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ARE DEWLAP COLOR AND DISPLAY BEHAVIOR HONEST INDICATORS OF MALE QUALITY IN *ANOLIS* LIZARDS?

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A DEPARTMENT HONORS THESIS SUBMITTED TO THE
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Abstract

Colorful ornaments such as the pattern of a butterfly wing or the plumage of a peacock's tail are among the most stunning products of evolution. Color, and the behaviors during which color is advertised, have come to serve important signaling functions for many species. Because color is often influenced by ecological factors such as diet or parasite load, the quality of an individual's ornamental color can serve as an honest indicator of aspects of advertiser condition. For this thesis, I have investigated the potential for ornamental coloration and display behavior to serve as honest indicators of male quality as determined by ectoparasite load and body condition in three species of Caribbean *Anolis* lizards. Male lizards of these species possess dewlaps, brightly colored throat fans extended for use during behavioral interactions such as courtship or territory defense. I conducted two studies in the Dominican Republic in which I performed focal behavioral observations, quantified dewlap coloration using spectrometry, and estimated the ectoparasite loads and body conditions of lizards. In the first study, I examined individual variation in the red-orange dewlap coloration and display behavior among a population of *Anolis brevirostris* lizards, and found that individuals with more parasites exhibited dewlaps of higher brightness, were of lower body condition, and performed fewer dewlap displays than did individuals with fewer parasites. In the second study, I examined variation in dewlap color and display behavior in populations of *Anolis cybotes* and *Anolis distichus* lizards distributed at different elevations across two mountain chains. I observed that ectoparasite load differed between mountain chains, and that dewlap color increased with elevation for both species on both chains. Because measures of male quality were associated with aspects of color and behavior, the potential remains for dewlap color and display behavior to serve as honest indicators of male quality.

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CHAPTER 1

INTRODUCTION: DEWLAP COLOR AS A SIGNAL IN *ANOLIS* LIZARDS

Elaborate ornaments such as the brilliant plumage of a peacock's tail or the massive horn of a scarab beetle are among the most visually stunning products of evolution. Colorful ornaments are not simply decorative—for many ornamented species, these traits serve as signals, and are thus critical components of communication within these species (Bradbury and Veherencamp 1998). Signals are traits that contain information and are used to increase an organism's fitness by influencing the behavior of the individual receiving and interpreting the information contained in the signal (Guilford and Dawkins 1991). Signals are both widespread and highly variable among different organisms, and may be comprised of physical structures such as a weapon, behavioral patterns such as a courtship display, or a combination of physical and behavioral attributes. The information contained in signals is nested within these attributes or combinations of attributes. For example, characteristics such as the size or color of a structure or the quality of a behavioral performance may provide information that a receiver observing the signaling individual may be able to perceive, interpret, and use to "inform" future behavior. If the influenced future behavior of the receiver involves such outcomes as choosing to mate with the signaler, signals may have important fitness implications for these organisms.

Honest signals, or those which contain information about an advertising individual that cannot be faked, are of particular interest to investigators of animal communication. A signal may be "honest" for a variety of reasons. Some signals may only be produced by individuals of particular physical condition—red deer (*Cervus elaphus*) stags of larger body size, for example, are able to perform calls of acoustic quality that are both attractive to females and impossible for males of smaller body size to perform (reviewed in Reby and McComb 2003). Other signals may be honest because they are costly to produce or maintain, perhaps requiring that an individual allocate valuable resources to the development of a large structure or endure increased predation risk due to the maintenance of a flashy characteristic. Thus, such signals are honest due to the "handicap" principle – because of the costs associated with these traits, only individuals of superior quality such as those with ample access to resources or robust immune systems, for example, should be able to maintain high quality signals (Zahavi 1975).

Charles Darwin noted in his theory of sexual selection that females of many species exhibited preference for more elaborately ornamented males, and that as a result, males with a particular quality of ornamentation were better able to attract mates than were males with other traits (Darwin 1871). Since its proposition, this theory has gained support from examples from a variety of taxa that demonstrate with strong evidence that females exhibit preference and that males experience differing degrees of reproductive success associated with ornament quality (reviewed in Andersson 1994). This trend is particularly apparent in species possessing brilliantly colored ornamentation, in which vibrantly colored males tend to attract more mates than do more dully colored conspecifics (e.g., Godin and Dugatkin 1996; Hill 1990). Why might females pay attention to male coloration?

While genetics may contribute to the quality of an individual's coloration, ornamental coloration is often influenced by environmental factors such as an individual's body condition, quality of diet, or health. Hamilton and Zuk (1982) proposed that ornamental coloration may be affected by an individual's parasite load, and that by assessing the relative quality of ornamental coloration among potential mates, females might be able to select mates that are less affected by parasites. A large body of evidence indicates that the presence of parasites reduces the quality of individual ornamental coloration (e.g., Ressel and Schall 1989), and suggests that females discriminating between males based on ornamental coloration may be able to select mates with fewer parasites (e.g., Houde and Torio 1992). The relationship between parasites and ornamental coloration, and the potential for colorful ornaments to serve as honest signals, have been well investigated in birds and fish in particular, but remain relatively unexplored in other groups.

Reptiles are among the most colorful species in nature, and many reptiles actively advertise ornamental colors during behavioral interactions such as courtship and territory defense (e.g., Martins 1993). The use of these colors in these behavioral contexts, which have the potential to influence reproductive success, suggests that they may be signals utilized by these species to communicate. Ornamental colors are highly variable across reptiles, and in many cases members of the same species exhibit considerable variation. Despite these observations, reptiles are one large group for which direct investigation of the potential for ornamental coloration to serve as an honest signal remains limited for many species.

In this thesis, I investigated the potential for ornamental coloration and display behavior to serve as honest indicators of male quality as determined by parasite load and body condition in male Caribbean *Anolis* lizards. Lizards in the *Anolis* genus possess dewlaps, brightly colored throat fans that are extended for use during behavioral interactions such as courtship and territory defense that have long been implicated as important components of communication among anoles (Losos 2009). Dewlap color varies widely throughout the *Anolis* genus, and many species exhibit considerable within-species variation in either dewlap color or pattern (Nicholson et al. 2007). Different species also exhibit distinctive display patterns during which the dewlap is extended for advertisement. Several hypotheses have been proposed in an attempt to discern the communicative function of dewlap color and display behavior, including the use of color or pattern and display behavior in species recognition (Jenssen 1977; Losos 1985; Ng et al. 2013). Whether dewlap color or display behavior play important signaling roles in terms of sexual selection, however, remains to be directly determined.

I began this investigation during June and July of 2011, during which I traveled to the Dominican Republic and investigated individual variation in dewlap coloration and display behavior among members of a population of *Anolis brevirostris* lizards. *Anolis brevirostris* are primarily trunk-dwelling lizards that exhibit yellow dewlaps with a red-orange patch of highly variable size and shape (Figure 1.1; Case 1990). Many anoles in the Dominican Republic, including members of our study population, are naturally parasitized by ectoparasitic mites (Trombiculidae spp.), which reside in varying densities within folds of skin under limbs, in the cloacal vent, and on the dewlap skin. Investigations of similar mites infesting birds revealed that they are parasitic and thrive by using resources derived from host tissues (reviewed in Proctor and Owens 2000). These results suggest that the mites I observed in the Dominican Republic may have similarly negative implications for infested anole hosts. Using behavioral observations, morphological measurements, and color spectrometry, I investigated the potential for these parasites to influence dewlap coloration and display behavior in this population of *Anolis brevirostris* lizards. I found that heavily parasitized lizards exhibited less vibrant dewlaps and displayed less frequently than lizards with fewer parasites. This study is the focus of chapter 2.

To further explore the potential for anole dewlap color and display behavior to serve as an honest indicator of male quality, I expanded my focus in a second study to include multiple populations of several *Anolis* species. The Dominican Republic was an ideal setting in which to do this for several reasons. First, a variety of *Anolis* species are endemic and widely distributed throughout the Dominican Republic, and many coexist in populations comprised of multiple species at different localities (Schwartz and Henderson 1991). Second, previous work conducted in the Dominican Republic suggests that the ectoparasite loads of *Anolis* lizard tend to increase with elevation (Zippel et al. 1996). Several major mountain chains span the Dominican Republic, and populations of various *Anolis* species can be found at different elevations on multiple mountain chains. The distribution of lizards and the tendency for parasite loads to differ with elevation combine to produce a unique natural laboratory in which to expand our investigation to better understand how ectoparasites may be affecting *Anolis* dewlap coloration and display behavior.

For this second study, I focused on two geographically widespread species—*Anolis cybotes* and *A. distichus*. *Anolis cybotes* is a large trunk-ground dwelling anole, primarily residing on the trunks of trees but also venturing onto the forest floor, and exhibits a large dewlap of white to yellow color (Figure 1.2). *Anolis distichus* is a trunk-dwelling sister taxon of *A. brevirostris* (the focus of our first study; Rabosky and Glor 2010), and exhibits a similar yellow dewlap with a red-orange patch of highly variable size and shape (Figure 1.3; Case 1990). Populations of both species may be found along the coasts at sea level, at least as high as 1200 meters in montane forests, and in many locations, populations of both species coexist in the same geographic location (*pers. obs.*). For this study, I sampled populations of both species across elevational transects spanning two mountain chains—the Cordillera Central located in the central Dominican Republic, and the Sierra de Baoruco located near the southwestern coast of the Dominican Republic (Figure 1.4). I sampled from sites of corresponding elevation on both chains, and studied members of both populations at the same location wherever possible. These species were parasitized by Trombiculid mites, as the *A. brevirostris* from the first study. I used similar techniques to investigate the potential for dewlap color and display behavior to serve as honest indicators of male quality as determined by parasite load and body condition, and to determine whether altitudinal differences determine or influence relationships between color, behavior, and quality in *Anolis* lizards. I found that ectoparasite prevalence differed considerably among mountain chains, and that habitat elevation was a better predictor of dewlap color than ectoparasite load in these species. This study is the subject of chapter 3.

Together, the results of these studies demonstrate the potential for dewlap coloration and display behavior to serve as honest signals in *Anolis* lizards. My observation that parasite load and body condition are associated with color and behavior suggest that information about male quality may be conveyed by these signals. This information may be interpreted by observers of dewlaps and display behavior—such as potential mates, rivals, or predators—and may therefore have important implications for individual fitness. My observation that variability in dewlap coloration is associated with elevation and geographic location suggest that habitat characteristics may play an important role in the evolution of dewlap variability. Further exploration is needed to fully understand these relationships and their potential implications, and the findings presented here demonstrate that such explorations are warranted. Ultimately, the results of these studies demonstrate that we must expand our investigation and understanding of the function of colorful ornaments and associated behaviors to include such taxa as *Anolis* lizards, and major groups such as reptiles.

References

Bradbury, J. W., Vehrencamp, S. L. 1998 Principles of animal communication. *Behav. Ecol.* **12**, 283-286.

Case, S. M. 1990 Dewlap and other variation in the lizards *Anolis distichus* and *A. brevirostris* (Reptilia: Iguanidae). *Biol. J. Linn. Soc.* **40**, 373-393.

Darwin, C. 1874.*The Descent of Man and Selection in Relation to Sex*. 2nd edn. London: John Murray.

Godin, J., Dugatkin, L. A. 1996 Female mating preference for bold males in the guppy, *Poecilia reticulata. PNAS* **93**, 10262-10267.

Guilford, T., Dawkins, M. S. 1991 Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1-14.

Hamilton, W. D., Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384-387.

Hill, G. E. 1990 Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* **40**, 563-572.

Houde, A. E., Torio, A. J. 1992 Effect of parasitic infection on male color pattern and female choice in guppies. *Behav. Ecol.* **3**, 346-351.

Jenssen, T. A. 1977 Evolution of anoline lizard display behavior. *Am. Zool.* **17**, 203-215.

Losos, J. B. 2009 *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*: Univ of California Press.

Martins, E. P. 1993 A comparative study of the evolution of *Sceloporus* push-up displays. *Am. Nat.* **142**, 994-1018.

Ng, J., Landeen, E. L., Logsdon, R. M., Glor, R. E. 2013 Correlation between *Anolis* lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* **67**, 573-582.

Nicholson, K. E., Harmon, L. J., Losos, J. B. 2007 Evolution of *Anolis* lizard dewlap diversity. *PLoS One* **2**, e274.

Proctor, H., Owens, I. 2000 Mites and birds: diversity, parasitism and coevolution. *Trends Ecol. Evolut.* **15**, 358-364.

Rabosky, D. L., Glor, R. E. 2010 Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *PNAS* **107**, 22178-22183.

Reby, D., McComb, K. 2003 Vocal communication and reproduction in deer. *Adv. Behav.* **33**, 231-264.

Ressel, S., Schall, J. 1989 Parasites and showy males: malarial infection and color variation in fence lizards. *Oecologia* **78**, 158-164.

Schwartz, A., Henderson, R. W. 1991 *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*: University Press of Florida.

Zahavi, A. 1975 Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**, 205-214.

Zippel, K., Powell, R., Parmerlee, J., Monks, S., Lathrop, A., Smith, D. 1996 The distribution of larval *Eutrombicula alfreddugesi* (Acari: Trombiculidae) infesting *Anolis* lizards (Lacertilia: Polychrotidae) from different habitats on Hispaniola. *Caribb. J. Sci.* **32**, 43-49.

Figure Legends

Figure 1.1. *Anolis brevirostris* male displaying dewlap (Photograph by Michele Johnson)

Figure 1.2. *Anolis cybotes* male displaying dewlap (Photograph by Michele Johnson)

Figure 1.3. *Anolis distichus* male displaying dewlap (Photograph by Jose Rivas, from http://turismoverde.wordpress.com).

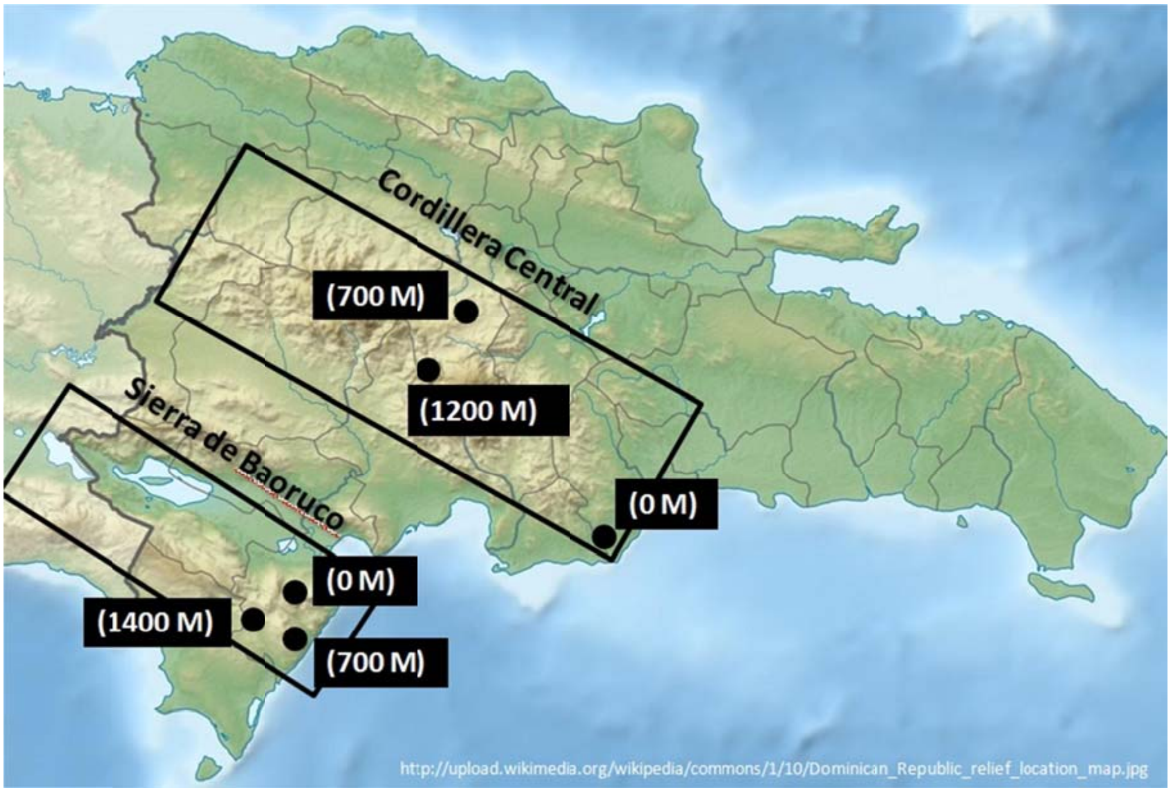
Figure 1.4. Map depicting geographic locations of mountain chains and sampling sites. The Cordillera Central chain is referred to as the Central chain, and Sierra de Baoruco as the Southwestern chain, throughout the thesis. Sampling sites are referenced according to elevation (e.g., Low, Mid, and High elevation) within each chain. (Map from http://commons.wikimedia.org/wiki/File:Dominican_Republic_relief_location_map.jpg)

Figure 1.1

Figure 1.2

Figure 1.3

Figure 1.4



http://upload.wikimedia.org/wikipedia/commons/1/10/Dominican_Republic_relief_location_map.jpg

CHAPTER 2

HIGHLY-PARASITIZED CARIBBEAN LIZARDS (*ANOLIS BREVIROSTRIS*) EXHIBIT LESS COLORFUL, LESS FREQUENT SOCIAL DISPLAYS

Introduction

Ectoparasites survive by drawing from the resources produced by a host, and as a result, can affect organismal fitness in a variety of ways (Lehman 1993). Colorful ornaments are often particularly vulnerable targets of the negative effects of ectoparasites (e.g., Fitze and Richner 2001) because color expression is linked to physiological processes underlying condition (Hill 2009). Taxa as diverse as insects, fish, birds, and reptiles use coloration to communicate quality and status, and thus the effects of ectoparasites on these ornaments are particularly important (Bradbury and Vehrencamp 1998, Hamilton and Zuk 1982).

Color can be produced via a variety of mechanisms, either structurally or by the deposition of pigments such as melanins or carotenoids (Jawor and Breitwisch 2003). Carotenoid-based colors are of particular ecological interest because these pigments must be obtained from diet and serve important physiological functions. For example, carotenoids function to boost the immune system, and act as free-radical scavengers (Britton 1995), and this antioxidant property may convey important immune benefits (Burton 1989). Pigment allocation to ornaments reduces the availability of these bioactive pigments for use in mounting immune responses (McGraw and Ardia 2003).Among parasitized host populations, only individuals with fewer parasites or increased ability to combat infestation should be able to allocate sufficient pigment resources to produce high-quality coloration. As a result, coloration may serve as a signal that indicates the level of parasite infestation or the preparedness of the host’s immune system (Lozano 1994). In addition, parasites also affect host metabolism and energetics (e.g., Booth et al. 1993), and so parasites can directly influence energy allocated towards display behavior (Kennedy et al. 1987). 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.

Anolis lizards are an excellent group in which to investigate the potential for ectoparasites to influence both ornamental coloration and the use of the color signal in a behavioral display. Most lizards in this genus possess dewlaps, often brightly colored throat fans that are primarily extended during courtship and territory defense (Jenssen 1977). The dewlap has long been implicated as an important communication signal for these species. For example, dewlap size is a good predictor of male bite force (Vanhooydonck et al. 2005), which is associated with male fighting ability (Lailvaux et al. 2004), and males that perform dewlap extensions are better able to attract mates than individuals that do not display (Crews 1975). However it remains unclear what role is played by dewlap color (Nicholson et al. 2007). Furthermore, it is unknown how signal color and display behavior interact, and whether both of these components serve as indicators of advertiser condition.

Here, I investigated the effects of ectoparasites on dewlap coloration and display behavior in male *Anolis brevirostris* lizards. *Anolis brevirostris* are trunk dwelling lizards, and exhibit yellow dewlaps with a red-orange patch of variable size and shape (Case 1990). Dewlap pigmentation has not been explicitly identified for *A. brevirostris*, but previous work with *A. sagrei* of similar dewlap coloration demonstrates that carotenoids are one of the pigment classes found to produce red-orange coloration in anole dewlaps (Steffan and McGraw 2007). In my study population, individuals were naturally parasitized by ectoparasitic mites (Trombiculid spp.) residing primarily in the folds of the dewlap and the axillae. I tested the hypothesis that dewlap color and display behavior have the potential to signal parasite load and body condition. Specifically, I tested the prediction that heavily parasitized individuals exhibit less vibrantly colored dewlaps, have lower body condition, and perform fewer dewlap display behaviors than less parasitized individuals.

Methods

I studied 30 adult male *A. brevirostris* lizards at CoralSol Resort in Barahona, southwestern Dominican Republic (N 18° 12.474, W 71° 5.977) from July 2 to July 11, 2011. I located lizards by scanning the trunks of large trees. To avoid sampling the same individuals more than once, I observed lizards in areas where lizards were not previously observed. I visually identified individuals as adult males based on their body size and the presence of a large dewlap (the dewlap is reduced in females, Johnson and Wade 2010). I then performed focal 30 - 60 min (mean = 58.9, standard error = 1.01) behavioral observations for each lizard. I recorded all behaviors of the focal lizard, focusing on dewlap display behaviors. I quantified display rate as the number of dewlap extensions per minute.

After the observation period, I captured each lizard by hand or noose, and confirmed its sex by the presence of hemipenes (male copulatory organs). I measured each lizard's snout-vent length, and measured its mass using a Pesola spring scale. I used digital calipers to measure the length of the second ceratobranchial cartilage, a linear proxy for dewlap size (Johnson and Wade 2010). I performed a linear regression with body length and mass to calculate standardized residuals as an estimate of body condition (Jakob et al. 1996). Using a hand lens, I counted the number of ectoparasitic mites on each animal (range = 0-34). Lizards were kept in individual bags for 1-32 hours (mean = 7.31 hrs, standard error = 1.48) until measures of dewlap color were taken. Holding time was not associated with any measure of dewlap coloration (results not shown).

I measured dewlap coloration for each lizard using an Ocean Optics 20001 spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin FL). I 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 the amount of ambient light included in reflectance measures, and allowed the researcher to maintain a consistent distance between the probe and dewlap during each measurement. Reflectance was quantified as the proportion of light reflected off of 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), and I calibrated the system against this standard and a dark standard prior to measuring each individual. I took five reflectance measurements of each individual's dewlap, distributed haphazardly across the left, lateral side of the fully extended dewlap.

Using the mean reflectance curve for each individual, I calculated the following tristimulus variables with CLR 1.05 (table 3.2, Montgomerie 2006): brightness (measured as the mean reflectance within the 320-700 nm range), hue (the wavelength corresponding to the mid-reflection value), and red and yellow chroma (reflectance within the 605-700 and 550-325 nm ranges, divided by mean brightness).

I performed a series of linear regressions to determine whether ectoparasite load predicted lizard body condition, tristiumulus measures of dewlap color, or dewlap display rate. I also performed a series of linear regressions to determine whether measures of color were associated with dewlap display rate. All statistics were performed using SPSS. One individual performed no dewlap extensions during behavioral observations, and was excluded from analyses because this individual’s dewlap rate was more than two standard deviations below the mean.

Results

Ectoparasites, color and condition

Eight of the 29 males were non-parasitized. Among the parasitized males, the number of mites per individual varied from 1-34 (mean = 7.62, standard error = 1.68). Ectoparasite load was significantly positively related to dewlap brightness ($F_{1,29} = 6.07$, $p = 0.02$, $R^2 = 0.18$; Fig. 2.1). Visual inspection of the color spectra of highly parasitized (parasites > mean) and less (parasites ≦ mean) or non- parasitized individuals indicated that dewlaps of parasitized lizards were more reflective across the entire spectrum (i.e., dewlaps were more white; Fig 2.2). Parasite load was not significantly correlated with hue ($F_{1,29} = 1.72$, $p = 0.20$), red ($F_{1,29} = 2.58$, $p = 0.12$) or yellow saturation ($F_{1,29} = 0.05$, $p = 0.81$). There was a significant negative relationship between ectoparasite load and condition ($F_{1,29} = 14.0$, $R^2 = 0.34$, $p = 0.001$; Fig. 2.3), but body condition was not significantly related to any measure of dewlap color (all $p > 0.18$).

Ectoparasites and display rate

Ectoparasite load was significantly negatively correlated with dewlap display behavior. Individuals with fewer parasites performed more dewlap extensions than individuals with more parasites ($F_{1,29} = 4.38$, $p = 0.046$, $R^2 = 0.13$, Figure 2.4).

Display rate, color and condition

Individuals with lower brightness performed more dewlap extensions than individuals with brighter dewlaps ($F_{1,29} = 7.22$, $p = 0.012$, $R^2 = 0.19$; Fig. 2.5). Dewlap display rate was not associated with hue or saturation (all $p > 0.12$). Individuals with higher body condition displayed significantly more frequently than lower condition individuals ($F_{1,29} = 9.78$, $p = 0.004$, $R^2 = 0.27$, Fig. 2.6).

Discussion

Overall, the findings of this study demonstrate a potential for dewlap coloration and display behavior to serve as honest indicators of male quality among male *Anolis brevirostris* lizards. In particular, the observation that ectoparasite load is negatively associated with display behavior and dewlap brightness suggests that these traits may convey information about the advertiser. This information may be interpreted by receivers such as potential mates or rivals, and may thus affect mating success and social interactions, both of which strongly influence individual fitness.

Our observation that heavily parasitized individuals have dewlaps with a greater degree of whiteness (i.e., higher brightness across the spectrum) seems likely to indicate that these hosts have less light-absorbing pigments deposited in their dewlap. Brightness is a measure of the amount of light reflected off of a surface, and pigments act by in a subtractive manner by absorbing certain wavelengths (see Britton 1983). If highly-parasitized individuals are in fact depositing less carotenoids into their dewlaps, this may indicate that they are allocating more pigment resources to immune function to combat parasitism. This proposed mechanism for color differences between individuals with different levels of parasitism is highly speculative, as there are other mechanisms that could account for these color differences. For example, dewlap brightness could be influenced by the deposition of other pigments, including pterins which have been identified in the anole dewlap in addition to carotenoids (Steffan and McGraw 2007), Additionally, the white scales that cover the dewlap could vary in structural-based white color (as has been shown in bird feathers, see Shawkey and Hill 2005), and so the brightness of the white background could vary between individuals. It is also worth considering that dewlap color could be influenced by vascularization or blood flow under the thin skin flap of the dewlap (as is true for some red traits in other species, e.g., Hunt et al. 2003), and individuals may circulate blood to the periphery differently depending on their level of parasitism. Future research is necessary to understand the mechanisms in color variation in this species.

Ectoparasite infestation may influence *A. brevirostris* dewlap coloration and display behavior via a variety of mechanisms. Our finding indicating that heavily parasitized individuals were in poorer body condition than individuals with fewer parasites is consistent with the hypothesis that the presence of these mites negatively affects condition. Mites may influence condition by directly using host resources – Trombiculid mite species parasitizing birds obtain resources by liquefying host tissue (reviewed in Proctor and Owens 2000), thus siphoning resources from the pool otherwise available for host use for processes such as growth. Mites infesting *A. brevirostris* may obtain resources in a similar fashion, and as a result, heavily parasitized lizards may be of lower condition due to resource loss to these mites. In addition, the presence of ectoparasites may also elicit an immune response from a host (e.g., Goldberg and Bursey 1991), wherein the host allocates resources to combating the negative effects of parasite infestation rather than to other metabolic processes. Allocation of resources to immune function may account for the effect of ectoparasites on dewlap coloration.

Parasite infestation has important implications for host behavior. Heavily parasitized individuals often exhibit reduced display behaviors (e.g., Kennedy et al. 1987) compared to individuals with fewer parasites. Our observation that lizards with more parasites displayed their dewlaps at lower rates suggests ectoparasites negatively influence display behavior, perhaps due to reduced resources or energy available to allocate to performing these behaviors due to parasite infestation. Future work exploring whether ectoparasites impose direct energetic challenges for lizards, which may influence individual behaviors including display behaviors, is needed to fully understand the implications of parasite infestation on this aspect of anole communication.

Taken together, these results reveal the potential for dewlap coloration and dewlap display behavior to serve as honest indicators of male quality as determined by ectoparasite load and body condition in *A. brevirostris* lizards.

References

Booth, D. T., Clayton, D. H., Block, B. A. 1993 Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *P. Roy. Soc. Lond. B* **253**, 125-129.

Bradbury, J. W., Vehrencamp, S. L. 1998 Principles of animal communication. *Behav. Ecol.* **12**, 283-286.

Britton, G. 1983 *The biochemistry of natural pigments*: Cambridge University Press.

Burton, G. W. 1989 Antioxidant action of carotenoids. *J. Nutr.* **119**, 109.

Britton, G. 1995 Structure and properties of carotenoids in relation to function. *The FASEB Journal* **9**, 1551-1558.

Case, S. M. 1990 Dewlap and other variation in the lizards *Anolis distichus* and *A. brevirostris* (Reptilia: Iguanidae). *Biol. J. Linn. Soc.* **40**, 373-393.

Fitze, P. S., Richner, H. 2002 Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behav. Ecol.* **13**, 401-407.

Fleishman, L. J., Leal, M., Persons, M. H. 2009 Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *J. Comp. Physiol. B.* **195**, 1043-1060.

Goldberg, S. R., Bursey, C. R. 1991 Integumental lesions caused by ectoparasites in a wild population of the side-blotched lizard (*Uta stansburiana*). *J. Wildl. Dis.* **27**, 68-73.

Hamilton, W. D., Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384-387.

Hill, G. E., Hood, W. R., Huggins, K. 2009 A multifactorial test of the effects of carotenoid access, food intake and parasite load on the production of ornamental feathers and bill coloration in American goldfinches. *J. Exp. Biol.* **212**, 1225-1233.

Jakob, E. M., Marshall, S. D., Uetz, G. W. 1996 Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61-67.

Jawor, J. M., Breitwisch, R. 2003 Melanin ornaments, honesty, and sexual selection. *Auk.* **120**, 249-265.

Jenssen, T. A. 1977 Evolution of anoline lizard display behavior. *Am. Zool.* **17**, 203-215.

Johnson, M. A., Wade, J. 2010 Behavioural display systems across nine *Anolis* lizard species: sexual dimorphisms in structure and function. *P. Roy. Soc. Lond. B.* **277**, 1711-1719.

Kennedy, C., Endler, J., Poynton, S., McMinn, H. 1987 Parasite load predicts mate choice in guppies. *Behav. Ecol. Sociobiol.* **21**, 291-295.

Lehmann, T. 1993 Ectoparasites: direct impact on host fitness. *Parasitol. Today.* **9**, 8-13.

Lozano, G. A. 1994 Carotenoids, parasites, and sexual selection. *Oikos* **70**, 309-311.

McGraw, K. J., Ardia, D. R. 2003 Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *Am. Nat.* **162**, 704-712.

Montgomerie, R. 2006 Analyzing Colors. *Vol. 1: Mechanisms and measurements*. Ed. G.E. Hill, K.J. McGraw. Cambridge, MA: Harvard University Press.

Nicholson, K. E., Harmon, L. J., Losos, J. B. 2007 Evolution of *Anolis* lizard dewlap diversity. *PLoS One* **2**, e274.

Proctor, H., Owens, I. 2000 Mites and birds: diversity, parasitism and coevolution. *Trends Ecol. Evolu.* **15**, 358-364.

Steffen, J. E., McGraw, K. J. 2007 Contributions of pterin and carotenoid pigments to dewlap coloration in two anole species. *Comp. Biochem. Phys. B.* **146**, 42-46.

Figure Legends

Figure 2.1. The relationship between ectoparasite load and dewlap brightness in *Anolis brevirostris*. Trend line based on a standard linear regression analysis ($p = 0.02$, $R^2 = 0.18$)

Figure 2.2: Mean dewlap reflectance calculated at each wavelength (nm) for lizards with ectoparasite loads less than or equal to the mean (7.62) parasite load (low parasites) and lizards with ectoparasite loads greater than the mean (high parasites). Error bars represent standard error.

Figure 2.3. The relationship between ectoparasite load and body condition in *Anolis brevirostris*. Trend line based on a standard linear regression analysis (, $p = 0.001$, $R^2 = 0.34$)

Figure 2.4. The relationship between ectoparasite load and dewlap display rate in *Anolis brevirostris*. Trend line based on a standard linear regression analysis ($p = 0.046$, $R^2 = 0.13$)

Figure 2.5. The relationship between dewlap brightness and dewlap display rate in *Anolis brevirostris*. Trend line based on a standard linear regression analysis ($p = 0.012$, $R^2 = 0.19$)

Figure 2.6. The relationship between lizard body condition and dewlap display rate in *Anolis brevirostris*. Trend line based on a standard linear regression analysis ($p = 0.004$, $R^2 = 0.27$)

Figure 2.1

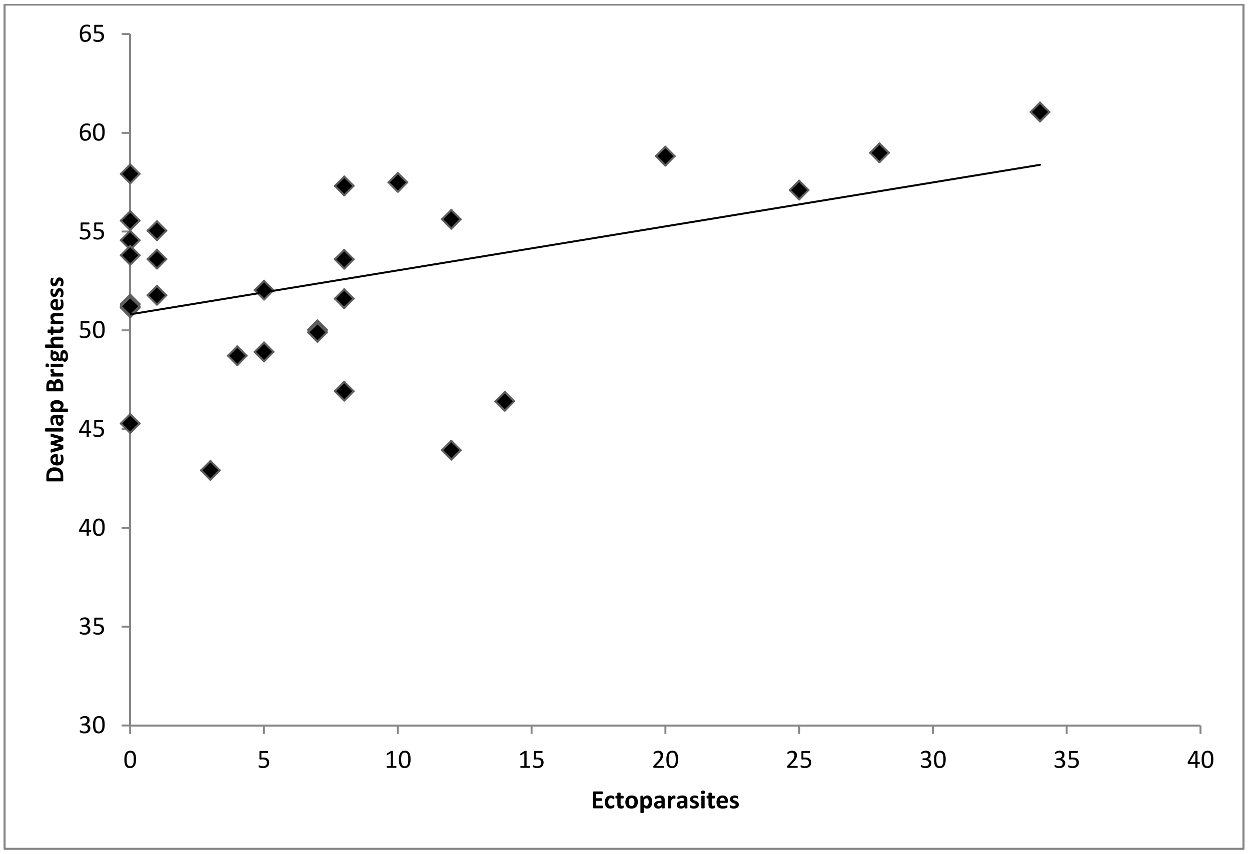
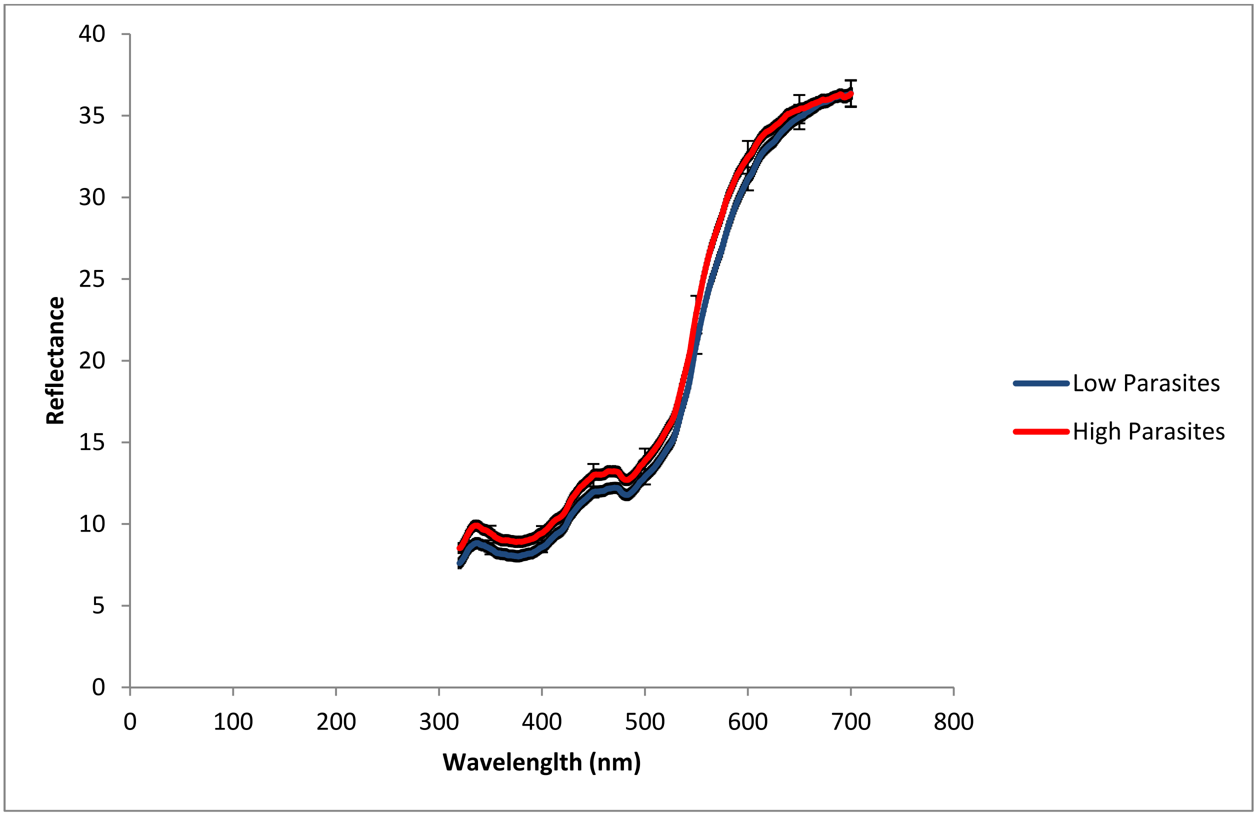
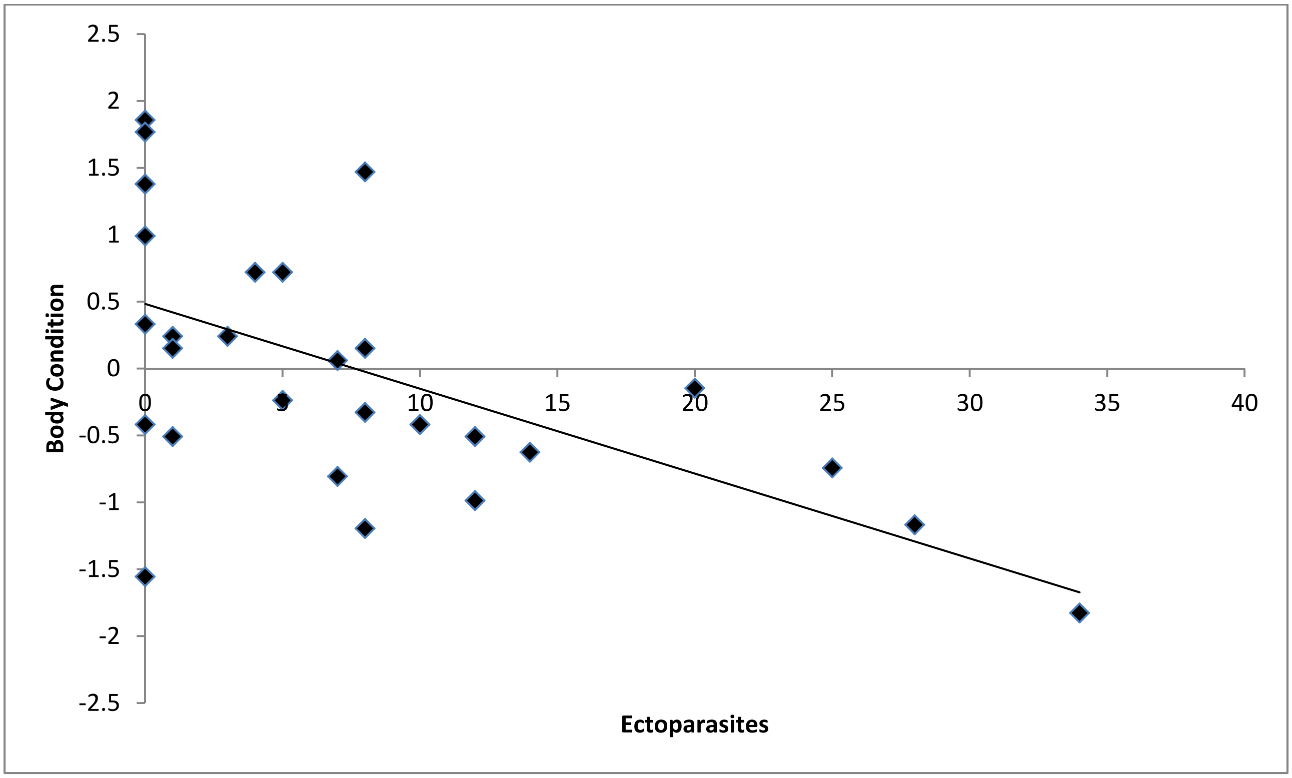

Dewlap Brightness
65
60
55
50
45
40
35
30
0
5
10
15
20
25
30
35
40
Ectoparasites

Figure 2.2



40
35
30
25
20
15
10
5
0
Reflectance
0
100
200
300
400
500
600
700
800
Wavelenglth (nm)
Low Parasites
High Parasites

Figure 2.3


2.5
2
1.5
1
0.5
0
-0.5
-1
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-2.5
Body Condition
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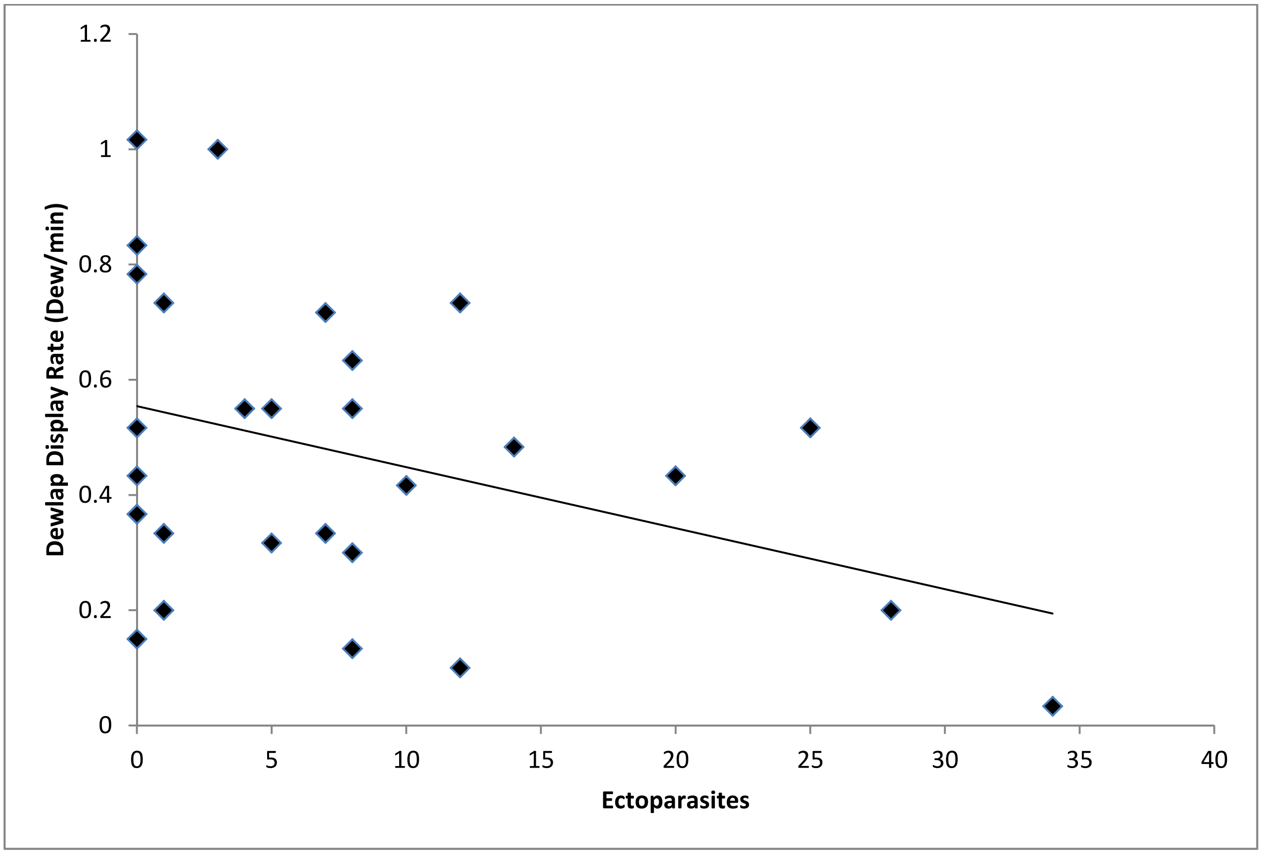
5
10
15
20
25
30
35
40
Ectoparasites

Figure 2.4


1.2
1
0.8
0.6
0.4
0.2
0
Dewlap Display Rate (Dew/min)
0
5
10
15
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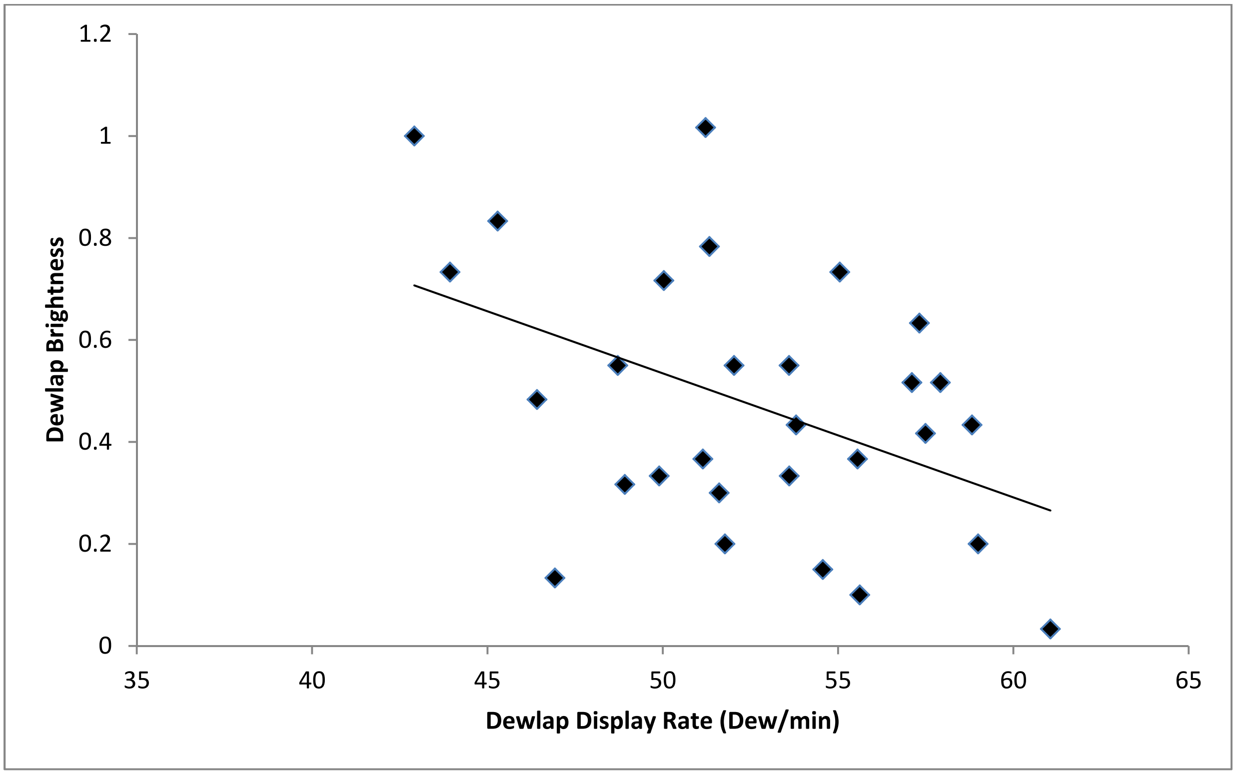
25
30
35
40
Ectoparasites

Figure 2.5


1.2
1
0.8
0.6
0.4
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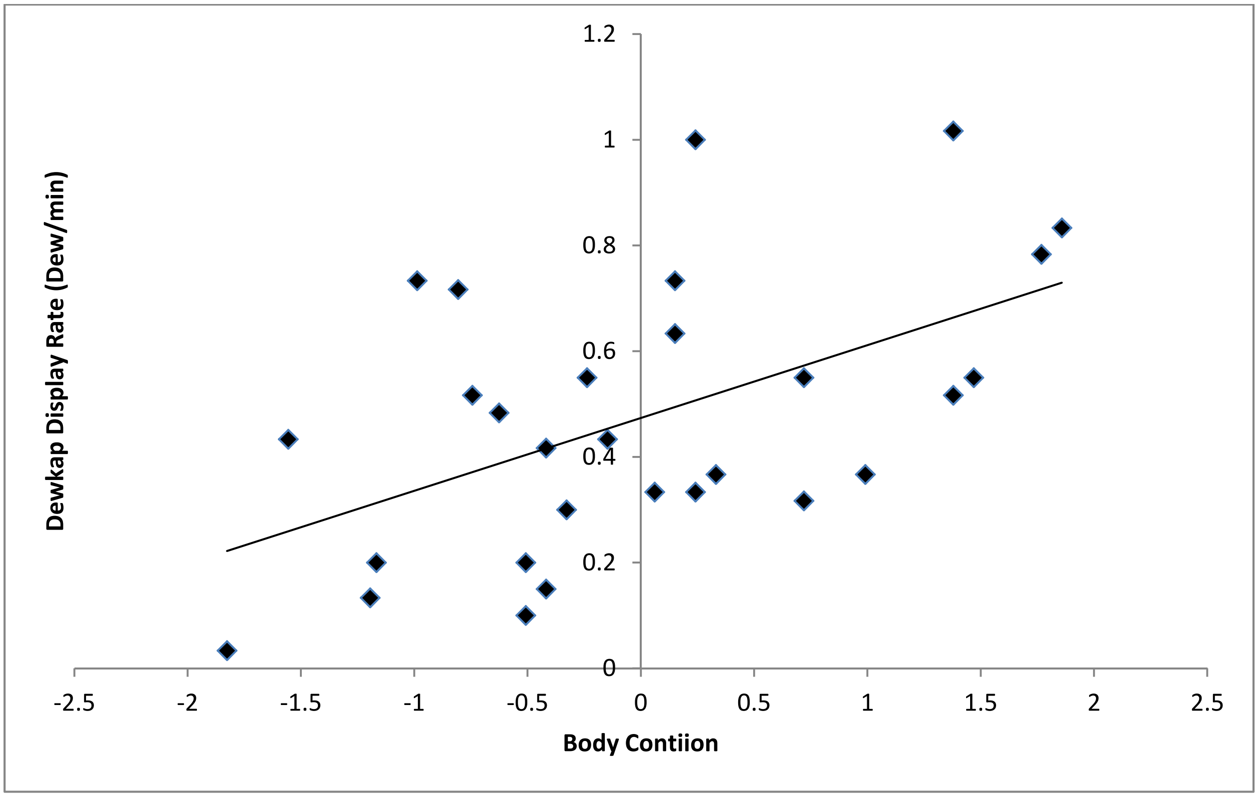
0
Dewlap Brightness
35
40
45
50
55
60
65
Dewlap Display Rate (Dew/min)

Figure 2.6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0.6
0.4
0.2
0
-2.5
-2
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-0.5
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0.5
1
1.5
2
2.5
Dewkap Display Rate (Dew/min)
Body Contiion

CHAPTER 3

DEWLAP COLOR AND PARASITE LOAD IN *ANOLIS* LIZARDS ACROSS ELEVATIONAL GRADIENTS

Introduction

Reptiles are a flashy group of animals—a variety of reptile species exhibit brilliantly colored ornaments, and many perform distinctive behavioral displays to advertize these colors to other animals. Lizards in the genus *Anolis* are no exception. Most species in this group possess dewlaps, vibrantly colored throat fans which they will extend during behavioral interactions such as courtship and territory defense. Dewlap coloration (Nicholson et al. 2007) and display behavior patterns (Jenssen 1977) vary widely across the genus, and in many cases, members of the same species may exhibit considerable individual variation (e.g., Ng and Glor 2011). The dewlap and its use by anoles during behavioral interactions have long been implicated as potentially sexually selected traits, particularly in male-male competition (Vanhooydonck et al. 2009). Whether male dewlap color or display behavior play a role in female mate choice, however, has been explored but not directly determined (e.g., Tokarz et al. 2005), and it remains unclear what factors influence the variation we observe among these lizards. The results of my previous research (Chapter 2) suggested that in male *A. brevirostris* lizards, infestation with ectoparasitic mites influences individual variation in physical condition, dewlap color, and display behavior. These findings provide evidence that that dewlap color and display behavior may therefore serve as honest indicators of aspects of male quality, and that other lizards observing an individual's dewlap and display behavior may be receiving information about the individual's quality.

To further explore what information is communicated by dewlap color and display behavior, I expanded the focus of my investigation to include two additional species of Hispaniolan anoles—*Anolis distichus* and *A. cybotes*. *Anolis distichus* is a trunk-dwelling anole exhibiting a yellow dewlap with a red-orange patch of highly variable size and shape, similar in ecology, morphology, and dewlap color to its sister taxon *A. brevirostris* (Losos 2009). *Anolis cybotes* is a trunk-ground dwelling species, and exhibits a large dewlap that is white to yellow in coloration. Both species are widely distributed throughout the island, and populations coexist in a variety of different geographic locations and habitats from dry coastlines at sea level to montane tropical forests as high as 1600 m in elevation (Schwartz and Henderson 1991*)*.

Previous work conducted in the Dominican Republic demonstrated that the prevalence of ectoparasitic mites increases with elevation, and that *Anolis* lizards in populations at high elevations are more heavily parasitized on average than *Anolis* lizards occurring at lower elevations (Zippel et al. 1996). The combination of this trend in parasitism and the distribution of *A. distichus* and *A. cybotes* on multiple mountain chains across different elevations generate a unique natural laboratory in which to further explore how ectoparasites and elevation influence dewlap coloration, display behavior, and physical condition in anoles.

Here, I tested the hypothesis that dewlap coloration and dewlap display behavior serve as honest indicators of male quality as determined by individual body condition and ectoparasite load in *A. distichus* and *A. cybotes* distributed across elevational gradients. In accordance with previous work conducted in the area (Zippel et al. 1996), I predict that populations residing at high elevations will be more heavily parasitized than populations at lower elevations. Consistent with my own previous findings, I predict that heavily parasitized lizards will be of lower body condition, will exhibit less colorful dewlaps, and will display their dewlaps less frequently than individuals with fewer parasites.

Methods

During the 2012 summer anole breeding season, I sampled adult male *Anolis cybotes* and *A. distichus* lizards from populations distributed across an elevational gradient on two mountain chains in the Dominican Republic (total *A. cybotes* N=110, *A. distichus* N= 94; Figure 1.4; Table 3.1). I sampled from localities in which populations of both species coexisted at all sites apart from the Low site from the Southwestern chain, at which *A. distichus* was absent.

I located lizards by scanning trees and other suitable perches throughout the sites, avoiding areas in which I had previously observed individuals to prevent collecting data from the same lizard more than once. I identified male individuals using their approximate body size and the presence of a large dewlap (males are generally of larger body size and the dewlap is highly reduced in females of both species). I then performed 30-60 min (*A. cybotes:* mean=58.6min, SE=0.47; *A distichus:* mean=57.97min, SE=0.79) focal behavioral observations for each lizard, during which I recorded all behaviors by the lizard, focusing on dewlap extensions and other display behaviors. I collected behavioral observations for both species at 4 of the sampling sites (Central Low, Mid, and High; Southwestern High; Table 3.1), and for only *A. cybotes* at the 2 remaining sites (Southwestern Low and High; Table 3.1). I calculated dewlap extension rate (i.e., dewlaps per minute) for each lizard.

Immediately following a behavioral observation, I captured each individual by hand or noose and confirmed sex by the presence of hemipenes (the male copulatory organ). At the Southwestern Mid elevation site, I collected *A. distichus* for measurement but did not perform behavioral observations. We measured each lizard's body size (snout-to-vent length, the distance from the tip of the snout to the middle of the cloacal vent), and used a spring Pesola to measure mass. I used digital calipers to measure the length of the second ceratobranchial cartilage, a proxy for dewlap size (Johnson and Wade 2010). I calculated body condition using standardized residuals from linear regressions of SVL and mass for each lizard, a standard index of body condition (Jakob et al. 1996). I counted the number of ectoparasitic mites (Trombiculid spp.) present on each individual using a hand lens. Lizards were kept in individual bags until we measured dewlap color.

I used an Ocean Optics 20001 spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin FL) to measure dewlap color. I used a fiber optic probe fitted with a plastic probe holder secured with screws at a 90° angle to light the sample and measure reflectance. The probe holder was used to minimize ambient light included in reflectance measures, and it allowed me to maintain a consistent distance between the tip of the probe and dewlap skin during each measurement. Reflectance was quantified as the proportion of light reflected off of the dewlap skin at 1nm increments within the lizard visible range (320-700 nm, see Fleishman et al. 1997). Reflectance was measured relative to a Spectralon white reflectance standard (Labsphere Inc., NH), and I calibrated the system prior to measuring each individual using this white standard (to represent 100% reflectance) and a dark standard (black velvet, to represent 0% reflectance). I took five measurements of each individual's dewlap, distributed haphazardly across the left, lateral side of the dewlap held fully extended.

Using the mean reflectance curve for each individual, I calculated the following trisitumulus variables using the program CLR 1.05 (Montgomerie 2008): brightness (mean reflectance within the 320-700 nm range), hue (the wavelength corresponding to the highest reflection), and red, and yellow chroma (i.e., saturation, or respective reflectance within 605-700 and 550-325 range divided by the mean brightness). Additional details on these measures of tristimulus variables can be found in Montgomerie (2006).

I performed a multivaraiate analysis of variance (MANOVA) to determine whether ectoparasite load and measures of dewlap color varied between populations of the two species from the different mountain chains. I also used a series of univariate analyses of variance (ANOVAs) to determine whether differences in these traits existed between lizards from the different elevational sites within the mountain chains, and whether interactions existed between mountain chain and elevation.

Results

The averages for each measure of dewlap color, physical condition, ectoparasite load, and dewlap display rate for populations of each species sampled at the different altitudinal sites are listed in Tables 3.2 and 3.3.

Populations from the two mountain chains differed substantially in the prevalence of ectoparasites. On the Central chain, almost no sampled lizards of either species were parasitized— two *Anolis cybotes* and one *A. distichus* from the Low elevation site were the only three lizards with parasites from this chain (Tables 3.2 and 3.3). On the Southwestern chain, every lizard sampled from both species had ectoparasites. *Anolis cybotes* sampled from Mid and High elevations from the Southwestern chain had significantly higher parasite loads than individuals from the Low elevation site ($F_{2,56} = 7.39$, $p = 0.001$; Table 3.2); ectoparasite load did not significantly differ between the Mid and High elevation sites. Ectoparasite load did not significantly differ between *A. distichus* sampled from Mid and High elevation sites; no *A. distichus* were present at the Low Southwestern site (Table 3.3).

Within the sites with high ectoparasite prevalence (i.e., Southwestern sites), lizard ectoparasite load did not significantly predict any measure of dewlap color (dewlap brightness, red saturation, or yellow saturation) or dewlap display behavior among lizards of either species. I found that site elevation and mountain chain were better predictors of dewlap color for lizards of both species sampled from both mountain chains.

For *A. cybotes*, populations from the two mountain chains differed in multivariate measures of color (Wilks $\lambda = 0.51$, $p < 0.001$). For *A. cybotes* from the Central mountain chain, dewlap red saturation increased with elevation ($F_{2,48} = 3.63$, $p = 0.034$). Yellow saturation ($F_{2,48} = 2.79$, $p = 0.072$) and dewlap brightness ($F_{2,48} = 0.63$, $p = 0.53$) were not significantly associated with elevation. For *A. cybotes* from the Southwestern chain, dewlap brightness was associated with elevation ($F_{2,56} = 8.17$, $p = 0.001$), with *A. cybotes* from the Mid elevation exhibiting the lowest dewlap brightness and *A. cybotes* from the Low and High elevation sites the highest brightness. Red saturation ($F_{2,56} = 2.17$, $p = 0.124$) and yellow saturation ($F_{2,56} = 2.34$, $p = 0.105$) were not significantly associated with elevation. There was a significant interaction between elevation and mountain chain for red saturation ($F_{2,104} = 5.04$, $p = 0.008$), but there were no significant interactions between elevation and chain for yellow saturation or brightness (both $p > 0.1$).

For *A. distichus*, relationships among color variables differed overall between populations from the two mountain chains (Wilks $\lambda = 0.28$, $p < 0.001$). For *A. distichus* from the Central mountain chain, red saturation ($F_{2,50} = 16.75$, $p < 0.001$) and yellow saturation ($F_{2,50} = 31.55$, $p < 0.001$) increased with elevation, and dewlap brightness decreased with elevation ($F_{2,50} = 11.98$, $p < 0.001$). I observed similar relationships for *A. distichus* from the Southwestern chain: red saturation ($F_{1,39} = 30.55$, $p < 0.001$) and yellow saturation ($F_{1,39} = 19.20$, $p < 0.001$) increased with elevation, and brightness decreased with elevation ($F_{1,39} = 23.77$, $p < 0.001$). There was a significant interaction between elevation and mountain chain for yellow saturation ($F_{1,89} = 4.21$, $p = 0.043$; Figure 3.1) and dewlap brightness ($F_{1,89} = 6.47$, $p = 0.013$; Figure 3.2), but there was no significant interaction between elevation and chain for red saturation ($p = 0.11$).

Discussion

The results presented here suggest that habitat elevation may influence variability in dewlap color in *Anolis cybotes* and *A. distichus*. I found that dewlap coloration increased with elevation for both species. Additionally, I found that there were differences in the relationships between site elevation and measures of dewlap color for the different mountain chains. Although geographic location has been classically explored to explain variability among populations of *Anolis* lizards (e.g., Rand and Williams 1970 and Thorpe et al. 2008), and *A. distichus* in particular (e.g., Ng and Glor 2011), previous studies have not specifically investigated whether elevation is associated with dewlap color variability. To my knowledge, these results are the first to demonstrate that habitat elevation is significantly associated with individual variation in dewlap color and display behavior in *Anolis* lizards.

Habitat elevation can have important implications for the conditions experienced by organisms residing in particular habitats. Climatic factors such as temperature and precipitation are often strongly associated with elevation (Stage and Salas 2007), and these factors can play significant roles in determining other habitat characteristics. One such characteristic affected by altitudinal differences in temperature and precipitation is species composition, which has been classically demonstrated to change with elevation for a variety of taxa, including plant species (reviewed by Rahbek 1995). Differences in climatic variables and vegetation associated with habitat elevation may have played an important role in the evolution of the variable dewlap color and display behavior that I observed across and within the *Anolis* populations I studied.

In previous investigations of dewlap color and display behavior, it has proposed that variability in these traits may have evolved in accordance with differences in such habitat characteristics as incident light and substrate composition (e.g., Fleishman et al. 2009), both of which may be strongly influenced by climate and vegetation composition. Vegetation type and resulting canopy cover, for example, determines the amount of light that infiltrates a habitat (e.g., e.g, Fetcher et al. 1985). The amount of incident light experienced by an anole while displaying, combined with the contrast of the dewlap against the substrate on which the anole is displaying from, may affect the efficacy of the dewlap in terms of visibility (e.g., Leal and Fleishman 2004). In other words, a particular dewlap and display pattern may be most effective in a particular set of habitat conditions, while another dewlap may be most effective in the opposite conditions. As a result, variable signals may have arisen over time due to differences in effectiveness (Guilford and Dawkins 1991) in particular habitats and particular habitat conditions (e.g., Ord et al. 2007).

My findings indicate that incorporating climate and other ecological data about the sites where I collected lizards may further inform the relationships I observed. Understanding how vegetation composition and canopy cover changes with elevation across my sampling sites, for example, may explain my observation that dewlap color tended to increase with sampling elevation. Such factors, in addition to various climactic variables, may also be influencing the discrepancy in ectoparasite incidence I observed between the two mountain chains. My finding that there are significant interactions between elevation and mountain chain for measures of dewlap color suggests that differences between the chains overall may be influencing these relationships. Although I did not observe that ectoparasite load directly predicted dewlap color, the chains differ substantially in parasite load, and my observation that some elevation-color relationships differed by mountain chain suggest that ectoparasite prevalence may be contributing to these differences. I will incorporate precipitation, temperature, and vegetation composition data into these analyses to determine whether these factors are associated with variability in parasite incidence, dewlap color, or display behavior.

Dewlap color and display behavior have long been implicated as important components of communication for *Anolis* lizards. However, much remains to be understood about how these traits function as signals, and exactly what information they communicate. The findings I present in this thesis provide both novel insight and evidence in support of existing hypotheses concerning the factors that influence variability in these traits. My observation that ectoparasite load may directly influence dewlap coloration and display behavior suggests that these traits may be more dynamic within individuals than has been previously considered, and generates the potential for these traits to serve as honest signals of quality. My finding that habitat elevation is associated with dewlap color provides support for the hypothesis that dewlap color varies according to geography, and provides important impetus for further exploring what geographic factors play a role in determining signal efficacy and the evolution of variability over time.

References

Burton, G. W. 1989 Antioxidant action of carotenoids. *J. Nutr.* **119**, 109.

Fleishman, L. J., Leal, M., Persons, M. H. 2009 Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *J. Comp. Physiol. B* 195, 1043-1060.

Garben, A., van Bronswijk, J., Van Ebbenhorst Tengbergen, T. 1977 Distribution and dispersal of the chigger *Neotrombicula autumnalis* (Shaw, 1790) (Trombiculidae, Acari). Part I. The behaviour of the unfed and feeding larva. *Neth. J. Zool.* **28**, 193-205.

Guilford, T., Dawkins, M. S. 1991 Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1-14.

Fetcher, N., Oberbauer, S. F., Strain, B. 1985 Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *Int. J. Biometeorol.* **29**, 145-155.

Jakob, E. M., Marshall, S. D., Uetz, G. W. 1996 Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61-67.

Jenssen, T. A. 1977 Evolution of anoline lizard display behavior. *Am. Zool.* **17**, 203-215.

Losos, J. B. 2009 *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*: Univ of California Press.

Lozano, G. A. 1994 Carotenoids, parasites, and sexual selection. *Oikos* **70**, 309-311.

Montgomerie, R. 2008. CLR version 1.05. Queen's University, Kingston, Canada. (available at http://post.queensu.ca/~mont/color/analyze.html)

Ng, J., Glor, R. E. 2011 Genetic differentiation among populations of a Hispaniolan trunk anole that exhibit geographical variation in dewlap colour. *Mol. Ecol.* **20**, 4302-4317.

Nicholson, K. E., Harmon, L. J., Losos, J. B. 2007 Evolution of *Anolis* lizard dewlap diversity. *PLoS One* **2**, e274.

Olson, V. A., Owens, I. P. 1998 Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol.* **13**, 510-514.

Ord, T. J., Peters, R. A., Clucas, B., Stamps, J. A. 2007 Lizards speed up visual displays in noisy motion habitats. *P R Soc B.* **274**, 1057-1062.

Rahbek, C. 1997 The relationship among area, elevation, and regional species richness in neotropical birds. *Am. Nat.* **149**, 875-902.

Rand, A. S., Williams, E. E. 1970 An estimation of redundancy and information content of anole dewlaps. *Am. Nat.* **104**, 99-103.

Schwartz, A., Henderson, R. W. 1991 *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*: University Press of Florida.

Stage, A. R., Salas, C. 2007 Interactions of elevation, aspect, and slope in models of forest species composition and productivity. *For. Sci.* **53**, 486-492.

Thorpe, R. S., Surget-Groba, Y., Johansson, H. 2008 The relative importance of ecology and geographic isolation for speciation in anoles. *Philos T Roy Soc B.* **363**, 3071-3081.

Tokarz, R. R. 1985 Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.* **33**, 746-753.

Vanhooydonck, B., Herrel, A., Meyers, J., Irschick, D. 2009 What determines dewlap diversity in *Anolis* lizards? An among-island comparison. *J. Evol. Biol.* **22**, 293-305.

Zippel, K., Powell, R., Parmerlee, J., Monks, S., Lathrop, A., Smith, D. 1996 The distribution of larval *Eutrombicula alfreddugesi* (Acari: Trombiculidae) infesting *Anolis* lizards (Lacertilia: Polychrotidae) from different habitats on Hispaniola. *Caribb. J. Sci.* **32**, 43-49.

Tables

Table 3.1. Geographic descriptions and sample sizes for each species (CYB/DIS) from sites from which lizards were sampled.

Mountain Chain	Site	Reference	GPS Coordinates	Elevation (m)	CYB/DIS
Central	Caamano	Low	N18 26.119 W70 35.546	43	21/16
Central	Jarabacoa	Mid	N19 05.976 W70 36.807	649	14/18
Central	Constanza	High	N18 53.623 W70 45.213	1156	16/19
Southwestern	Los Patos	Low	N17 57.300 W71 11.288	13	19/0
Southwestern	Guyalluyal	Mid	N18 03.387 W71 0.8557	734	20/20
Southwestern	Polo	High	N18 07.188 W71 41.870	1236	20/21

Table 3.2. Average parasite load, physical condition, and color measurements for *Anolis cybotes* from each sampling site

Mountain Chain	Site	Elevation	Average (Max) Ectoparasites	Lizards Parasitized (# Lizards Sampled)	Av. SVL (mm)	Av. Mass (g)	Av. Body Condition	Av. Dewlap Rate
Central	Low	43	0 (13)	2 (21)	61.98	8.59	$-2.1*10^{-17}$	0.35
	Med	649	0 (0)	0 (14)	56.15	5.78	0.05	0.33
	High	1156	0 (0)	0 (16)	59.16	7.84	$6.25*10^{-7}$	0.12
Southwestern	Low	13	29.36 (78)	19 (19)	62.87	8.17	$-5.3*10^{-7}$	0.08
	Mid	734	99.35 (354)	20 (20)	66.47	10.43	-0.03	0.26
	High	1236	108.35 (274)	20 (20)	64.77	10.25	$1*10^{-6}$	0.27

Mountain Chain	Site	Elevation	Av. Brightness (B2)	Av. S1R	Av. S1Y	Av. S1G	Av. S1B	Av. Hue
Central	Low	43	0.33	0.27	0.23	0.29	0.24	342.28
	Med	649	0.32	0.29	0.24	0.30	0.22	346.64
	High	1156	0.33	0.29	0.24	0.30	0.21	341.81
Southwestern	Low	13	0.41	0.28	0.23	0.28	0.24	343.84
	Mid	734	0.34	0.28	0.23	0.28	0.23	346.40
	High	1236	0.37	0.27	0.23	0.28	0.23	341.45

Table 3.3. Average parasite load, physical condition, and color measurements for *Anolis distichus* from each sampling site.

Mountain Chain	Site	Elevation	Average (Max) Ectoparasites	Lizards Parasitized (# Lizards Sampled)	Av. SVL (mm)	Av. Mass (g)	Av. Body Condition	Av. Dewlap Rate
Central	Low	43	0 (9)	1 (16)	50.60	3.32	-0.68	1.80
	Mid	649	0 (0)	0 (18)	46.68	3.22	-0.04	1.14
	High	1156	0 (0)	0 (19)	48.08	3.75	0.83	1.62
Southwestern	Mid	734	17.2 (72)	20 (20)	48.91	3.45	-0.02	N/A
	High	1236	38.76 (71)	21 (21)	47.98	3.29	-0.16	0.47

Mountain Chain	Site	Elevation	Av. Brightness (B2)	Av. S1R/S1Y	Av. S1Y	Av. S1G	Av. S1B	Av. Hue
Central	Low	43	0.25	0.38	0.28	0.32	0.21	449.00*
	Mid	649	0.21	0.40	0.30	0.34	0.21	449.00*
	High	1156	0.20	0.44	0.31	0.33	0.15	448.36
Southwestern	Mid	734	0.17	0.37	0.28	0.33	0.21	448.40
	High	1236	0.13	0.44	0.31	0.31	0.14	372.95

Figure Legends

Figure 3.1. Mean yellow dewlap saturation of *Anolis distichus*. There was a significant interaction between elevation and mountain chain for yellow saturation, suggesting that the increase in yellow situation with elevation differs between the two mountain chains. Error bars represent standard error.

Figure 3.2. Mean yellow dewlap brightness of *Anolis distichus*. There was a significant interaction between elevation and mountain chain for brightness, suggesting that the decrease in brightness as elevation increases differs between the two mountain chains. Error bars represent standard error.

Figure 3.3: Mean red dewlap saturation for *Anolis cybotes*. There was a significant interaction between elevation and mountain chain for red saturation, suggesting that the increase in red saturation with elevation differs between the populations from the two mountain chains. Error bars represent standard error.

Figure 3.1

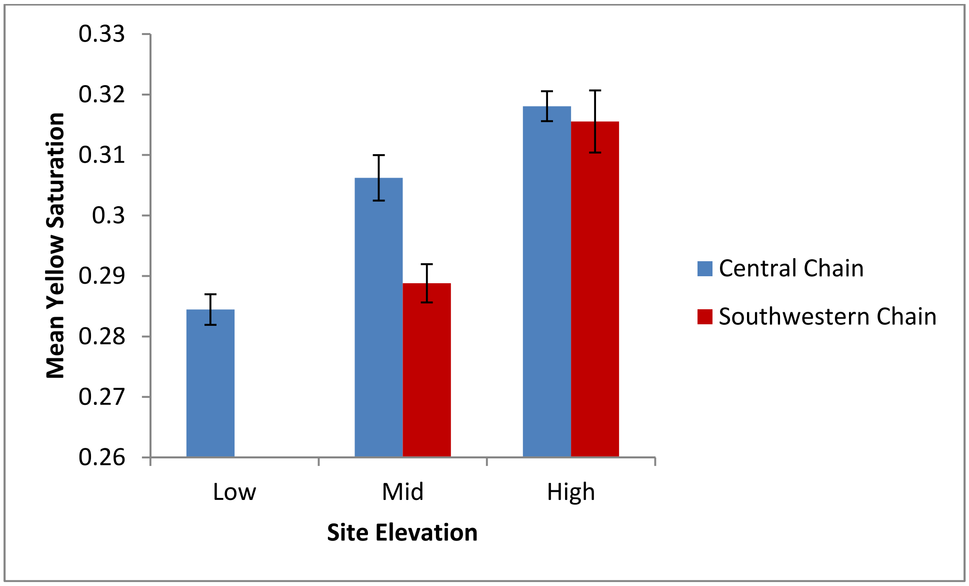

0.33
0.32
0.31
0.3
0.29
0.28
0.27
0.26
Mean Yellow Saturation
Low
Mid
High
Site Elevation
Central Chain
Southwestern Chain

Figure 3.2

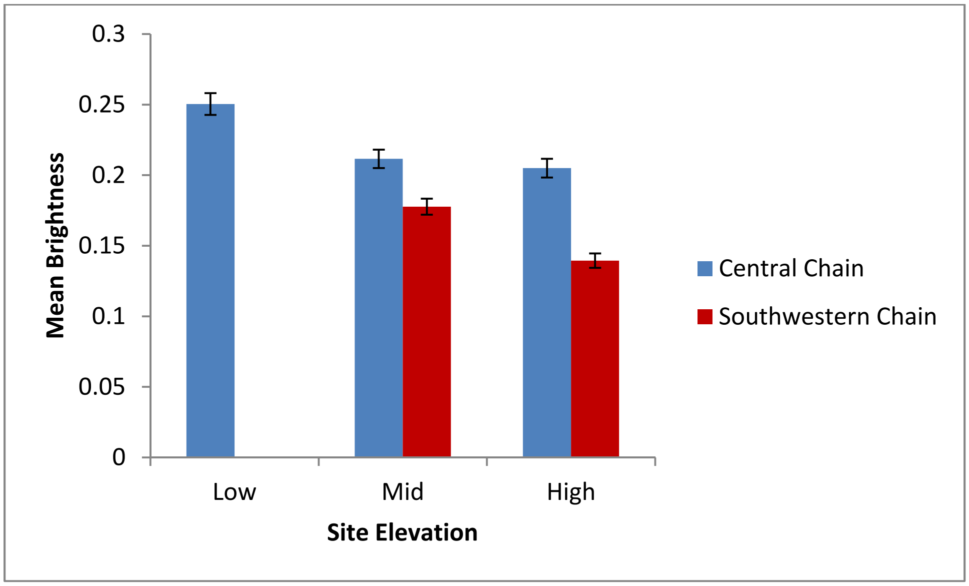
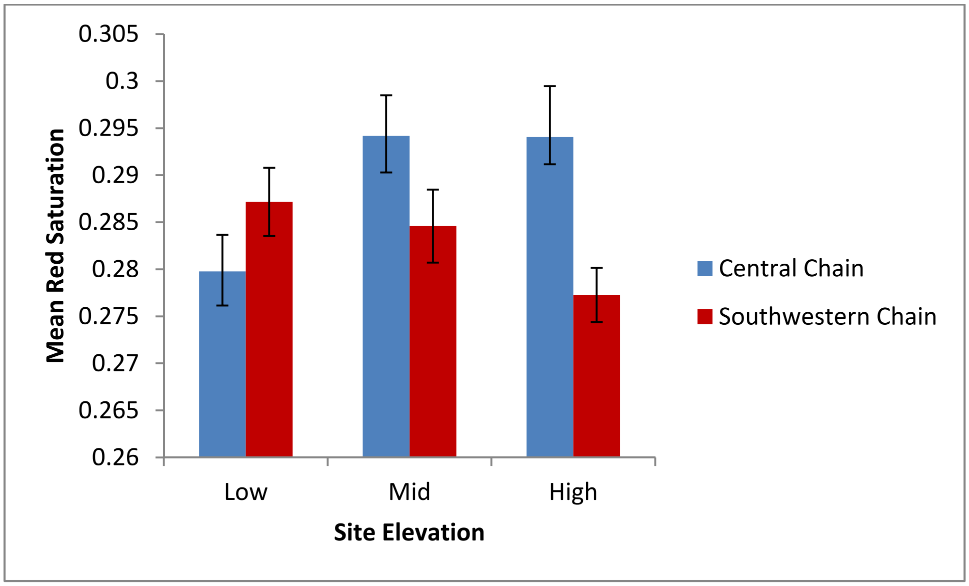

0.3
0.25
0.2
0.15
0.1
0.05
0
Mean Brightness
Low
Mid
High
Site Elevation
Central Chain
Southwestern Chain

Figure 3.3



0.305
0.3
0.295
0.29
0.285
0.28
0.275
0.27
0.265
0.26
Mean Red Saturation
Low
Mid
High
Site Elevation
Central Chain
Southwestern Chain