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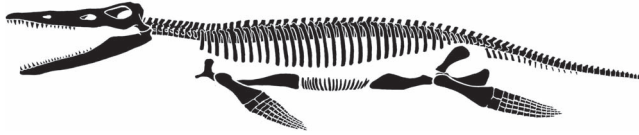
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FEMALE SIGNAL VARIATION IN THE *ANOLIS LEMURINUS* GROUP

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ABSTRACT. Within the lizard genus *Anolis*, color variation in the dewlap, an important signaling trait, can indicate local adaptation or divergence between populations. Most research on anole dewlaps has taken aim at males rather than females. Despite several publications of unrelated lizard genera with links between female signal color polymorphisms and fecundity, variation in female anole dewlaps has received less inquiry. We compiled dewlap photographs of females from several populations of the *Anolis lemurinus* group, characterized color variants through visual assignment, and tested for associations of dewlap color to body size and dewlap area. We describe the first case of polymorphic dewlap color in females and relatively monomorphic dewlap color in males within a group of anoles. Our survey found that female dewlap color variation in the group is more similar between geographically proximate northern populations of *A. lemurinus* and *A. bicaorum* than between populations ascribed to *A. lemurinus* from different regions. Additionally, we provide evidence that female body size in this group may correlate with dewlap coloration. Our findings support the need for further taxonomic research within the *A. lemurinus* group, as well as research into the potential mechanisms driving and maintaining color polymorphism in female signaling traits.

KEY WORDS: *Anolis lemurinus*; *Anolis*; sexual selection; sexual dimorphism; female signals; female dewlaps

INTRODUCTION

Anolis lizards (anoles), widely known as a classic example of adaptive radiation in the West Indies, are increasingly being used as

model species for a wide range of ecological and evolutionary studies (Losos, 2009, and references therein). Anoles have incredible variability in sexual dimorphism, often-prominent signaling ornaments, and high species diversity. These traits make them ideal targets for addressing hypotheses related to sexual selection, behavior, diversification, and trait evolution. Furthermore, an abundance of background research on natural history and ecology of these lizards allows evolutionary questions to be more

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easily addressed (Losos, 2009; but see Kamath and Losos, 2017).

Among the most charismatic of anoline traits is the dewlap, an ornament believed to play a prominent role in sexual selection (Losos, 2009). Dewlaps are extendable throat fans that come in a variety of colors and sizes (Nicholson et al., 2007; Ingram et al., 2016); males primarily use the dewlap for species recognition (Rand and Williams, 1970; Williams and Rand, 1977; Losos, 1985, 2009), predator deterrence (Leal, 1999), territory defense (Vanhooydonck et al., 2005) and to signal mate quality (Cook et al., 2013). In female anoles, some species are reported to use dewlaps for social signaling, territory, and courtship (Jenssen et al., 2000; Leal and Losos, 2000; Cook, personal communication). Between species, structure and function of dewlaps is much more variable in females than males (Harrison and Poe, 2012), an observation that could have resounding implications for evolutionary and ecological mechanisms of diversification in the group.

Female dewlaps tend to be diminutive in size and mirror the coloration of male conspecific dewlaps (Harrison and Poe, 2012). Because of this trend, few studies to date have focused on the evolution and diversity of female anole dewlaps. However, the findings of Harrison and Poe (2012) suggest that in *Anolis* lizards, female dewlap area can be an important predictor of habitat use and size differences between the sexes. Moreover, signaling traits in color polymorphic female lizards of the unrelated genera *Lacerta* and *Urosaurus* can be important predictors of female body size and reproductive output (Zucker and Boecklen, 1990; Vercken et al., 2007).

Female dewlap color polymorphisms in *Anolis* appear to be quite rare. They have been reported only in populations of *Anolis lemurinus* (Savage, 2002) and *A. salvini* in

Costa Rica and Panama (Bienentreu et al., 2013). Recently, a handful of populations have been elevated to species status within the range of *A. lemurinus*: *A. bicaorum* (Köhler, 1996), *A. roatanensis* (Köhler and McCranie, 2001), *A. serranoi* (Köhler, 1999), and *A. lyra* (Poe et al., 2009). These species belong to a monophyletic group (Poe et al., 2017) that includes *A. vittigerus* (Cope, 1862), herein referred to as the *A. lemurinus* group (Poe et al., 2017). Within the *A. lemurinus* group, males are described as possessing dewlaps with various shades of red (Köhler, 1999; Poe et al., 2009; McCranie and Köhler, 2015), whereas dewlaps of females are reported as either absent, red, white, or similar to male dewlap coloration (Köhler, 1996, 1999; Köhler and McCranie, 2001; Savage, 2002; McCranie and Köhler, 2015).

Here we report a high degree of within-population dewlap color variation in females of the *A. lemurinus* group. We surveyed dewlaps of females in the northwestern portion of the species' range (Belize and Mexico) and within two heavily sampled populations in Honduras and Costa Rica, and we tested for associations between female dewlap color and body size and dewlap area. Female *A. lemurinus* from Belize and Mexico and the closely related *A. bicaorum* from Honduras exhibit high dewlap color polymorphism, whereas female *A. lemurinus* from our Costa Rican population are color monomorphic. In all three populations, we find that dewlap color correlates with body size, but not dewlap area.

MATERIAL AND METHODS

Field observations

We sampled *A. lemurinus* from Belize, Costa Rica, Honduras, and southern Mex-

ico between 2010 and 2017. Sampling was conducted through visual surveys during the day or night and captures made by either hand or noose. Fieldwork was conducted under the authority of collecting permit FAUT-0243 issued to Uri O. García-Vázquez by the Secretaría de Medio Ambiente y Recursos Naturales, FAUT-0093 issued to Adrián Nieto-Montes de Oca, and DE-MP-090-2017 and 043-2017-ACC-PI issued by the Honduran Instituto de Conservación Forestal (ICF) and the Costa Rican Ministerio de Ambiente y Energía (MINAE) and Comisión Nacional para la Gestión de la Biodiversidad (CONAGEBIO), respectively, to Sofia Prado-Irwin. Any specimens collected were deposited in the Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México.

Dewlap color assignment

For all populations, we grouped by geographic proximity and classified female dewlap color by eye as either red, orange, gray, or cream (Figs. 1, 2). In the presence of patterning, grouping was based on the color that made up the majority of the dewlap area (Fig. 2H). Although we realize this is a subjective binning of potentially continuous color variation and that dewlap patterns can be a compounding factor (see Nicholson et al., 2007), most individuals were easily scored into color groups because of low proportions of secondary coloration (Figs. 2A–G). For the populations in Costa Rica and Honduras, we quantified dewlap area from photographs taken in the field with the image processing software FIJI (Schindelin et al., 2012). We calculated relative dewlap size for those individuals by dividing dewlap area by snout-vent length (SVL). For individuals in Mexico and Belize, ImageJ (Schneider et al., 2012) was used to calculate

dewlap area and head length, and relative dewlap size was calculated using head length (HL) in place of SVL (Ingram et al., 2016).

Statistical analysis

To determine whether dewlap size or body size differed between females of different morphs, we performed three separate analyses. First, we used a combined data set of Costa Rican and Utilan (Honduras) animals, for which we had SVL data and dewlap photos, which allowed for the calculation of relative dewlap area from photos ($n = 106$). Second, because the Costa Rican population only contained one morph, we performed a separate analysis on the Utilan population to test whether dewlap size and body size varied between individuals with different colored dewlaps. Third, for individuals from Belize and Mexico, we used head length as a proxy for body size (see Ingram et al., 2016) and tested whether head length and relative dewlap area varied between individuals with different colored dewlaps.

For the combined Costa Rica and Utilan analysis, dewlap size was normally distributed (Shapiro-Wilk test; dewlap size: $W = 0.98764$, $P = 0.439$) but SVL was not (Shapiro-Wilk test; $W = 0.97398$, $P = 0.03515$). We therefore performed a one-way ANOVA using dewlap color (red, orange, gray, or cream) as the independent variable and dewlap size as the dependent variable, and a non-parametric Kruskal-Wallis test using dewlap color as the independent variable and body size as the dependent variable. We then performed post hoc Dunn tests to determine how group means varied.

For the within-population analysis of Utilan females only, all data were normally distributed (Shapiro-Wilk test for dewlap size: $W = 0.97103$, $P = 0.08686$; SVL: $W = 0.97316$, $P = 0.1163$). We performed one-way

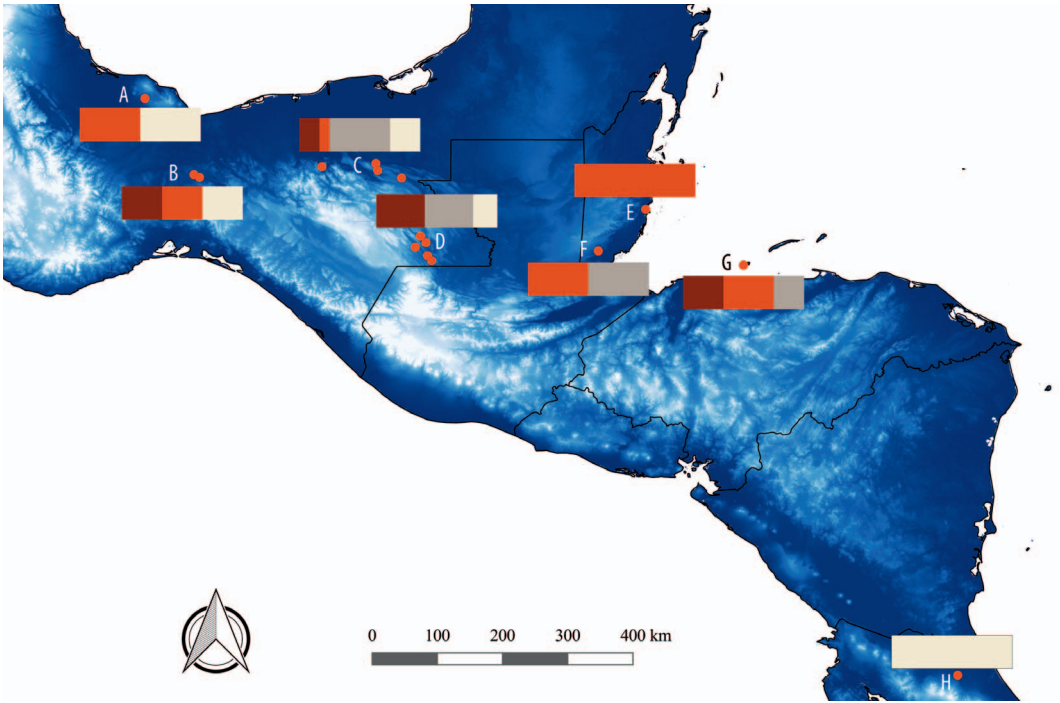


Figure 1. Sampling map showing individuals as orange dots and elevation continuously from low elevation (0 meters) in blue relative to high elevation (approximately 2600–5600 meters) in white. Bar graphs indicate the percentage of female dewlap color morphs (red, orange, gray, and cream) within populations for localities: (A) Salto de Eyipantla, Mexico ($n = 2$), (B) Chinantla, Mexico ($n = 3$), (C) El Panchan, Mexico ($n = 12$), (D) San Quintin, Mexico ($n = 5$), (E) Hopkins, Belize ($n = 1$), (F) Lubaantun, Belize ($n = 2$), (G) Utila, Honduras ($n = 90$), and (H) La Selva, Costa Rica ($n = 18$).

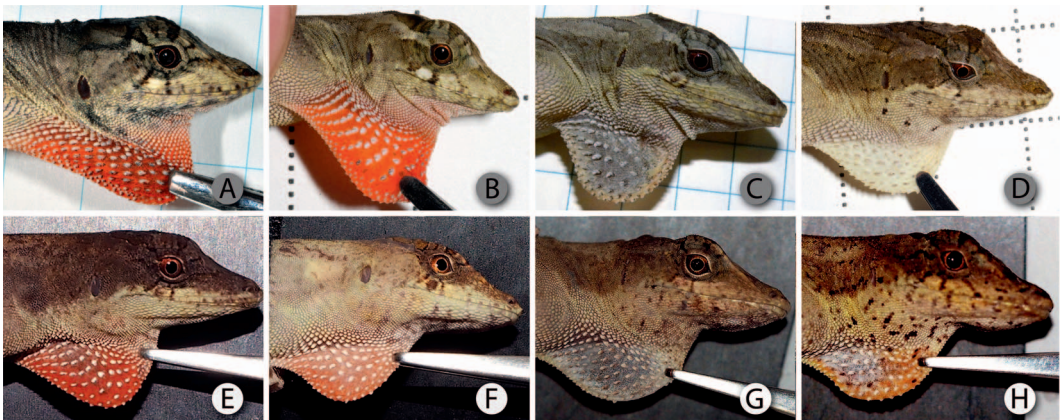


Figure 2. Representative female *A. lemurinus* color morphs from Belize and Mexico: red (A), orange (B), gray (C), cream (D); and female *A. bicaorum* from Utila, Honduras: red (E), orange (F), gray (G), divided orange with gray (H).

analyses of variance (ANOVAs) using dewlap color (red, orange, or gray) as the independent variable and dewlap size and body size as the dependent variables, respectively. We then performed post hoc Tukey honestly significant difference (HSD) tests to determine how group means varied.

For individuals from Belize and Mexico, we used head length as a proxy for body size (Ingram et al., 2016) and tested whether dewlap size and head length varied between individuals with different colored dewlaps. We only used females for which dewlap size and head length could be calculated from photos ($n = 23$). Head length and relative dewlap area were normally distributed (Shapiro–Wilk test; HL: $W = 0.9555$, $P = 0.3788$; relative dewlap area: $W = 0.97672$, $P = 0.8434$), so we performed one-way ANOVAs to test whether head length or dewlap area differed among females with different colored dewlaps. We then performed post hoc Tukey HSD tests to determine how group means varied.

RESULTS

We collected a total of 25 females from several localities in Belize and Mexico, 84 females from Utila, Honduras, and 18 females from La Selva, Costa Rica (Fig. 1). Overall, we identified four color morphs ranging from continuous (or nearly so) variation between red, orange, gray, or cream (Fig. 2). The heavily sampled population on the Honduran island of Utila ($n = 84$) contained three of the color morphs (red, orange, and gray) found in our sample sites from northern Central America (Figs. 2E–G). A number of Utilan females had partially cream dewlaps, but these contained a majority of gray area and were thus classified as gray. The population from La Selva exhibits substantially less variation, with all samples possessing cream dewlaps (n

$= 18$). The only variation seen at La Selva was in the number of black gorgetal scales on the dewlap (Fig. 3).

The combined analysis of Utilan and Costa Rican females ($n = 106$) showed that the relative sizes of dewlaps of different colors were significantly different (ANOVA $F = 3.358$, $df = 3$, $P = 0.022$). Cream dewlaps were smaller than red dewlaps (Tukey HSD $P = 0.018$) and slightly smaller than orange dewlaps, although this difference was not statistically significant (Tukey HSD $P = 0.097$); Figs. 4IA, IB). Additionally, females with different dewlap colors had significantly different body sizes (Kruskal–Wallis $\chi^2 = 10.606$, $df = 2$, $P = 0.004977$; Figs. 4IIA, IIB): females with gray dewlaps were significantly larger than all others (Dunn test $P < 0.001$), females with orange dewlaps were smaller than those with gray dewlaps but larger than those with red dewlaps (Dunn test orange-red $P = 0.06228$; Fig. 4IB), and cream-dewlapped Costa Rican females were significantly smaller than all others (Dunn test orange-cream $P < 0.001$; Figs. 4IIA, IIB). However, it is important to note that Costa Rican females, all of which had cream dewlaps, also had significantly smaller body sizes (Wilcoxon rank sum test $W = 189$, $P < 0.001$; Figs. 4IIA, IIB) overall than the Utilan females and displayed somewhat greater variance in dewlap size (Fligner–Killeen test of homogeneity of variances $\chi^2 = 3.22$, $df = 1$, $P = 0.073$; Figs. 4IA, IB).

To remove the confounding effects of the color monomorphic Costa Rican population, we analyzed the polymorphic Utilan population separately. Among the Utilan females ($n = 74$), dewlaps of different colors were not significantly different in relative area (ANOVA $F = 1.027$, $P = 0.363$; Fig. 4IB). However, females with different dewlap colors had significantly different body sizes ($n = 74$; ANOVA $F = 12.72$, $P < 0.001$): females with gray dewlaps were larger than

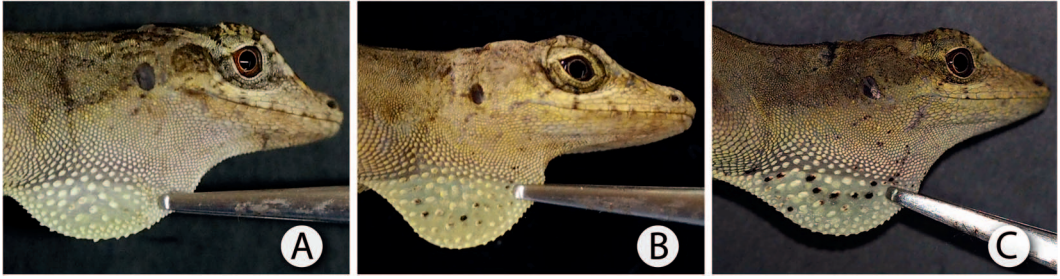


Figure 3. Variation in the amount of black gorgetal scales of *A. lemurinus* females from La Selva, Costa Rica.

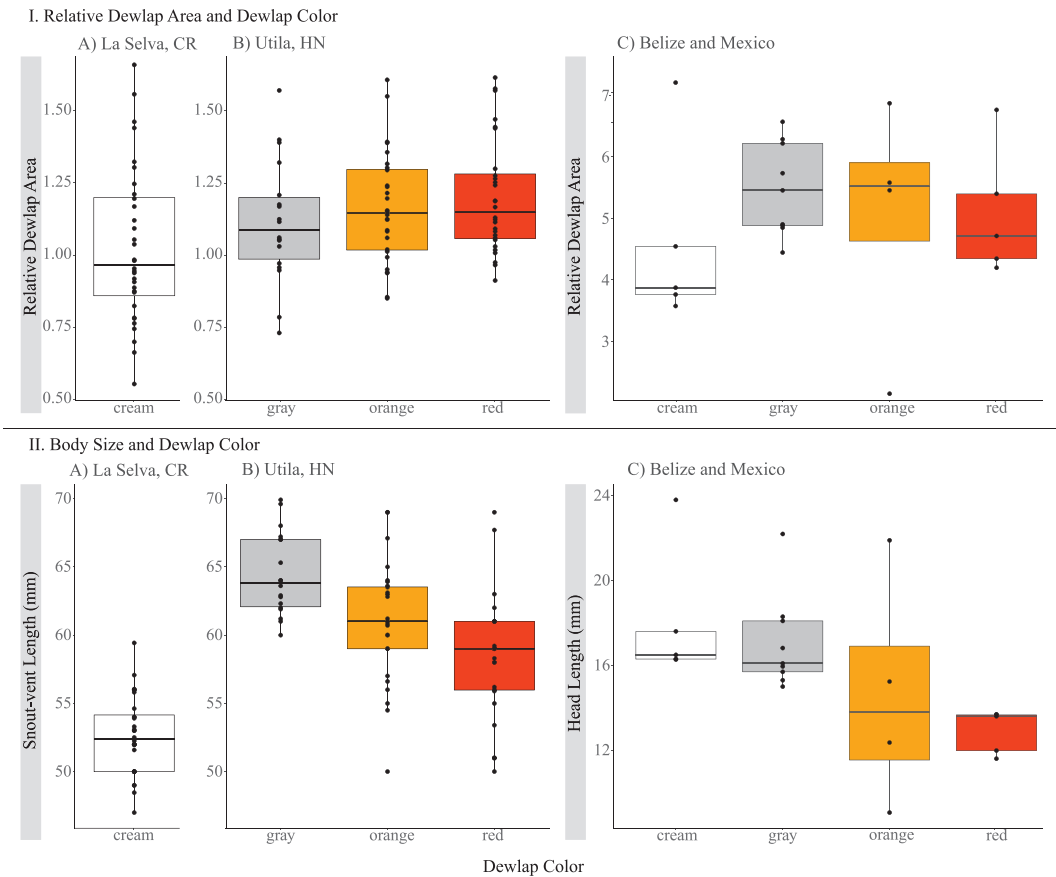


Figure 4. Relative dewlap area (I) and body size (II) for each color morph in female *A. lemurinus* group populations from La Selva, Costa Rica (A), Utila, Honduras (B), and Belize + Mexico (C). Relative dewlap area was calculated for each individual as dewlap area divided by body size, using scaled photographs in ImageJ software. Snout-vent length is used as a proxy for body size in samples from populations (A) and (B), and head length is used as a proxy for body size in samples from population (C).

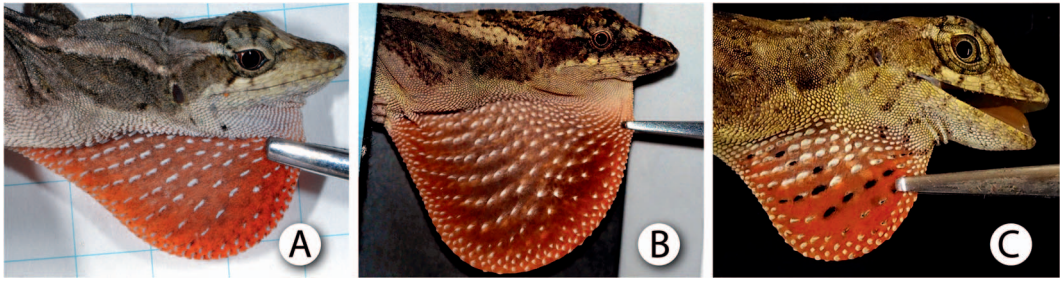


Figure 5. Representative male dewlaps from (A) *A. lemurinus*, San Quintin, Mexico; (B) *A. bicaorum*, Utila, Honduras; and (C) *A. lemurinus*, La Selva, Costa Rica.

those with either red or orange dewlaps (Tukey HSD $P < 0.01$), and females with orange dewlaps were larger than those with red dewlaps (Tukey HSD $P < 0.01$; Fig. 4IIB).

Like Utilan females, for Belize and Mexico, we found that dewlaps of different colors were not significantly different in relative dewlap area (Kruskal–Wallis $\chi^2 = 7.2841$, $df = 3$, $P = 0.0644$; Fig. 4IC), but females with different colored dewlaps did have significantly different body sizes ($n = 23$, ANOVA $F = 3.131$, $P = 0.0498$; Fig. 4IIC). Post hoc Tukey HSD tests showed that this result is driven by the difference in body size between females with red dewlaps (smaller body size) and cream dewlaps (larger body size; $P = 0.06$), whereas body sizes of females with gray and orange dewlaps were not statistically distinguishable from the other groups ($P > 0.1$).

DISCUSSION

In our surveys of multiple *A. lemurinus* group populations, we identified polymorphic female dewlap color in populations from northwestern Central America and a contrasting lack of female dewlap color variation at a site in southeastern Central America (Costa Rica). We identified four distinct dewlap color morphs among females—red, orange, gray, and cream. However, we also observed color variation

between those color morphs, with individuals between gray and cream being most difficult to differentiate. In these few cases, majority color was selected as the morph category, which might suggest that female dewlap color is a continuous trait. To our knowledge, this is one of only two cases of significant intraspecific female dewlap color variation, the first being *A. salvini* (Bientre et al., 2013). In contrast to this previous case, we found that in the *A. lemurinus* group, female dewlap color variation was not consistent across its range. In populations from Belize, Honduras, and Mexico, female dewlaps were polymorphic in color (Fig. 2), whereas the study population in Costa Rica was nearly color monomorphic (Fig. 3). Unlike male dewlap coloration in *A. salvini*, male dewlap color variation appears to be relatively uniform across the *A. lemurinus* group, with slight variations in brightness and gorgetal scales (Fig. 5). This unique case of dewlap color polymorphism in the female sex and relative color monomorphism in the male sex may not only lend significant insight into the ecology and biogeography of the *A. lemurinus* group, but also has implications for the study of female dewlap form and function in *Anolis* as a whole.

There are a number of potential explanations behind the pattern of female dewlap color variation in the *A. lemurinus* group.

Our data from the polymorphic populations (not Costa Rica) suggest that dewlap color is correlated with body size, which may relate to fecundity, as is common in other species exhibiting color polymorphism (Fig. 4; Gray and McKinnon, 2007). For instance, polymorphic ventral coloration and body size in the lizard genus *Lacerta* correlates with clutch success and sex ratio (Vercken et al., 2007), and in the genus *Urosaurus*, female throat color and body size are predictive of clutch size (Zucker and Boecklen, 1990). Such morphologic traits may also be associated with behavioral strategies, as seen in males of the genus *Uta* (Sinervo and Lively, 1996), a system with phenotypically and behaviorally distinct morphs that exhibit different resource use, reproductive strategies, or both (Losey et al., 1997; Andrés et al., 2002; Pruitt et al., 2008). Alternatively, the relationship we observed between body size and dewlap color is also consistent with a change in dewlap color over ontogeny, which has also been seen in female *Urosaurus* (Carpenter, 1995). In populations of *Urosaurus*, the smallest and therefore youngest females have orange throats, which fade to yellow with age. However, in anoles, juveniles hatch without a dewlap and develop it as they mature, and there is no evidence for dewlap color change after sexual maturity in any *Anolis* species to date. Moreover, carotenoid supplementation trials in *A. distichus* and *A. sagrei* show no diet effects on dewlap color (Steffen et al., 2010; Ng et al., 2013). Future work investigating whether female anoles with different dewlap colors exhibit distinct reproductive behavior or resource use strategies, or instead belong to different age classes, would inform our knowledge of sex-specific selection pressures and the genetic basis of this trait.

Our results may also shed light into the patterns of biogeographic variation within the *A. lemurinus* group generally. As ex-

plained above, the *A. lemurinus* group is made up of multiple species, including the two island species *A. bicaorum* (Utila, Honduras) and *A. roatanensis* (Roatán, Honduras), and the four mainland species *A. lemurinus* (Mexico through Panama), *A. lyra* (Ecuador and Colombia), *A. serranoi* (El Salvador, Guatemala, and Mexico), and *A. vittigerus* (Panama and Colombia). Although *A. lemurinus* populations throughout their entire range are still considered conspecific, morphologic evidence suggests that a significant genetic break may exist between northwestern and southeastern populations (Savage, 2002), although this hypothesis has not been fully explored. Our results, showing female dewlap color polymorphism in both *A. bicaorum* and *A. lemurinus* populations in Mexico and Belize supports the idea that these species share more similarities with each other than they do with the population sampled in Costa Rica. Research on female dewlap form and function is lacking (Harrison and Poe, 2012), so we can only speculate that the difference in female dewlap color variation between northwestern and southeastern *A. lemurinus* populations may reflect separate evolutionary trajectories.

Our findings in Costa Rica contrast with previous reports by Savage (2002), which suggest that red-dewlapped *A. lemurinus* females exist in Costa Rica as well. It is possible that we did not find any red-dewlapped females because the color polymorphism is regionally variable and our population is color monomorphic. Alternatively, the ratio of red- to cream-dewlapped females may be much lower in the Costa Rican population, such that our limited sampling was unable to detect any red-dewlapped females. For instance, we are confident color polymorphism occurs in Hopkins, Belize, because our single sample from this population is not isolated from

Lubaantun, Belize, where we did detect variation. For this reason, more extensive surveys, particularly in the southern range of *A. lemurinus*, would be informative to determine the extent of color monomorphism in Costa Rica. Although we can only speculate as to the source of these differences, it is possible that ecological factors differing between the Costa Rican and Utilan habitats or communities impart different selection pressures, such that color polymorphism may be either beneficial in the island context or detrimental in the mainland context, or both. Further evaluation of the function of the female dewlap is of paramount importance for understanding the potential selective pressures acting on this female display trait.

SUMMARY

Here we publish the first record of female-only polymorphic dewlap coloration in an anole species group and the first evidence of a correlation between body size and dewlap coloration within females of an anole species. A cursory look at variability within females of other mainland species (Gray, personal observation) suggests variation in female coloration may be more common than in males. However, most of the within-species variation known thus far for female anoles consists of either no color or light coloration similar to males of the species. The patterns revealed here make clear that research into the structure and function of female dewlaps is greatly needed, because we can currently only speculate as to what mechanisms may be responsible for the color variation we observed. Further investigations should include molecular data, more in-depth analyses of populations, quantifiable color measurements, and modeling of dewlap pattern over geographic and environmental space.

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