

Condition dependence of shared traits differs between sympatric *Anolis* lizards

John David Curlis¹  | Ryan William Davis² | Emily Zetkulic³ | Christian L. Cox¹

¹Department of Biology, Georgia Southern University, Statesboro, Georgia

²Department of Biology, Grinnell College, Grinnell, Iowa

³Department of Biology, Reed College, Portland, Oregon

Correspondence

John David Curlis, Department of Biology, Georgia Southern University, Statesboro, GA.
Email: jc12430@gorgiasouthern.edu

Abstract

In many species, sexually selected combat and display traits can confer dramatic fitness benefits to males by aiding in mate acquisition, so individuals maximally invest energy into their growth and maintenance. Such traits are deemed condition-dependent, as the energy that is available for investment depends on the health and condition of the individual. Condition dependence is present in a wide range of traits across many taxa, but the extent to which condition dependence varies among shared traits in closely related species is poorly understood. We tested for condition dependence in two *Anolis* lizards, the ground anole (*Anolis humilis*) and the slender anole (*Anolis limifrons*). Specifically, we measured dewlap area, jaw length, jaw width, and sprint speed, and then regressed one of two indices of body condition on each of these traits for both species. We found that dewlap area and jaw width exhibited condition dependence in ground anoles, but not in slender anoles. Sprint speed and jaw length were not condition-dependent in either species. The presence of condition dependence in ground anoles, but not slender anoles, implies evolutionary liability in the condition dependence of shared traits. Additionally, the fact that condition dependence was only detected in ground anoles, which have a greater relative dewlap size, suggests a potential role for signal evolution or strength of sexual selection in the evolution of condition dependence. Finally, our research suggests that variation in condition dependence of sexually selected traits could have implications for the evolution of dewlap diversity among *Anolis* species.

1 | INTRODUCTION

Sexual selection can give rise to exaggerated phenotypic traits by conferring a fitness advantage, but the costs associated with such traits can be high (Andersson, 1994; Emlen, 2001; Grether, 1997; Johnstone, Rands, & Evans, 2009; Kotiaho, 2000; Rowe, Evans, & Buchanan, 2001; Ryan, 1998). While these traits are often costly in terms of increased mortality due to predation (Andersson, 1982b; Grether, 1997), they can also be energetically costly through their production, maintenance, and use (Kotiaho, 2000; Mappes, Alatalo, Kotiaho, & Parri, 1996; Møller, 1989). Nevertheless, if mating success and reproductive output are tightly linked to these sexually selected traits, individuals should invest in them maximally. Thus, these traits are often energy-limited and dependent on the energetic condition of the individual, or condition-dependent (Andersson, 1982b; Mappes et al., 1996; Tomkins, Radwan, Kotiaho, & Tregenza, 2004). This can be adaptive for potential mates because a high quality of these expensive and exaggerated secondary sexual traits is often reflective of the condition of that individual (Andersson, 1994; Grafen, 1990; Iwasa, Pomiankowski, & Nee, 1991; Kahrl & Cox, 2015; Nur & Hasson, 1984; Zahavi, 1975).

Although condition dependence has been demonstrated across a wide range of taxa and characters (Hill, 2011; Rowe & Houle, 1996), examining variation in condition dependence among shared traits in closely related species is important for understanding the evolution of sexually selected traits.

Condition-dependent traits that arise and persist due to sexual selection are generally associated with display, combat, or both (Kodric-Brown & Brown, 1984; Nur & Hasson, 1984; Price, Schluter, & Heckman, 1993; Rowe & Houle, 1996). Display traits include enlarged morphological features (i.e., tails in birds, Andersson, 1982a; Møller, 1988; fins in fish, Basolo, 1990; Bischoff, Gould, & Rubenstein, 1985), vibrant colors (i.e., plumages of birds, Hill, 1991; dewlaps in lizards, Sigmund, 1983; beaks in birds, McGraw & Ardia, 2003; pigmentation patterns in fish, Kodric-Brown, 1985), and intricate courtship behaviors (i.e., nest building in bowerbirds, Uy & Borgia, 2000; song in birds, frogs, and insects, Searcy & Andersson, 1986; salamander courtship, Arnold, 1977). Such traits are used by males in many species to convey to females their suitability as potential mates. Additionally, because mate acquisition can be heavily influenced by male–male combat, traits that confer a physical advantage over rivals can be favored (Andersson,

1994; Berglund, Bisazza, & Pilastro, 1996; Emlen, 2001; Husak, Lappin, & Van Den Bussche, 2009; Le Boeuf, 1974). Although condition dependence is most often studied in the context of sexual selection, it is possible for traits to be condition-dependent as a result of natural selection, and some argue that most traits exhibit condition dependence to some extent (Johnstone et al., 2009). Nevertheless, condition dependence has been shown to be more weakly expressed in nonsexual traits (Bonduriansky & Rowe, 2005; Cotton, Fowler, & Pomiankowski, 2004a).

The term “condition” has multiple definitions and has been studied in several ways in previous research. We broadly define condition as the amount of energy available to an organism (Jakob, Marshall, & Uetz, 1996; Schulte-Hostedde, Zinner, Millar, & Hickling, 2005), which it can invest in growth, maintenance, and reproduction. The most direct way to assess condition in an operational context is through measurement of lipid stores via volumetric, mass, or chemical means, but this requires that the animal is sacrificed or that only dead animals are analyzed (Ardia, 2005; Blanckenhorn, Kraushaar, & Reim, 2003; Blanckenhorn, Kraushaar, Teuschl, & Reim, 2004; Lockyer, McConnell, & Waters, 1985; Pangle, Sutton, Kinnunen, & Hoff, 2004). Alternatively, while condition can be measured experimentally by altered feeding (Stirling, 1976; Uetz, Papke, & Kilinc, 2002) or manipulation of energy via fat body ablation (Cox, Lovern, & Calsbeek, 2014), these tests cannot adequately represent what happens in nature. A third method of assessing condition is using quantitative magnetic resonance, which generally produces highly accurate results (Warner, Johnson, & Nagy, 2016), but requires specialized equipment that is not practical for field research. Finally, condition is often measured using indices obtained by analyzing residuals of a regression of body mass on some linear index of body size, such as length (Cox & Calsbeek, 2015; Schulte-Hostedde et al., 2005). The principal advantage to these approaches is that they can be easily measured in the field with no specialized equipment, and they can be measured while only minimally disturbing the animal. Because we were interested in condition dependence of traits in natural populations, we used a combination of condition indices as a noninvasive method to study the role of body condition on the expression of morphological and performance traits.

We studied condition dependence in *Anolis* lizards, which possess a number of sexually selected and naturally selected traits that are shared among species. Anole species exhibit a high degree of diversity, but are generally characterized as being relatively small in body size and mostly arboreal (Williams, 1983). In many species, males are territorial (Butler & Losos, 2002; Lailvaux, Herrel, Vanhooydonck, Meyers, & Irschick, 2004; Schoener & Schoener, 1982; Trivers, 1976) and signal to both potential mates and rival males using a dewlap, an extendable throat fan that is often brightly colored (Sigmund, 1983; Trivers, 1976). Traits of the dewlap are associated with mate acquisition in anoles (Crews, 1975; Greenberg & Noble, 1944; Sigmund, 1983; Vanhooydonck, Herrel, Van Damme, & Irschick, 2005), suggesting that this feature is a target for sexual selection (Irschick, Herrel, Vanhooydonck, & Damme, 2007). Similarly, male head shape and jaw morphology are subjected to sexual selection as well, as male–male combat often escalates into biting and jaw locking (Lailvaux et al., 2004; McMann, 1993). These traits are also influenced by natural

selection, however, as the jaws are used for obtaining prey (Herrel, Joachim, Vanhooydonck, & Irschick, 2006) and deterring predators (Leal & Rodriguez-Robles, 1995). Although anoles may attempt to bite a potential predator, most species rely on their sprinting abilities to escape (Irschick & Losos, 1998). Because maximum sprint speed is ecologically relevant and affects survival probability in many reptiles, it is likely influenced by natural selection (Jayne & Bennet, 1990), but also by sexual selection, as faster males lizards have been shown to sire more offspring and better defend territories (Husak, Fox, & Van Den Bussche, 2008; Husak, Fox, Lovern, & Bussche, 2006). The potential for contributions of sexual and natural selection to the evolution of these aforementioned traits makes the genus *Anolis* an ideal system with which to study condition dependence.

We tested for condition dependence of sexually and naturally selected traits in two *Anolis* species: the ground anole (*Anolis humilis*) and the slender anole (*Anolis limifrons*). While these two species are similar in size and shape, ground anoles are generally shorter-bodied and stockier, whereas slender anoles, as their name suggests, are more elongate and gracile (Guyer & Donnelly, 2005; Savage, 2002; Fig. 1). These two anole species are closely related to one another, albeit not sister taxa (Pyron, Burbrink, & Wiens, 2013). Additionally, these species are sympatric throughout much of their respective ranges and inhabit the same types of rainforest habitats (Guyer & Donnelly, 2005; Savage, 2002). We note that statistical comparisons of only two species have limited inference capability, as any difference between species cannot be attributed to any single factor (Garland & Adolph, 1994). Rather, our research investigates condition dependence of traits in two species to test for evolutionary variation in condition dependence, as opposed to attributing any differences to particular ecological or evolutionary elements. Specifically, we measured body size, dewlap size, jaw morphology, and sprint speed to test whether combat, display, and performance traits exhibit condition dependence, as well as the extent to which condition dependence varies between these two species.

2 | MATERIALS AND METHODS

We conducted this study from September 24 to 26, 2014, at La Selva Biological Station, Costa Rica, an area classified as tropical lowland wet forest (sensu Holdridge, 1947). Lizards were captured by hand and noose along the edges of the Sendero Tres Rios, Sendero Las Vegas, and Sendero Occidental, which included areas of abandoned silviculture plantations, known as the Huertos plots, where these two species are locally abundant. Ground anoles were more frequently found basking in sunflecks or hiding under leaf litter on the forest floor, while slender anoles were often encountered on stems and trunks of plants, positioned 0.25–0.5 m from the ground (J. D. Curlis, pers. obs.). We determined the life stage (juvenile vs. adult), sex, and species using the criteria set forth in Savage (2002) and Guyer and Donnelly (2005). Each morning following an experimental trial, individuals were marked with nonpermanent ink to avoid recapture, then released back to their respective locations of capture.

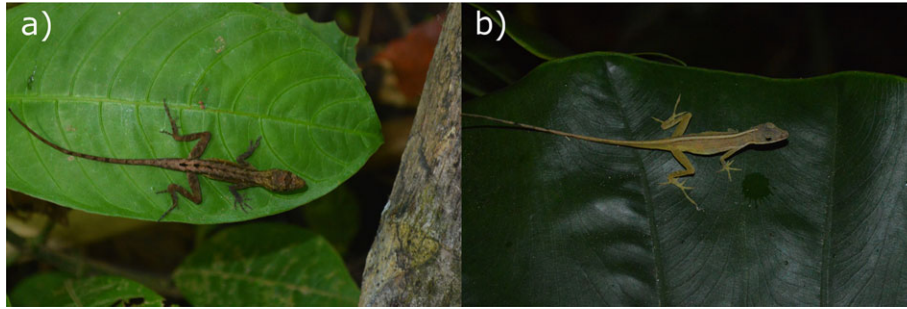


FIGURE 1 Photographs of (a) a male ground anole (*Anolis humilis*) and (b) a male slender anole (*Anolis limifrons*) in La Selva, Costa Rica. Photographs by J. D. Curlis [Color figure can be viewed at wileyonlinelibrary.com]

2.1 | Morphological measurements

We measured morphological traits including snout-vent length (SVL), jaw width, and jaw length to the nearest 0.1 mm using digital calipers (Mitutoyo Corporation, Aurora, IL). Snout-vent length was measured from the tip of the snout to the venter, or the opening of the cloaca. We measured jaw length from the tip of the snout to the point halfway between the ear and the edge of the mouth, and jaw width as the distance between these two points on either side of the head. To measure dewlap area, we used rubber-coated forceps to extend the dewlap of each animal over graph paper, where it was then traced with a pencil. These tracings were digitally scanned and total area was obtained using the “freehand line tool” in ImageJ (Schneider, Rasbadd, & Eliceiri, 2012). Lastly, we measured the mass of each individual to the nearest 0.1 g using an electronic balance (Scout II, Ohaus Corporation, Pine Brook, NJ).

2.2 | Performance measurements

To measure maximum sprinting speed, we placed each individual on a 1-m demarcated wooden dowel set at an approximately 25° incline and motivated the lizard to run by following it closely with our hand. Each sprint trial was video-recorded using a Nikon® D3200 camera (Nikon Corporation, Melville, NY) at a rate of 29 frames per second and saved as a .MOV file. While a greater frame rate is often better-suited for measures of maximum sprinting speed, the small body sizes and low sprinting speeds attained by these lizards allowed our frame rate of 29 frames per second to be sufficient. In virtually all of our videos, we were able to determine the exact moment in time when the tip of a lizard’s snout crossed a marking on the dowel. We analyzed these videos frame-by-frame using Eagle Eye Pro Viewer® software (Eagle Eye Digital Video; LLC, Saint Paul, MN), which allowed for the computation of each lizard’s maximum sprinting speed, in meters per second, over 10 cm. Although ambient temperature was unlikely to significantly vary during data collection, we measured this variable to the nearest 0.01°C using a mercury thermometer, as temperature is known to affect sprint speed in lizards (Artacho, Jouanneau, & Le Galliard, 2013).

2.3 | Statistical analysis

Data were analyzed only for adult males of each species. We calculated two conventional indices of body condition: the residual index (R_i) and

the scaled mass index (M_i). The residual index (R_i) was calculated using ordinary least squares (OLS) regressions of \log_{10} body mass on \log_{10} SVL (Cox & Calsbeek, 2015). We calculated the scaled mass index (M_i) using the equation:

$$M_i = M \times \left[\frac{\text{SVL}_0}{\text{SVL}} \right]^{b_{\text{SMA}}}$$

where M and SVL represent the mass and SVL of the individual, SVL_0 is the arithmetic mean population SVL, and b_{SMA} is the standardized major axis slope from the regression of the natural log of mass on the natural log of SVL for the population (Cox & Calsbeek, 2015; Peig & Green, 2009, 2010). Alternatively, b_{SMA} can be calculated indirectly as the slope of the OLS regression divided by Pearson’s correlation coefficient (Cox & Calsbeek, 2015; Peig & Green, 2009, 2010), as was done in this study.

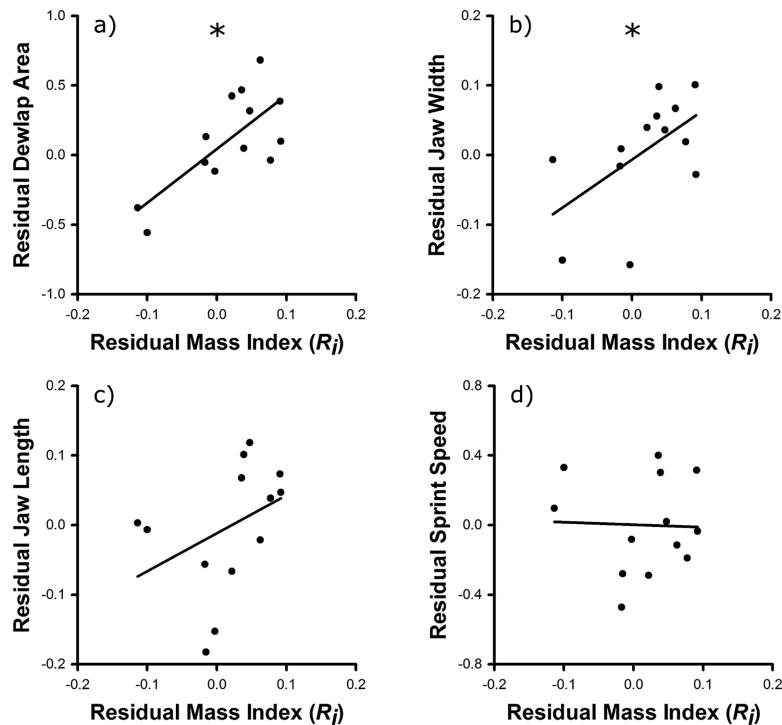
Jaw width, jaw length, dewlap area, and sprint speed were all \log_{10} -transformed to fulfill the assumption of normality for parametric statistics and because weapons and ornaments often scale allometrically, rather than linearly (Kodric-Brown, Sibly, & Brown, 2006). For all four of these log-transformed variables, residuals were calculated from linear regressions with \log_{10} -transformed snout-vent length to control for body size within each species (Supporting Information Table S1). We then used bivariate linear regression to test the effect of body condition on residual jaw width, residual jaw length, residual dewlap area, and residual sprint speed. Direct morphological comparisons between species were done using independent t -tests. All statistical tests were conducted using JMP Pro 11 (SAS, 2014).

3 | RESULTS

We found that ground anoles have a shorter body size but a greater mass than slender anoles, and that ground anoles have larger dewlaps than slender anoles (Table 1). Within ground anoles, we found a significant positive correlation between the residual index (R_i) and residual jaw width, and between R_i and residual dewlap area (Fig. 2; Table 2). However, we found no relationship between R_i and residual jaw length or residual sprint speed (Fig. 2; Table 2). Similarly, we found a significant positive relationship between the scaled mass index (M_i) and residual dewlap area, but not between M_i and residual jaw width, residual jaw length, or residual sprint speed (Table 2). In contrast, we found

TABLE 1 Morphological comparisons between *Anolis humilis* and *Anolis limifrons*

Trait	Mean		Standard Error		t-Ratio	df	P-value
	<i>A. humilis</i>	<i>A. limifrons</i>	<i>A. humilis</i>	<i>A. limifrons</i>			
Mass (g)	0.862	0.721	0.041	0.040	-2.443	25	0.022*
SVL (mm)	31.354	35.229	0.541	0.522	5.154	25	<0.001*
Dewlap area (cm ²)	6.607	2.726	0.449	0.433	-6.219	25	<0.001*
Jaw width (mm)	6.015	5.721	0.119	0.115	-1.771	25	0.089
Jaw length (mm)	8.562	8.850	0.241	0.232	0.864	25	0.396

**FIGURE 2** The relationship between body condition (calculated using the residual index, R_i) and (a) residual dewlap area, (b) residual jaw width, (c) residual jaw length, and (d) residual sprint speed in the ground anole, *Anolis humilis*. Dewlap area, jaw width, jaw length, and sprint speed were \log_{10} -transformed and linearly regressed on \log_{10} -transformed snout-vent length to generate residuals. Body condition was significantly correlated with residual jaw width and residual dewlap area, but not with residual jaw length or residual sprint speed (see Table 2); $N = 13$

no significant relationships between either measure of body condition (R_i or M_i) and residual dewlap area, residual jaw width, residual jaw length, or residual sprint speed in slender anoles (Fig. 3, Table 3). For confirmation, we ran all bivariate analyses using residuals of non-log-transformed dewlap area, jaw length, jaw width, and sprint speed, and all tests produced congruent results (all P -values were concordant).

4 | DISCUSSION

Our results suggest that the forces driving energetic limitation of traits can vary among traits and in a species-specific fashion. We found that jaw width, a trait important for bite force and male combat, and dewlap size, a trait important for sexual signaling, are condition-dependent at least for ground anoles (in addition to mixed evidence for jaw width in slender anoles, Table 3). While natural selection can influence the evolution of condition-dependent traits (Johnstone et al., 2009), naturally

selected traits tend to express condition dependence more weakly than sexually selected traits (Bonduriansky & Rowe, 2005; Cotton et al., 2004a). In our study, we found no relationship between body condition and either jaw length or sprint speed in either species, which could indicate a relatively greater contribution of natural selection, rather than sexual selection, in governing the evolution of these two traits in both ground anoles and slender anoles. Performance measures are often considered traits that are most influenced by natural selection because of their importance for capturing prey and escaping predation (Herrel, Van Damme, & De Vree, 1996; Jayne & Bennet, 1990; Miles, 2004). However, they can also be important for male fitness in the context of male–male combat and potentially subjected to the forces of sexual selection (Herrel, Moore, Bredeweg, & Nelson, 2010; Husak et al., 2006; Lailvaux & Irschick, 2006; Peterson & Husak, 2006). Indeed, most performance traits are likely acted upon by a complex mixture of sexual and natural selection (Lailvaux & Irschick, 2006; Miles, Snell, & Snell, 2001).

TABLE 2 Statistical results of bivariate linear regressions of body condition and residual dewlap area, residual jaw width, residual jaw length, and residual sprint speed in ground anoles (*Anolis humilis*). Residuals were used in order to control for body size and were generated from linear regressions of these variables (after \log_{10} -transformation) and \log_{10} -transformed snout-vent length

Index of Body Condition	Variable Measured	F-statistic	df	P-value	R ²
Residual (R_i)	Residual Dewlap Area	12.586	12	0.005*	0.534
	Residual Jaw Width	5.031	12	0.047*	0.314
	Residual Jaw Length	1.951	12	0.190	0.151
	Residual Sprint Speed	0.012	12	0.915	0.001
Scaled Mass (M_i)	Residual Dewlap Area	6.238	12	0.030*	0.362
	Residual Jaw Width	3.687	12	0.081	0.251
	Residual Jaw Length	1.608	12	0.230	0.128
	Residual Sprint Speed	0.003	12	0.956	<0.001

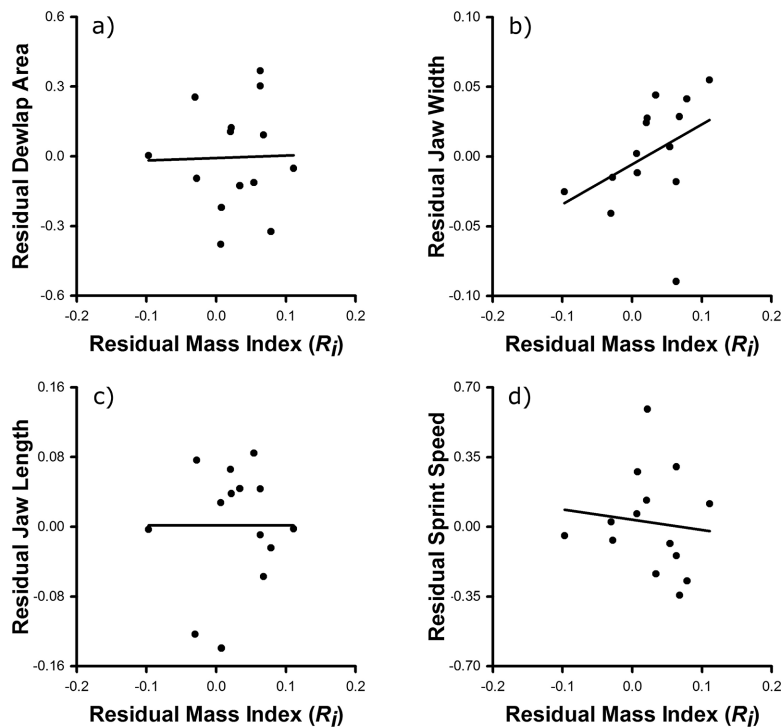


FIGURE 3 The relationship between body condition (calculated using the residual index, R_i) and (a) residual dewlap area, (b) residual jaw width, (c) residual jaw length, and (d) residual sprint speed in the slender anole, *Anolis limifrons*. Dewlap area, jaw width, jaw length, and sprint speed were \log_{10} -transformed and linearly regressed on \log_{10} -transformed snout-vent length to generate residuals. There were no significant correlations between body condition and any of the traits measured (see Table 3); $N = 14$

Our results agree with previous research demonstrating that alternative indices of body condition can produce highly congruent results with regard to inferences about selection and fitness (Cox & Calsbeek, 2015). The residual index (R_i) has been used historically, but the scaled mass index (M_i) has recently emerged as a purportedly superior measurement (Cox & Calsbeek, 2015; Peig & Green, 2009, 2010). We recovered the same statistical result using either index in seven out of eight analyses, suggesting that these indices are largely interchangeable in these two species of anole. A broader critique of using mass-SVL regressions (or related techniques) is that they do not necessarily reflect the energetic condition of individuals (Vervust, Lailvaux, Grbac, & Van Damme, 2008) and can be easily confounded by variation in body shape (Cox & Calsbeek, 2015). While we agree that energetic condition can be most accurately assessed by dissect-

ing and quantifying total organism lipid stores, there is a tradeoff in that the study organisms must be sacrificed (Blanckenhorn et al., 2003, 2004). Mass-size regressions usually satisfy the critical assumptions that a linear relationship exists between body mass and body size and that the proportion of mass associated with energy reserves is independent of body size, which suggests that condition indices can be useful measures of body condition (Schulte-Hostedde et al., 2005). Additionally, research aimed at validating the accuracy of condition indices has shown that these indices are indeed positively related to absolute estimates of fat stores, albeit with the potential for inflated error (Warner et al., 2016). Because assessing whole-organism lipid stores is not practical for research in which the individuals cannot be killed and quantitative magnetic resonance is not practical in remote field settings, we recognize the utility of proxies such as the residual

TABLE 3 Statistical results of bivariate linear regressions of body condition and residual dewlap area, residual jaw width, residual jaw length, and residual sprint speed in slender anoles (*Anolis limifrons*). Residuals were used in order to control for body size and were generated from linear regressions of these variables (after \log_{10} -transformation) and \log_{10} -transformed snout-vent length

Index of Body Condition	Variable Measured	F-statistic	df	P-value	R ²
Residual (R_i)	Residual dewlap area	0.008	13	0.931	0.001
	Residual jaw width	2.190	13	0.165	0.154
	Residual jaw length	0.123	13	0.928	0.011
	Residual sprint speed	0.146	13	0.710	0.012
Scaled mass (M_i)	Residual dewlap area	0.007	13	0.935	0.001
	Residual jaw width	0.519	13	0.485	0.041
	Residual jaw length	0.025	13	0.887	0.002
	Residual sprint speed	1.275	13	0.281	0.096

index and scaled mass index for studying energetic tradeoffs among traits.

While we found that both dewlap size and jaw width are positively correlated with body condition in ground anoles, we found no evidence of these relationships in slender anoles, suggesting evolutionary lability in the condition dependence of shared traits. Furthermore, the dewlap is larger in ground anoles than in slender anoles, despite the fact that ground anoles are shorter in body length. This pattern could suggest that either altered intensity of sexual selection (i.e., directional sexual selection driving the evolution of a larger dewlap in ground anoles exclusively; Bonduriansky & Rowe, 2005; Cotton, Fowler, & Pomiankowski, 2004b) or that signal evolution (i.e., microhabitat differences favoring different dewlap characteristics; Harrison & Poe, 2012; Leal & Fleishman, 2002) may drive the evolution of the dewlap in these two species. In either case, our findings imply that variation in the forces driving dewlap evolution can lead to varying expression of condition dependence among shared traits in a comparative context.

The condition dependence of dewlap size suggests that, at least in one species of *Anolis* lizard, the dewlap may be used by males to convey an honest indication of quality to potential mates. Previous research has found that some aspects of the dewlap are reflective of the overall health or physiological capabilities of the individual that possesses them (Lailvaux, Gilbert, & Edwards, 2012; Lailvaux & Irschick, 2007; Vanhooydonck et al., 2005; Vanhooydonck, Herrel, Meyers, & Irschick, 2009), which should cause sexual selection to favor such traits. However, in other cases, dewlap characteristics are not correlated with mate quality and thus do not translate to greater mating success (Greenberg & Noble, 1944; Lailvaux, Leifer, Kircher, & Johnson, 2015; Steffen, Hill, & Guyer, 2010; Vanhooydonck et al., 2005). Our results suggest that species with condition dependence of the dewlap are excellent candidates to test for female choice of honest indicators of male quality.

The dewlap is extraordinarily diverse among the species-rich lizard genus *Anolis* (Harrison & Poe, 2012; Nicholson, Harmon, & Losos, 2007). Despite the status of *Anolis* as an evolutionary ecology model system and the sizeable body of research on the dewlap, its role as a sexual and social signal remains enigmatic (Nicholson et al., 2007; Vanhooydonck et al., 2009). Previous research has found that the dewlap is often important for social signaling (Greenberg & Noble,

1944; Sigmund, 1983; Vanhooydonck et al., 2009; Williams & Rand, 1977), can be regulated in size and color by diet and testosterone (Cox, Hanninen, Reedy, & Cox, 2015; Steffen et al., 2010), can exhibit intraspecific polymorphism within and among populations (Glor & Laport, 2012; Lambert, Geneva, Luke Mahler, & Glor, 2013; Ng & Glor, 2011; Stapley, Wordley, & Slate, 2011), and varies in extent and presence among the genus *Anolis* (Harrison & Poe, 2012; Nicholson et al., 2007). Our work contributes to this work by suggesting that the size of the dewlap can be condition-dependent in some species. Indeed, within-species variation in the expression of the dewlap could be partially controlled by body condition and food availability. In a comparative context, the condition dependence of the dewlap in at least some species could theoretically increase the diversification of the dewlap (Lorch, Proulx, Rowe, & Day, 2003) and may be one of the many factors underlying the extraordinary diversity of the dewlap among *Anolis* species.

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