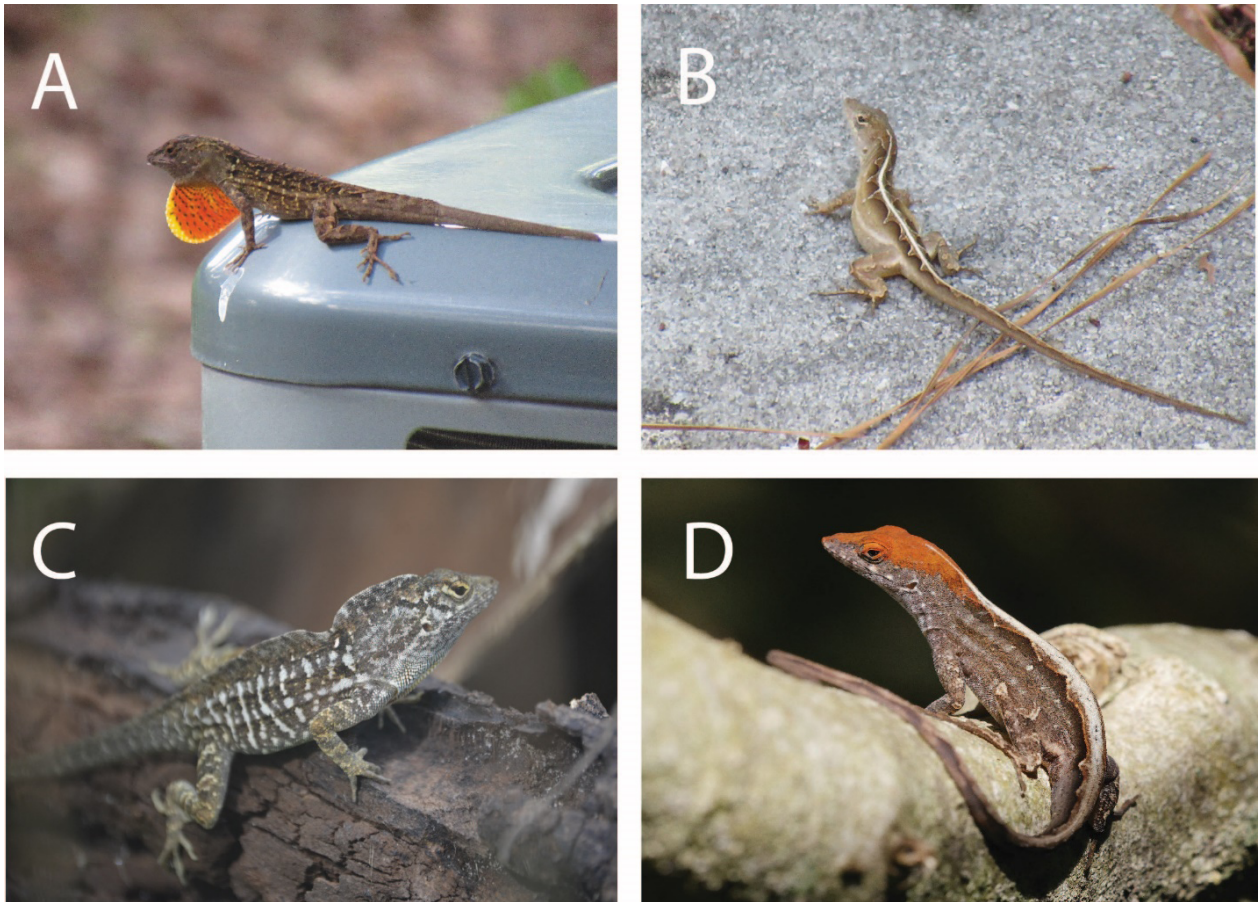
Brown anoles exhibit variation of colors but are typically light to dark brown with black markings on the dorsum and lighter colors as dorsal or lateral lines, spots or bars; females often have a light mid-dorsal stripe or an array of chevrons or diamonds (Fig. 1A, B). Other colors and patterns are also shown in Fig. 1. Males display a bright orange dewlap, which does not change with environmental or social conditions, and they sometimes develop a prominent dorsal ridge or crest extending from the neck to the tail (Figs. 1C; and see below 7, 8c). The crest varies in its development between different males and over time in some individuals.

### Methods

There are numerous publications concerning the colors of anoles, and these offer varied interpretations of causation and function. However, many of these studies present statistical analyses of previously published datasets or the use of museum specimens, and sightings and observations of wild anoles usually represent only brief snapshots in time. Here we report observations based on repeated sightings or continuous observation of individuals with attention to the details of background habitat and the context and behavior of the observed lizards. The observations took place at our residences and a few other locations in Gainesville and north-central Florida during the warmer months of the years 2021 through 2024.

### Results: A Case for Color Change and Crypsis

Body coloration of *Anolis sagrei* is variable in both hue and pattern (Figs. 1 through 9). The most frequently observed color is brown (Fig. 1A), but other colors are expressed in variable contexts (Schoener and Schoener 1976; Moon and Kamath 2019). Our observations indicate that attributes of color such as weaker hues, mottling, and changes in pattern on lizards can match similar attributes (solid or broken colors, shadows, variegated plant colors) of habitat that are generally not mentioned in analyses of *Anolis's* colors. These attributes might



**Fig. 1.** Variation of colors in *Anolis sagrei*. **A.** typical brown color with orange dewlap extended in a male. **B.** Typical brown color of a female with dorsal chevrons and white stripe extending onto the tail. This individual is rather light in color compared with that in A, likely owing to the light-colored background (cement patio). **C.** A mottled male with dorsal crest. **D.** An unusual female with a red head. Photos by HBL (A, B), Shauna Lillywhite (C), and T. J. Wronski (D).

be incidental or serve unknown functions, but they also appear relevant to possible enhancement of crypsis.

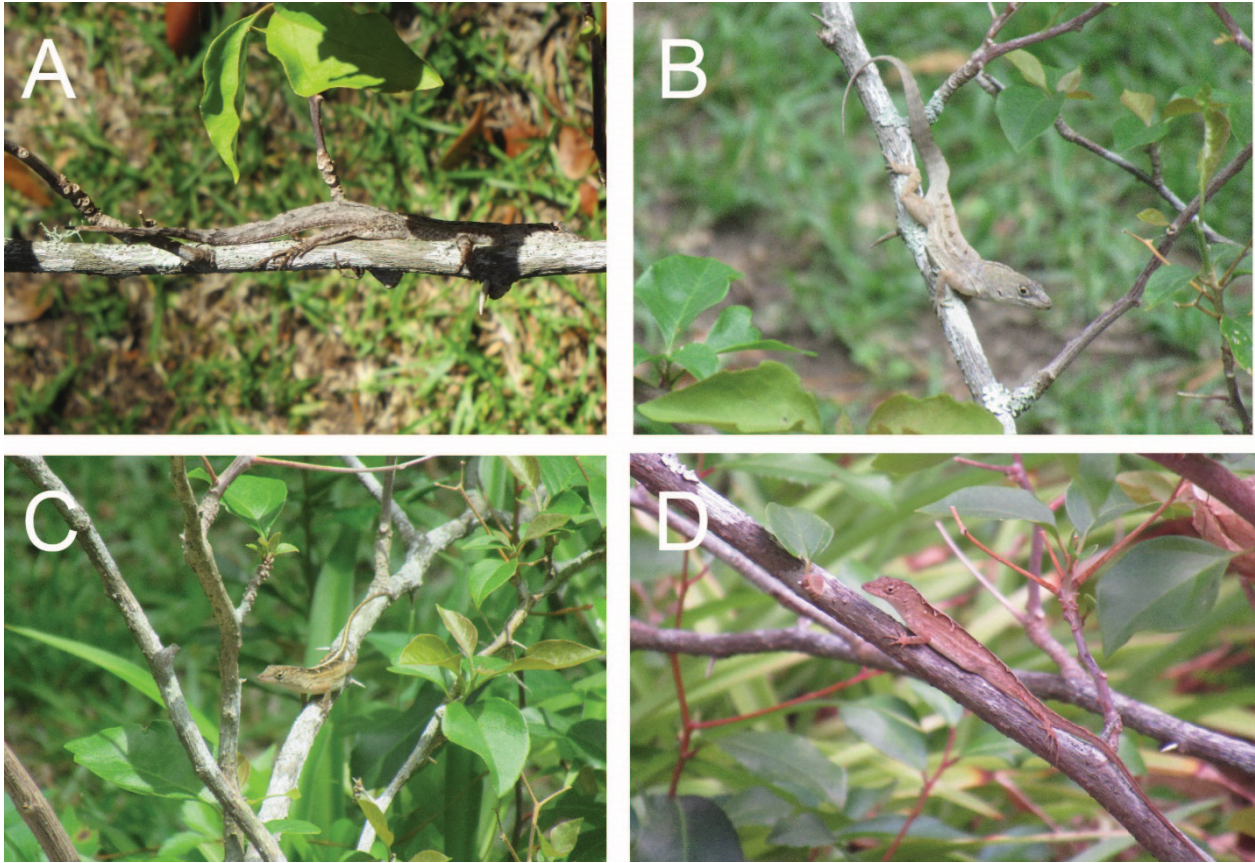
Figure 2 illustrates examples of *A. sagrei* that are perched on twigs in vegetation which were frequented by the respective lizards. Figure 2A and 2B feature two anoles that express light coloration when perched on twigs or branches having light gray color. With respect to the lizard featured in Fig. 2A, note that the animal has assumed a position and posture that enhances the camouflage considering the physical properties of the branch on which it rests. In Figs. 2C and 2D, the lizards express colors that do not closely match that of the twig on which they perch but exhibit green or reddish-brown colors that characterize the features of background that are prominent in their respective habitats. Hence, there are very likely cryptic elements of both foreground and background at play in how lizards might be viewed by predators and at what distance.

Figure 3 features two lizards that perched frequently on a reddish clay pot on a patio adjacent to a patch of green ferns. Much of the mid-dorsal body, head, and limb pattern of the lizards express an orange-red color that resembles that of the pot. The individual shown in the lower photo has a reddish colored head that is

sometimes seen in other individuals (Fig. 1D; context unknown).

One of these lizards shown in the figure (Fig. 3A) was periodically seen moving to the adjacent habitat of green ferns after it concluded basking and left the pot. We have never seen such a reddish-colored lizard within the fern patch but have noted female lizards with lighter gray dorsal patterns that were perched on a bush that grew among the ferns. It could not be determined whether one of the gray lizards seen among the ferns expressed the orange-reddish color when perching on the pot. That is, we cannot say whether the orange-reddish lizards that perched on the pot expressed lability of color change or had attained a fixed coloration during previous long-term association with the pot as a principal perch for basking. If the reddish colors were fixed, these individuals very likely were hiding during periods when they were within the ferns.

Figure 4 illustrates Brown anoles that were perching on light-colored objects, including the head of a clay tortoise sculpture (Fig. 4A), an air conditioning unit (Fig. 4B), and the trunk of a tree (Fig. 4C). Each lizard shown here had basked for some time previously and had assumed a lighter color without a prominent pattern



**Fig. 2.** *Anolis sagrei* perching on branches of shrubs, with variation in color providing camouflage related either to the color of the branch on which an individual is perched (A, B) or dominant colors of background vegetation (C, D). Photos by HBL.



**Fig. 3.** Two female *Anolis sagrei* that when basking habitually perched on a red clay pot adjacent to a thick-growth area of ferns. The lizards are shown under two different conditions of lighting (sun at top; partial shade with cloudy sky at bottom). Note the match with background of dorsal and lateral parts of the body. Photos by HBL.

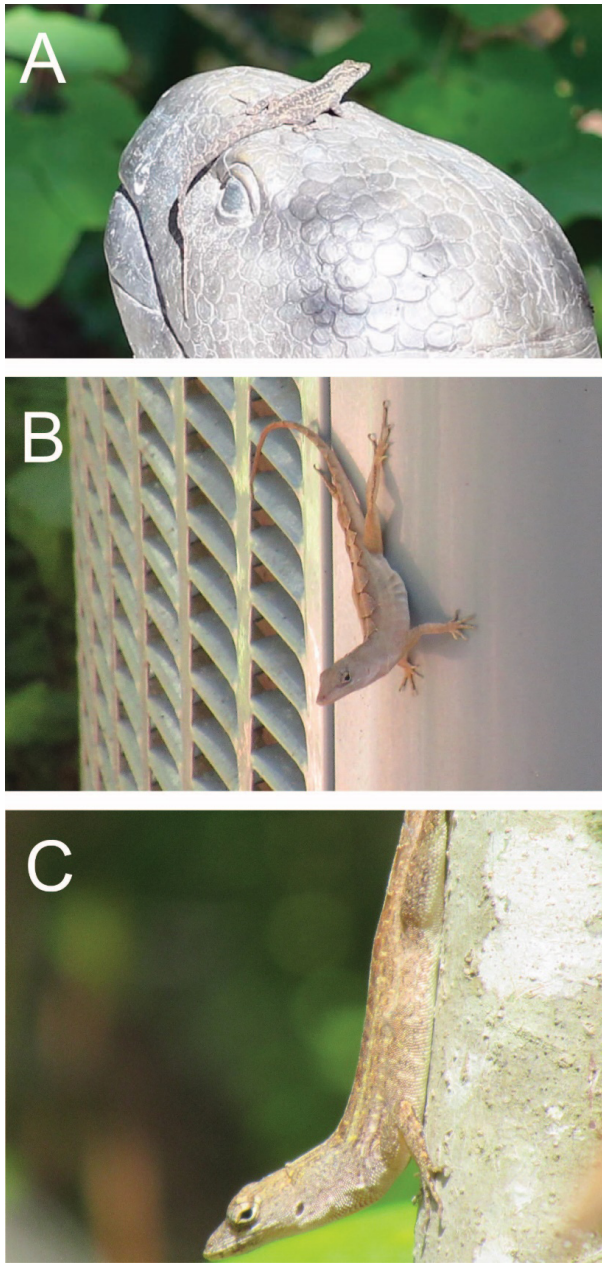
and matched the background on which it perched more closely than would the typical brown color of this species. Note the greenish tinges that suffused the lizard in Fig. 4C, thereby matching the light green colors of the bark that covered much of the tree trunk on which it perched.

The lizard featured in Fig. 5A illustrates an individual which had retained or adopted a brown color pattern that matched rather closely the brown colors of dead tree parts on which it was perched. The female lizard in Fig. 5B has a dorsal white stripe bordered by chevrons and brown colors with greenish tinges elsewhere on the body. When viewed from a distance  $>2$  m, the lizard appears cryptic in relation to the complexity of shapes and colors in the surrounding environment in which it is located.

Although we do not have photographs, we have noted remarkable matching of Brown anoles with background at three locations where pebble gardens are part of the landscaping. In all cases, the anoles were very light in color and were perched or moving among light-colored stones 3–5 cm in diameter with white, gray, or very light brown colors.

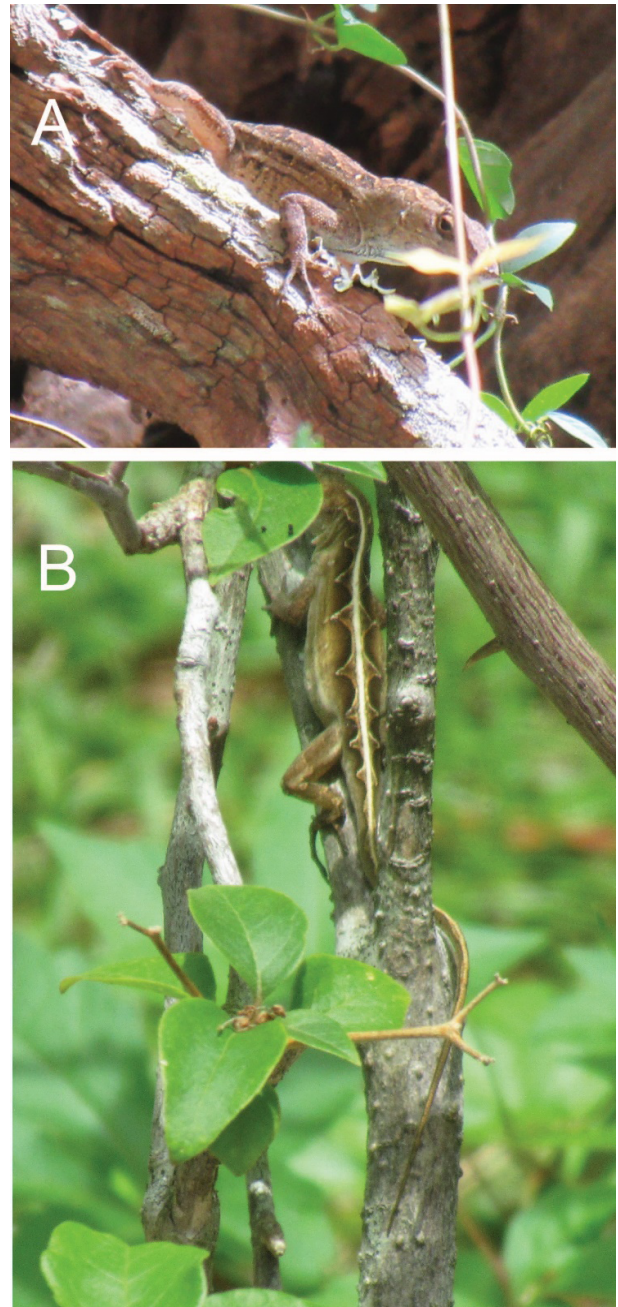
### ***Color change and background matching***

Here we report seven cases where we observed a lizard during a period in which it changed color and/or pattern that enhanced camouflage with respect to its background. Four of the cases were documented with photographs that are included in the descriptions that follow.



**Fig. 4.** Three *Anolis sagrei* variably color-matched to light-colored backgrounds. Compare the lizard shown in **B** with that shown in Fig. 1A (perched on same metal object). Note the greenish patches of skin on the lizard in **C**, including the venter which matches the color of green bark on the tree on which it is perched. Photos by ERJ (**A**) and HBL (**B**, **C**).

**Case 1:** April 28, 2023, ~ 1200 h at a restaurant in Gainesville, Florida (*Formaggio's Bistro*; now closed). The sky was mostly cloudy with intermittent sun. A Brown anole (presumed to be a female) jumped onto a patio table made of black metal mesh. The lizard was very dark in color, with a lighter mid-dorsal stripe. The perch height was ca. 80 cm. After just a few minutes the lizard crawled downward onto a thin, black electric cord that lay along a light reddish-tan brick floor with scattered bunches of yellowish-tan leaves. After ~ 7 minutes had elapsed, the lizard lightened perceptibly to a gray-tan color. After another 10 minutes, the lizard



**Fig. 5.** **A.** An *Anolis sagrei* perched upon, and adjacent to, dead wood pieces with colors that are also seen on the lizard. **B.** A female *A. sagrei* perched within variably colored twigs and branches associated with dominantly green vegetation. Photos by HBL.

moved to a position on a vertical black metal post that was part of a fence at the perimeter of the restaurant. It then again changed color to a dark brown typical of the species. No photographs are available.

**Case #2:** July 8, 2023, ca. 1130 h, Adult male Brown anole, backyard tables at a store (*Mosswood Farm Store and Bakehouse*) in Micanopy, Florida. A lizard was seen sitting at the edge of a wooden table that was light yellow-tan in color. The color of the lizard was a light yellow-brown. It sat on the table for ~12 minutes, occasionally displaying its orange dewlap. At ~ 11:45 h, the lizard jumped to a nearby metal table that was black

in color. During the course of ~10 minutes, the lizard darkened considerably to a dark brown color that better matched the table on which it rested. No photographs are available for this observation.

**Case #3:** April 26, 2023, 1158 h, front yard of HBL's residence, Gainesville, Florida. A male Brown anole was seen to climb upon the top of a lamp post that was metal and light tan-gray in color. The lizard was a characteristic dark brown color that was very conspicuous against the lighter background (Fig. 6A). Within 9 minutes, the color of the lizard changed from its brown color to a uniformly lighter gray color with almost no evident pattern (Fig. 6B). On another occasion, the same lizard was seen perching on a metal bench that was rusty brown in color. The color of the lizard at that time closely matched that of the bench on which it perched, and a pattern of lighter spots and faint stripes was evident (Fig. 6C).

**Case #4:** April 22, 2023, 1322 h, front yard of HBL's residence, Gainesville, Florida. A male Brown anole was observed as it perched head down on a wooden shutter on the front of HBL's house. The body of the lizard had a black crest with lateral dark color against yellowish hues (Fig. 7A). During the course of three minutes, the darker colors lightened and the color pattern on the sides of the lizard faded perceptibly, while the tail, venter, and head changed to a uniformly lighter gray color (Fig. 7C). The lizard appeared better camouflaged following these changes.

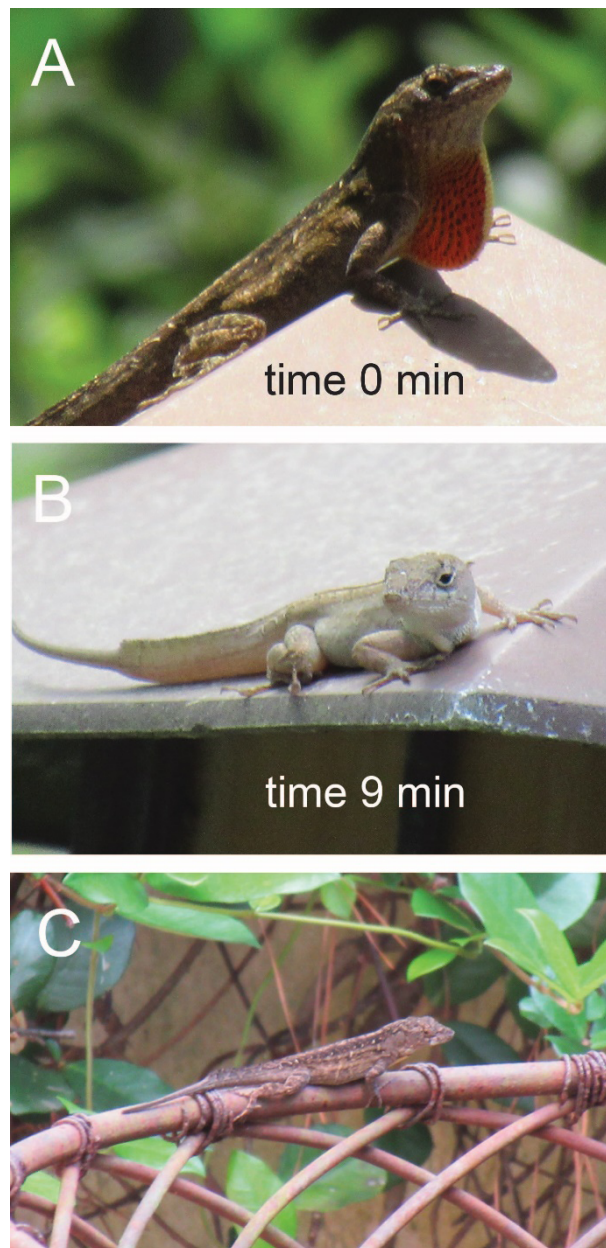
**Case #5:** March 15, 2024, 1608 h, backyard patio of HBL's residence, Gainesville, Florida. As in case #4, a male Brown anole crawled onto a gray plastic chair and perched on its arm. The lizard had a slight dorsal ridge and was quite dark with black patterning on its sides (Fig. 8A). Within one minute, the lizard lightened to a gray color with obscured pattern and some extension of the dorsal ridge to form a prominent crest (Fig. 8B). The change of color rendered this lizard less conspicuous while it was perched upon the chair. A second lizard (Fig. 8C) was seen later on the same chair with a light and matching color as in 8B.

**Case #6:** February 13, 2025, 1200 h, ChopStix restaurant, Gainesville, Florida. A very dark female anole jumped onto a white PVC pipe immediately adjacent to a light-green wall and perched lengthwise adjacent to a table with observers. After 15 minutes, this anole was observed to have changed to a much lighter brown color and what appeared to be a wider lighter area running the length of the dorsal torso. No photographs are available for this observation.

**Case #7:** June 26, 2021, 1726 h, fern garden in the front yard of HBL's residence, Gainesville, Florida. A dark brown male Brown anole was seen perching among ferns where it remained for some while. During the 92 minutes of periodic observation, the lizard changed color from its dark condition to a light green color which more closely resembled that of the background vegetation

in which it moved and perched (Fig. 9). This is one example in which lability of color in the Brown anole changed from brown to green, qualitatively similar to changes that are seen in the Green anole.

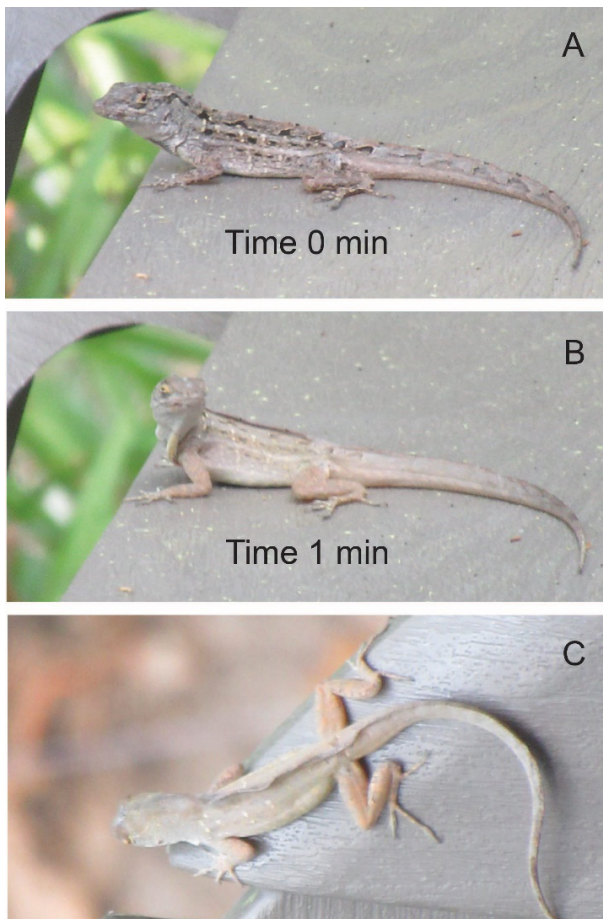
In addition to the above cases, two other observations are noteworthy. On May 14, 2025, HBL visited a *Steak and Shake* restaurant in Gainesville, Florida, where the landscape plantings were in beds of small white rocks. At 1330 h, a *A. sagrei* was observed moving intermittently over rocks between the plants. This individual lizard was color-matched with the white rocks in that its body color was extremely pale grey with almost no evident



**Fig. 6.** A male *Anolis sagrei* that was observed on 04/26/2023 when it crawled upon a tan-gray lamp post at 1158 h and within 9 minutes lightened from dark brown to light gray color to match its substrate (A, B). The same lizard on 05/13/2023, shown in C perching on a rust-brown metal which it tended to match in color, but with lighter, more reddish hues than that of the condition shown in A. Photos by HBL.



**Fig. 7.** A male *Anolis sagrei* perched on very light-gray-brown wood and lightened to better match the background in 3 minutes. Photographed on 04/22/2023 by HBL.



**Fig. 8.** A male *Anolis sagrei* that crawled upon a light gray patio chair and lightened in 1 minute to an almost solid light gray color that matched that of the chair on which it perched. The lizard featured in the lower photograph (C) is a different individual but also had assumed a light and largely solid color that closely matched that of the same chair shown in A and B. Photographed on 03/15/2024 by HBL.

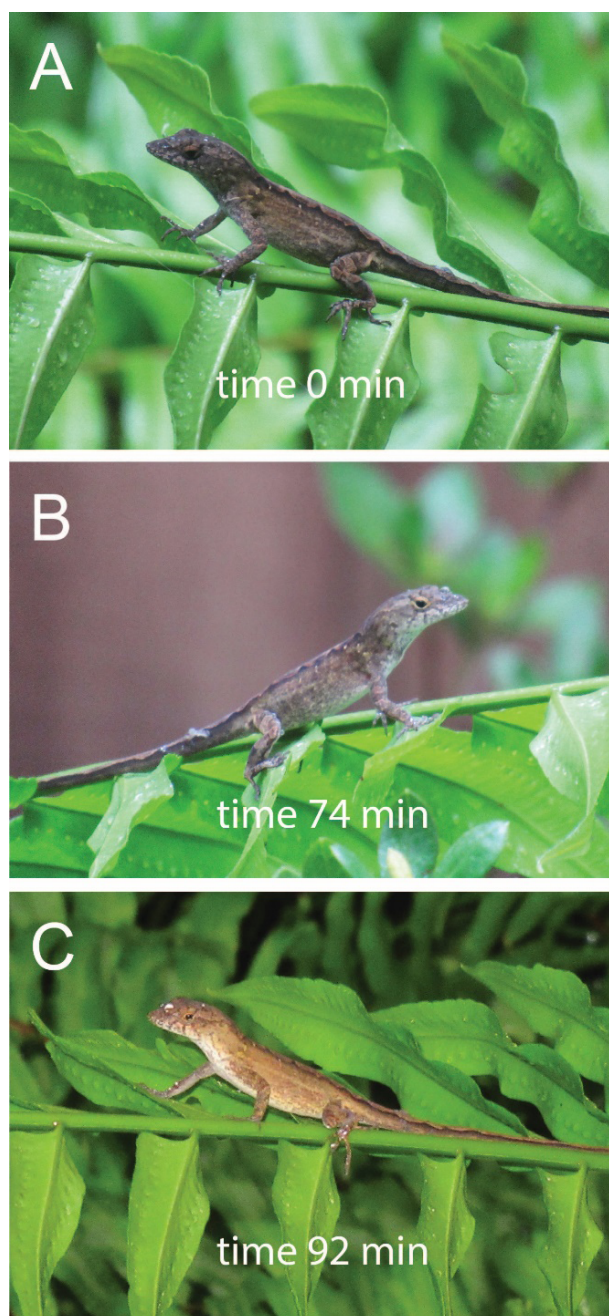
pattern. HBL watched this lizard for a few minutes, and it remained on the rocks and did not move onto a plant. We surmise that this lizard had either changed by means of plastic adjustment from its normal brown color to a nearly white match with the surrounding rocks, or perhaps its color was more permanently light because of prior living among the white rocks. A camera was not at hand to document the color of this particular lizard, but it resembled the individuals that are illustrated in Figs. 2B, 4A, 6B, and 8C.

Finally, on May 16, 2025 HBL visited a restaurant in northeast Gainesville, Florida, and sat at an outside table. It was soon noticed that two Brown anoles were sitting and periodically moving on the patio floor, which consisted of large insettings of stone that were very light gray to light pinkish-orange in color. Both of these anoles were a very light gray-brown color that matched the stone floor rather well. Simultaneously, a third Brown anole was noticed sitting vertically and head-down on a piece of dark tree branch that was part of a planter. This anole displayed its orange dewlap occasionally, and it was a very dark brown that matched the wood on which it perched. All three anoles were very likely active and associated with their respective backgrounds for some time before they were observed.

The data related to the timed changes of color in *A. sagrei* are summarized in Table 1.

## Discussion

Crypsis and background matching of coloration has a long history of discussion and acceptance in biology (Darwin 1794; Cott 1940; Endler 1978) and seems to be, in our many years of personal experience, quite common



**Fig. 9.** A presumed female *Anolis sagrei* seen perching among ferns, changing (on a scale of just tens of centimeters) location and position while being observed by HBL on 06/26/2021. When first seen, the lizard was a dark gray-brown in color but changed to a light green during 92 minutes of observation. The dark lizard (A) was conspicuous against the green background of fern leaves and stems, and the change of color was in a direction (green) to better match the background. Photos by HBL.

as an antipredator strategy in predator-prey systems involving squamates (see also Norris and Lowe 1964; Gibbons and Lillywhite 1981; Krohn and Rosenblum 2016; Marshall *et al.* 2016). Coloration of squamate reptiles can change in response to many environmental conditions and over many time scales, including rapid changes that reflect phenotypic plasticity and ‘physiological color change’ (Price 2006). To understand



**Fig. 10.** A wild *Anolis carolinensis* photographed while perching in green vegetation with cryptic color match and posture. Predatory snakes (e.g. *Nerodia* spp.) and birds (e.g., herons, hawks, various passerines) are numerous at this location. Photo taken at 1300h, 10/08/2023, Sweetwater Wetlands Reserve, Gainesville, Florida, by HBL.

the causation and significance of color changes in the wild, the variation of color patterns should be assessed with respect to geographic patterns, time scale and environmental context, and the possible role of plasticity (Price 2006). The variation of possible colors can provide a foundation for understanding the mechanisms underlying intraspecific variation and crypsis.

Here we discuss our observations in context of crypsis. Although our observations are consistent with the hypothesis that color changes contribute to camouflage, we also caution that causality cannot be established by observations alone. Moreover, multiple functions of coloration can be compatible or in conflict depending on the nature and consistency of selective pressures. For example, Sun *et al.* (2024) demonstrated that in adjacent populations of an agamid lizard, *Phrynocephalus putjatai*, dark and light dorsal coloration facilitates both thermoregulation and camouflage and in respective habitats that differ in substrate color and thermal quality (e.g. dark and cold vs. light and warm). It was found that a point mutation of a specific gene resulted in variations of skin coloration that were positively selected in contexts of both camouflage and thermoregulation. Analysis of

## Coloration and Color Change in the Brown Anole

**Table 1.** Summary of color changes when individuals of *Anolis sagrei* were observed over time.

| Date       | Habitat or microhabitat                   | Time begin, h | Background color              | Sex of lizard | Color change of lizard                                           | Elapsed time, min |
|------------|-------------------------------------------|---------------|-------------------------------|---------------|------------------------------------------------------------------|-------------------|
| 06/26/2021 | dense foliage of green ferns              | 1726          | green                         | M             | brown to light green                                             | 92                |
| 4/28/2023  | Patio with scattered leaves               | 1130          | yellowish-tan                 | F             | dark brown to gray-tan                                           | 7                 |
| “          | black metal post on patio                 | 1137          | black                         | F             | gray-tan to dark brown                                           | Est. 10           |
| 7/08/2023  | tables on patio                           | 1130          | Black                         | ?             | yellow-brown to dark brown                                       | Est. 10           |
| 04/26/2023 | Lamp post                                 | 1158          | Light tan-gray                | M             | dark brown to more uniform light gray                            | 9                 |
| 04/22/2023 | light wood shutter                        | 1322          | light gray-brown              | M             | black crest, dark sides w mottling to light gray w less mottling | 3                 |
| 03/15/2024 | gray plastic patio chair                  | 1608          | gray                          | M             | dark gray-brown w black mottling to lighter gray                 | 1                 |
| 02/13/2025 | white pvc pipe next to a light-green wall | 1200          | white adjacent to light green | F             | dark brown to lighter brown                                      | 15                |

the spectral properties of skin in *Anolis carolinensis* indicates that the reflectance of visible and near-infrared light increases with increasing temperature, suggesting that changes of body color not only serve functions of camouflage and social signaling but also assist thermoregulation (Hu *et al.* 2026).

Brown anoles that are invasive to Florida do not characteristically change color from very uniform brown to a nearly uniform green that renders two fundamentally contrasting color morphs as is seen characteristically in the native Green anoles. In our experiences in urban and suburban Florida environments, most sightings of Brown anoles are of brown individuals, hence the name “Brown” anole. Solidly green lizards resembling Green anoles are not seen, but individuals with greenish colors are sometimes observed in shrubs or trees with green vegetation (*e.g.*, Figs. 2C, 4C, 9C). Brown colors of varying patterns would seem appropriate as a fundamental or “baseline” color for a ground- and trunk-dwelling lizard. Dark colors are variable in Brown anoles, with stripes, mottling, or nearly uniform patterns that can match attributes of near-ground environments (Figs. 2D, 3, 5, 6, 8). More subtle aspects of matching patterns could be circumstantial, but we have noted them in multiple instances (Figs. 2, 4, 5, 7, 8). Matching of pattern as well as colors with background environments has been noted in other species of lizards (Gibbons and Lillywhite 1981).

Turning consideration to Green anoles, both brown and green colors seem appropriate for a species that perches among shrubs and trees where these colors are quite common in background habitat. Thus, it seems that both species of anole that are considered here express dominant colors that could be adaptive in context of camouflage and antipredator behaviors. Note that the immobile wild Green anole shown in Fig. 10 has expressed both a green color and postural behavior that appear to enhance camouflage in an environment where predatory birds and snakes are known to be common. Clearly, the strength of visual hiding (“camouflage index”) is maximally effective for a lizard that is perched in appropriate conditions of habitat (Kiladze 2019).

We do not intend to imply that Brown anoles

change color strictly to match backgrounds and minimize detection by predators. Social signaling and thermoregulation might also affect the coloration of Brown anoles. In instances where lizards changed to a lighter color when perched against a light or pale-colored background, a warming of body temperature while basking might also have influenced the color of a lizard (Norris and Lowe 1964). On the other hand, we have observed lizards either darken or lighten after changing perch locations on variably colored backgrounds during periods of sun exposure when basking levels of body temperature likely had already been attained. In a study of Green anoles, Yabuta and Suzuki-Watnabe (2011) reported that male lizards tended to be green (but some were brown) while perching at higher positions presumably to advertise social signals to broad areas. The green color was thought to be more conspicuous for social functions, but the movement and background history of individuals were not observed. Hence, the green colors (instead of brown) might also have been influenced either by the color of background vegetation and/or lightening attributable to basking (see also Medvin 1990). Advertisement of location and social signals are enhanced by bobbing movements and extension of a brightly colored dewlap, and these behavioral attributes of *Anolis* seem to us more important to signaling than are green colors that tend to match lizards with vegetation at any position within green foliage (Fig 10). However, it has generally been assumed that green coloration is a sign of social dominance (*e.g.*, Boyer and Swierk 2017). Importantly, a study of an Australian agamid species complex (Stuart-Fox *et al.* 2004) suggests that crypsis plays a substantial role in the evolution of color variation while color patterns also represent a balance between the need for conspicuousness for signaling and the need for crypsis to avoid predation.

The color of *Anolis* lizards can be influenced by conditions of ambient light intensity and the albedo of a surface on which a lizard is perched (Hadley and Goldman 1969). Temperature of the skin also directly affects its color and alters the rate at which the skin responds to hormones (Hadley and Goldman 1969). Color-matching with background might also extend

into invisible spectral regions such as UV (Norris 1967; Jacobs 1992). Hence, background color matching is a complex topic and one that deserves more detailed and continuous observations of individual lizards over appropriate time scales.

Changes in colors that match backgrounds of lizards can be rapid (minutes or hours) or slow (days) depending on the pigments and the mechanisms involved (see Sherbrooke 1997 and literature citations therein; see also Vaughan 1987). Our observations of wild lizards changing color to match features of background include both relatively rapid as well as longer time scales and include features of pattern as well as hue. Behavior can also optimize features of camouflage related to color (Fig. 2A), and lizards might prefer backgrounds on which camouflage related to color is enhanced by position or posture (Figs. 3, 5, 10) (Marshall *et al.* 2016). Whether a lizard best matches the immediate object on which it perches or the more general background (Figs. 2, 5) might depend on the visual field of the lizard, its body temperature, and the intensity of illumination, with the advantage of camouflage being further dependent on the distance and view of potential predators. This study illustrates the importance of continuous observations of lizards to identify features of color change that have potential significance as antipredator features but are challenging to observe, quantify, and interpret.

### The Importance of Observation and Details

Recently, it was demonstrated that 246 ecologists analyzing the same data sets reached widely varying conclusions, and some effects were found to be in totally opposite directions (Gould *et al.* 2025). Such lack of consensus is often related to differences in the choice or application of statistics, but we suggest that conclusions concerning behavior of organisms can also arise from the use of datasets without adequate attention to detailed observations. Evaluation of crypsis involving organisms changing color is a particular case in point.

The use of datasets involving positions and colors of organisms that are snapshots in time has the pitfall of not knowing the context of behavioral motivation just prior to the snapshot. Hence, judgments about color-matching of such organisms might include variable amounts of error depending on the dataset. Our observations of *A. sagrei* suggest that such errors might be considerable because these lizards characteristically perch for short periods and undertake considerable movement between pauses of motion while on vegetation or other objects. Moreover, in complex habitats or microenvironments having variable colors, knowing quantitatively just ‘how cryptic’ a lizard might be to potential predators depends on the position, distance, view, visual apparatus, and behavior of the predator, and these variables are difficult to quantify or even guess. Given the complexity of colors and shapes of objects in various environments, quantification of color matching often entails subjective

selection of data. We suggest that one could either support or refute a case for background color-matching depending on how the data are analyzed. What seems clear from our observations is that in those cases when a lizard is paused and stationary for more than a moment, the position, posture and color of the animal renders it less conspicuous than in cases where a lizard is engaged in periodic movement (Figures 2A and 10).

In consideration of these issues, here we do not attempt to quantify background color-matching, as the choice of analysis and conclusions are subject to variable interpretation. The points we demonstrate with rigor of observations are (1) *Anolis sagrei* change color, and (2) in cases where an animal is carefully observed, the directional change of color while on a particular perch and without disturbance is toward a better match with the immediate background. Finally, given what is known concerning the biology of *Anolis* lizards, conflicting selection pressures likely influence optical signaling (*e.g.*, crypsis and sexual recognition). Hence, one might demonstrate the uses of color in either system, but neither system is perfect. These findings corroborate the Schoener (1968, 1975) hypothesis that green body coloration provides crypsis.

### *Anolis sagrei* and Conservation

The Brown anole is invasive to Florida, but there is little hope and no coherent effort to control its populations. It is now the most common lizard in Florida and has competed well with native anoles and probably other species of lizards. Thus, today this species is a dominant and highly conspicuous element of the state’s herpetofauna. As such, we suggest this species has significance to conservation and managements largely in three contexts.

First, understanding the biology of *A. sagrei* will contribute to assessments of whether and how it successfully competes, suppresses, or displaces the native anole, *Anolis carolinensis*. Such evaluation has potential application to competitive relations and the invasive successes of this lizard not only in Florida, but at other locations as well.

Second, because of its widespread abundance in Florida, *A. sagrei* is an important candidate for detecting threats to the state’s herpetofauna generally, including impacts of storms, abundance of prey, disturbances to habitat, disease, and pesticides. Hence, it is a bioindicator of the health of rapidly changing ecosystems throughout Florida and beyond. Although we do not have quantitative data, it is our impression that local populations of *A. sagrei* are either less robust or absent in urban and suburban settings where pesticides are used compared with landscaped habitats that are free of pesticides. Moreover, we sometimes find lizards that are very thin and suspect that individuals with seemingly lower body condition do not find sufficient insects to prey upon. Issues of prey abundance might be causally

related to the impacts of pesticides, either locally or broadcast over larger areas. Bioindication of changes in the abundance of insects has numerous implications beyond any local issue related to demography of *A. sagrei* (Yang and Graton 2014; Hallman et al. 2017).

Third, and more generally, as sequelae to above, *A. sagrei* is potentially a model invasive vertebrate that may further understanding of invasive ecology applicable to any variety of ecosystems. Its utility as a model invasive organism is enhanced by its ease of introduction to novel habitats, capacity for dispersal, conspicuous behavior, reproductive potential, flexibility in choices of perching sites, and small but appropriate size for ease of observation. Understanding the variation of color in this species also is important because of related functions that affect individual fitness, especially the ecology of predator and prey relationships in context of crypsis (Endler 1978; Stevens and Merilaita 2011).

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