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Colorful displays signal male quality in a tropical anole lizard

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Abstract Parasites influence colorful ornaments and their behavioral display in many animal hosts. Because coloration and display behavior are often critical components of communication, variation in these traits may have important implications for individual fitness, yet it remains unclear whether such traits are signals of quality in many taxa. We investigated the association between ectoparasitic mite load and the color and behavioral use of the throat fan (dewlap) by male *Anolis brevirostris* lizards. We found that heavily parasitized lizards exhibited lower body condition, duller dewlaps, and less frequent dewlap displays than less parasitized individuals. Our results thus suggest that highly parasitized individuals invest less in *both* ornamental color and behavioral display of that color. Because the two components of the signal simultaneously provide information on male quality, this study provides novel support for the long-standing hypothesis that colorful traits may function as social or sexual signals in reptiles.

Keywords *Anolis* · Color · Dewlap · Display behavior · Ectoparasites

Introduction

Ectoparasites exploit a variety of host resources and can thus affect many aspects of host condition (Lehmann 1993). Colorful ornaments are often vulnerable targets of the negative effects of ectoparasites (Hamilton and Zuk 1982; Fitze and Richner 2002) because color expression is linked to physiological processes underlying condition (Hill et al. 2009).

Ectoparasites have been found to limit color expression (Tschirren et al. 2003) and behavioral display (Doucet and Montgomerie 2003); however, the degree to which ectoparasites affect fitness remains unclear (Proctor and Owens 2000). Among taxa as diverse as insects, fish, birds, and reptiles, individuals use coloration to communicate quality and status (Bradbury and Vehrencamp 2011), yet we lack a general understanding of whether ectoparasites alter the information signaled by colorful animal structures.

Anolis lizards are an excellent group in which to investigate the potential for ectoparasites to influence the coloration and behavioral use of a color signal. Most anoles possess colorful dewlaps (throat fans) primarily extended during courtship and territory defense (Jenssen 1977). The dewlap is a signal of male fighting ability (Vanhooydonck et al. 2005), and its behavioral use is thought to influence mating success (Tokarz et al. 2005). However, the communication role of dewlap color is not clear (Nicholson et al. 2007) and it is unknown whether signal color and display behavior interact to indicate advertiser condition.

Parasites may negatively affect both physical ornament properties such as color and behavioral investment in ornament display. Color can be produced via structural mechanisms or by deposition of pigments such as carotenoids and pterins (Steffen and McGraw 2007; San-Jose et al. 2013), all of which influence anole skin coloration (Macedonia et al. 2000; Steffen and McGraw 2007). Many pigments also serve important physiological functions, including acting as free radical scavengers (McGraw 2005). Pigment allocation to ornaments thus reduces the availability of these bioactive pigments for use in mounting immune responses (McGraw and Ardia 2003). Only individuals with fewer parasites or increased ability to combat infestation should allocate sufficient pigment resources to produce high quality coloration (but see Steffen et al. 2010). Coloration may then signal the level of a host's parasite infestation or the preparedness of its

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immune system (Lozano 1994). Parasites also affect host metabolism (Booth et al. 1993) influencing the energy allocated to behavior. In many taxa, ectoparasites are negatively associated with display behavior, such that heavily parasitized individuals display less frequently than individuals with fewer parasites (e.g., Clayton 1990). The simultaneous effect of parasites on color and behavior generates the potential for information about individual quality to be directly communicated by both colors and behavioral advertisement of these colors.

Here, we investigated the relationship between ectoparasite load, dewlap coloration, and display behavior in male *Anolis brevirostris*, trunk-dwelling lizards that have yellow to red-orange dewlaps. Lizards in our study population were naturally parasitized by ectoparasitic trombiculid mites in the folds of the dewlap and axillae. These body fluid-feeding mites may negatively affect hosts in a variety of ways, including inducing immune responses due to dermal inflammation and necrosis (Goldberg and Bursley 1991). We tested the hypothesis that dewlap color and display both signal male quality in *A. brevirostris*. Specifically, we predicted that heavily parasitized individuals exhibit less vibrantly colored dewlaps, lower body condition, and fewer dewlap displays than less parasitized individuals.

Materials and methods

We observed the behavior of 30 adult male *A. brevirostris* lizards at CoralSol Resort in Barahona, Dominican Republic in July 2011. We performed 30–60 min (mean=58.9 min) observations for each lizard recording all display behaviors of the focal lizard. After observation, we captured each lizard and confirmed its sex by the presence of hemipenes (male copulatory organs). We measured each lizard's snout-vent length, mass, and the length of the second ceratobranchial cartilage, a linear proxy for dewlap size (Johnson and Wade 2010). Using a hand lens, we counted each lizard's ectoparasitic mites. Prior to dewlap color measurement, lizards were held in individual bags for 1–35 h (mean=7.61 h). Holding time was not statistically associated with any subsequent measure of dewlap coloration (results not shown).

We measured dewlap coloration for each lizard using an Ocean Optics 20001 spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin FL). We used a fiber optic probe fitted with a plastic probe holder secured at a 90° angle to light the sample and measure dewlap reflectance. The probe holder minimized ambient light in reflectance measures and maintained a consistent distance between the probe and dewlap. Reflectance was quantified as the proportion of light reflected from the dewlap at 1 nm increments within the lizard visible range (320–700 nm, Fleishman et al. 1997). Dewlap reflectance was measured relative to a Spectralon white reflectance standard (Lapsphere Inc., NH) with the system

calibrated against this and a dark standard prior to measuring each individual. We took reflectance measurements at five haphazard locations within the central region of the dewlap, on the left, lateral side of the fully extended dewlap.

Using the mean reflectance curve for each individual, we calculated the following tristimulus variables with RCLR 9.33 (Montgomerie 2010): mean brightness (mean reflectance across 320–700 nm; herein “brightness”), hue (wavelength corresponding to $[\{\max \text{reflectance} - \min \text{reflectance}\} / 2]$), and red and yellow chroma (sum of reflectance from 605–700 and 325–550 nm, respectively, divided by brightness).

We used linear regressions to determine whether ectoparasite load predicted lizard body condition, tristimulus measures of dewlap color, or dewlap display rate and whether dewlap color was associated with dewlap display rate. To estimate body condition, we used standardized residuals from a linear regression with body length and mass (Jakob et al. 1996). One individual performed dewlap extensions at a rate greater than two standard deviations above the mean and was excluded. Except where noted, analyses with and without this individual were similar.

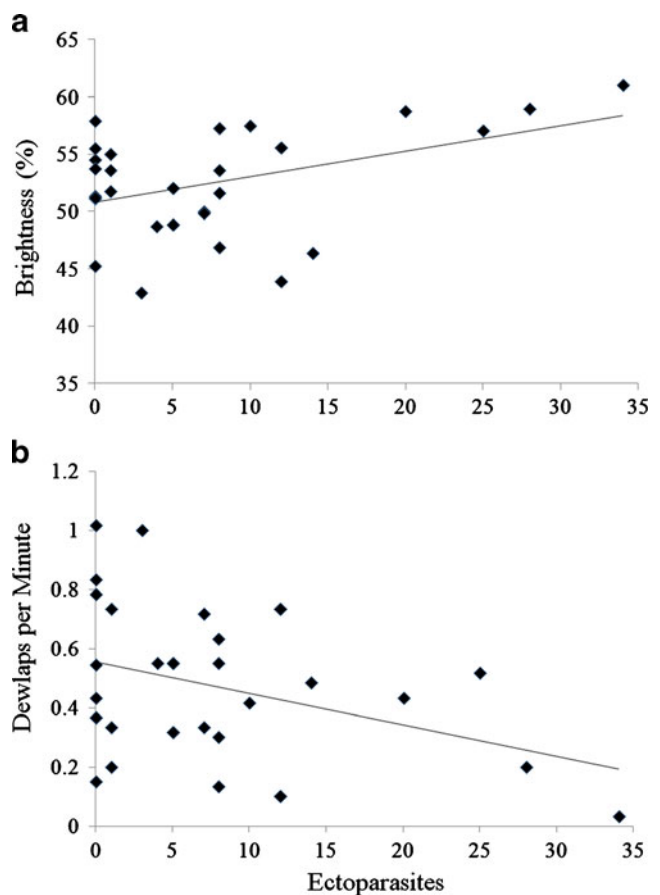


Fig. 1 Ectoparasite load predicts dewlap brightness and display rate. **a** Each individual's dewlap brightness represents the average brightness (mean reflectance between 320 and 700 nm) calculated using five measurements of each dewlap. **b** Dewlap display rates represent dewlap extensions performed per minute of focal observation

Results

Parasites and coloration

Twenty-two of the 30 males were parasitized by 1–34 trombiculid mites (mean=7.93, SE=1.68). Dewlap brightness increased with ectoparasite load ($F_{1,27}=6.07$, $p=0.02$, $R^2=0.18$; Fig. 1a), but parasite load was not associated with dewlap hue ($F_{1,27}=1.72$, $p=0.20$), red chroma ($F_{1,27}=2.58$, $p=0.12$), or yellow chroma ($F_{1,27}=0.05$, $p=0.81$).

Parasites and display behavior

Lizards with higher ectoparasite loads displayed their dewlaps less frequently than less parasitized lizards ($F_{1,27}=4.38$, $p=0.046$, $R^2=0.14$, Fig. 1b; with outlier included, $F_{1,28}=1.21$, $p=0.28$). More colorful (less bright) lizards performed more dewlap extensions than lizards with less colorful dewlaps ($F_{1,27}=6.48$, $p=0.017$, $R^2=0.19$; with outlier included, $F_{1,28}=1.06$, $p=0.31$). Dewlap display rate was not associated with hue or chroma ($p>0.12$).

Parasites and condition

Ectoparasite load was negatively associated with body condition ($F_{1,27}=14.0$, $p=0.001$, $R^2=0.34$), such that more parasitized lizards had lower condition, but body condition was not related to any measure of dewlap color (all tristimulus variables: $p>0.22$). Individuals with higher body condition displayed more frequently than lower condition individuals ($F_{1,27}=10.5$, $p=0.003$, $R^2=0.28$; with outlier included, $F_{1,28}=3.08$, $p=0.09$).

Discussion

This study demonstrates that dewlap coloration and display behavior may serve as honest indicators of male quality in lizards. Associations between the two components of dewlap display, ectoparasite load, and lizard condition indicate that coloration and behavior convey important information that may be interpreted by prospective mates and rivals, potentially affecting social interactions and reproductive success.

Our observation that heavily parasitized *A. brevivirostris* have brighter dewlaps suggests that these hosts' dewlaps may have fewer light-absorbing pigments. Brightness is a measure of the light reflected of a surface, and pigments act in a subtractive manner by absorbing certain wavelengths. If highly parasitized individuals are depositing fewer pigments in dewlaps, this may indicate that they are allocating more pigment resources to immune function to combat parasitism (McGraw and Ardia 2003). However, alternative mechanisms could also account for the observed color differences. For example, pigment-based ornamental colors are often enhanced by underlying structural color

components (Shawkey and Hill 2005) such as iridophores, and recent evidence suggests that color variability may be strongly influenced by differences in these underlying reflective surfaces rather than differences in pigment allocation alone (San-Jose et al. 2013).

Increased parasite loads were also associated with lower body condition and less frequent display behavior. Both of these relationships may result from mites reducing available host resources. This may occur as mites siphon resources by digesting host tissues, directly reducing the total resources available to the host, or infection by mites may stimulate a costly immune response drawing resources from other host metabolic processes (Bonneaud et al. 2003). Alternatively, low condition lizards may be more susceptible to parasite infection. Surprisingly, while both body condition and color were associated with parasitism, body condition itself was not associated with color, possibly indicating that coloration is more influenced by the direct effects of parasitism.

In many cases, the most valuable information about an animal's quality may be communicated by a combination of ornamental structures and the behaviors that display them (i.e., a multi-component signal; Johnstone 1995) rather than either trait alone. For example, female mate choice in guppies is influenced by both male coloration and display behavior such that the quality of these traits together determines mate choice (Kodric-Brown and Nicoletto 2001). This integration of information from the color of ornamental structures and their display also has the potential to influence social or sexual selection in reptiles. Future studies that manipulate anole parasite loads and measure changes in dewlap color and use would experimentally verify these results.

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