

## ORIGINAL ARTICLE

# Trait allometries generate super-honesty in *Anolis dewlaps* and may underlie sexual dimorphism

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## Abstract

Whether or not sexually selected traits consistently exhibit positive allometry (i.e. are disproportionately large in larger individuals) is an ongoing debate. Multiple models and exceptions to this rule suggest that the underlying drivers of sexual trait allometry are nuanced. Here, we compare allometries of sexual and non-sexual traits of a species (*Anolis aquaticus*) within a well-studied lizard genus to test the competing hypotheses that sexual traits are, or are not, defined by positive allometry. We further consider the relationships of trait functions, which are relatively well understood in the genus *Anolis*, and allometry to identify potential drivers of allometric patterns. In particular, we explore how trait allometries interact to influence total organism function and generate sexual dimorphism. We quantified size (of targeted traits) and color of a sexual signal (the dewlap) in *Anolis aquaticus* in the field. The dewlap conveyed information relevant to intra-sexual combat and exhibited positive allometry. Overall, our results suggest that using single-trait allometries as indicators of past selection provides only an incomplete understanding of trait evolution. Although the function of positive allometry in some individual sexual signals (e.g. those conveying “super-honest” information) may be straightforward, we illustrate how scaling relationships interact synergistically to influence the function of phenotypes and propose avenues for future research.

**Key words:** *Anolis* [*Norops*] *aquaticus*, color, morphology, reproductive strategy, scaling

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## INTRODUCTION

Identifying universal hallmarks of sexually selected traits across taxa has proven to be an elusive task (Darwin 1871; Andersson 1994). An idea that has gained popularity in recent decades is that sexually selected traits may be identified by their allometric scaling relationships (Petrie 1988, 1992; Simmons & Tomkins 1996; Green 2000; Kodric-Brown *et al.* 2006). Allometric scaling relationships describe how two trait measurements relate to one another, for example over development (ontogenetic allometry) or among individuals of

different sizes but the same life stage (static allometry). It has been proposed that condition-dependent traits under directional sexual selection consistently scale to an individual's body size with positive allometry (i.e. become disproportionately larger with an increase in body size [positive allometry hypothesis]). The rationale of this hypothesis cites the high costs to small individuals or the greater benefits to larger individuals of sexual trait production (Wallace 1987; Petrie 1992; Simmons & Tomkins 1996). Taken one step further, Kodric-Brown *et al.* (2006, p. 8737) suggest that positive allometry is “the inevitable result of differential allocation to structures that enhance mating success” and can serve as indicators of sexual selection (Simmons & Scheepers 1996; Green 2000).

Although the simplicity of this logic is attractive, re-assessments of the evidence for the positive allometry hypothesis have produced contradictory results. Bonduriansky and Day (2003) describe how almost any static allometric pattern may be produced by either ecological or sexual selection depending on a trait's unique selective regime. Overall, positive allometry should typically evolve when a given incremental increase in trait size produces a greater fitness advantage for larger rather than smaller individuals (but see Bello-Bedoy *et al.* 2015). As such, selection should produce a variety of sexual trait allometries because of the many ways in which this criterion precludes consistent selection for very large traits. For example, size-dependent conditional strategies may differentially exert selection on sexual traits depending on size class, or biomechanical or ecological constraints may limit the functionality of sexual traits at certain sizes (see Bonduriansky & Day 2003; Bonduriansky 2007; Eberhard *et al.* 2009 and references therein). This nuanced view is perhaps more representative of the empirical evidence; although classically exaggerated sexual traits often exhibit positive allometries (e.g. Gould 1973; Petrie 1988; McLain *et al.* 2003; McCullough *et al.* 2015), other sexual traits are isometric or even negatively allometric (e.g. Eberhard *et al.* 1998; Cuervo & Møller 2001; Eberhard 2002; Jennions & Kelly 2002).

Here, we examine sexual and non-sexual trait allometries in an *Anolis* lizard, a genus in which the ecological and sexual functions of morphological traits are relatively well understood (Losos 2009). Because of the wealth of information available on *Anolis* traits, use of a species within this genus enabled us to examine how trait allometries relate to: (i) trait function; and (ii) the hypothesis that sexual selection influences allometry

(Green 2000; Kodric-Brown *et al.* 2006). Furthermore, as morphological traits function interactively with one another to influence whole-organism performance and fitness, we illustrate how differential growth of two or more traits may produce intra-sexual and inter-sexual dimorphisms.

The anoline dewlap is a classic example of an exaggerated secondary sexual signal. Because of the dewlap's conspicuousness, physiological cost and fitness relevance, it is an ideal trait with which to investigate allometric scaling relationships. Used by males (and some females) of almost all *Anolis* species, the dewlap is a large, extendable and colorfully patterned structure on the throat (Nicholson *et al.* 2007; Losos 2009). The dewlap functions in species recognition (Williams & Rand 1977; Losos 1985) and to enhance conspicuousness (Persons *et al.* 1999; Fleishman & Persons 2001; Macedonia *et al.* 2003). Dewlap extensions are integral in both intraspecific (territory assertion, courtship; Crews 1975; Fleishman 1992; Tokarz 1995; Driessens *et al.* 2014) and interspecific (pursuit deterrence; Leal & Rodriguez-Robles 1997; Leal 1999) behavioral displays. In most anoles, dewlap size is an honest indicator of bite force (Vanhooydonck *et al.* 2005a,b). Dewlap color may correlate with condition, testosterone, immunity and contest success (Cook *et al.* 2013; Steffen & Guyer 2014; Cox *et al.* 2015; Driessens *et al.* 2015) and is a target of female choice (Sigmund, 1983; Cook *et al.* 2013). Consequently, the dewlap fulfills many of the criteria of a reliable indicator of individual quality (Vanhooydonck *et al.* 2007). Theory suggests that the underlying requirement for positive allometry is similar to the requirements for reliable signaling: higher-quality individuals receive a greater fitness return on their trait investment (Bonduriansky & Day 2003). We therefore sought to identify the information content of this classic sexual signal with respect to its allometric scaling.

We used the semi-aquatic anole, *Anolis aquaticus* Taylor, 1956, to examine this question and to test additional hypotheses regarding the interactions of sexual signals, sexual dimorphism and static allometry. *A. aquaticus* lives along streams and rivers on lowland and premontane slopes in south-western Costa Rica and north-western Panama (Savage 2005). This species is specialized to an aquatic habitat and is unique among mainland anoles in its use of vertical stream banks and boulders, a preference which is hypothesized to be facilitated by its proportionally shorter hind limbs and lower sprint speeds than the other mainland aquatics (Norops clade: *Anolis lionatus*, *Anolis oxylophus* and *Anolis poe-*

*cilopus*) (Nicholson *et al.* 2005; Muñoz *et al.* 2015). When threatened, *A. aquaticus* leap into streams and use an undulating motion and flattened rudder-like tails (Leal *et al.* 2002) to swim underwater (Eifler & Eifler 2010), or they escape by running along vertical surfaces of boulders and riverbanks to crevice retreats (personal observation). Male *A. aquaticus* are larger than females, bear orange-red “striped” (Nicholson *et al.* 2007) dewlaps, and defend territories encompassing the home ranges of 1 to 3 females (Márquez *et al.* 2005).

In this study, we predicted that properties of an exaggerated sexual signaling trait (the dewlap) would correlate to and exhibit positive allometric scaling with fitness-relevant morphologies (as per the positive allometry hypothesis of Kodric-Brown *et al.* 2006). If identified, positive allometry would suggest that this exaggerated trait is not merely an honest, but rather a “super-honest” (Wallace 1987) advertisement of male quality. “Super-honest” traits increase exponentially with body size (Bonduriansky 2007), and, therefore, they may be expected to serve as amplifiers of individual differences in quality. Second, we compared the competing predictions that: (i) positive allometry is a hallmark of sexually selected traits (positive allometry hypothesis; Green 2000; Kodric-Brown *et al.* 2006) versus (ii) positive allometry is not necessarily a consequence of sexual selection (Bonduriansky 2007). To approach this comparison, we calculated the allometric slopes of sexual and non-sexual traits in male and female *A. aquaticus*. The sexual traits that we tested were dewlap and head size of males (Vanhooydonck *et al.* 2010; Scharf & Meiri 2013) and female condition; heads are critically important weapons in anoline male contests (Stamps & Krishnan 1997; Jenssen *et al.* 2000; Lailvaux *et al.* 2004; Perry *et al.* 2004) and female lizard fat reserves fuel reproduction (Bonnet *et al.* 1998; Warne & Charnov 2008) and are preferred by males (Swierk *et al.* 2013). Tail size and limb length positively correlate with (i) swim speeds and (ii) jumping distances and sprint speeds, respectively (Losos & Sinervo 1989; Losos 1990a; Brossman *et al.* 2013). These locomotor traits have important fitness implications because of their relevance to predator avoidance and prey capture (Irschick & Losos 1998; Eifler & Eifler 2010). Consequently, we considered the tail and hind limbs primarily as non-sexual traits. We then examined the relationships of the allometric slopes of sexual and non-sexual traits in both males and females and offer interpretations for any deviations from isometry.

## MATERIALS AND METHODS

### Study site

This study was conducted from 29 June to 26 July 2015 at Las Cruces Biological Station (Organization for Tropical Studies), Puntarenas, in southern Costa Rica. The study site is located along the Rio Java (approximately 1200 m a.s.l.) within Las Cruces Biological Station. The forests surrounding the study site are a mixture of primary and secondary forests with substantial canopy cover over the river.

### Morphological measurements

We captured 81 adult *A. aquaticus* (male:  $\geq 54$  mm,  $N = 47$  and female:  $\geq 52$  mm,  $N = 34$ ; Márquez *et al.* 2005) from the field by hand or noose. Lizards were located during the day by searching under rock crevices and the sides of boulders with a flashlight. Immediately upon capture, we photographed each lizard (see “Photography” subsection below). We then measured snout-vent length (SVL), the length of the left hind limb from the body juncture to longest digit, and tail length starting at the cloaca using a clear plastic ruler. Mass was measured using a 10-g spring scale. All other measurements were taken with vernier calipers: we measured head length as the distance from the tip of the snout to the posterior edge of the parietal bone, head height and head width at their greatest points, and tail height and tail width at the base of the tail to the nearest 0.1 mm. A single researcher measured all lizards. Each lizard was then individually marked on the dorsal base of its tail using a unique combination of two drops of colored nail polish to prevent re-sampling and released at its site of capture.

### Photography

We used digital photography to quantify *A. aquaticus* dewlap color instead of alternative techniques, such as spectrophotometry. Digital photography as a method of studying animal coloration provides several advantages but requires careful interpretation (for recent reviews, see Troscianko & Stevens 2015; White *et al.* 2015). In brief, unlike digital photography, spectrophotometers are limited to measuring small areas of uniform color (Stevens *et al.* 2007) and are highly sensitive to measurement angle and distance to the subject (White *et al.* 2015), which may produce suboptimal results in the field. The multiple bright orange stripes on red *A. aquaticus* dewlaps are narrow and have poorly defined margins, rendering spectrophotometric measure-

ment imprecise in a field setting. We consequently chose to use digital photography, despite the fact that many *Anolis* species perceive and display ultraviolet colors (Fleishman *et al.* 1993; Fleishman & Persons 2001; Leal 2004). Although nothing is known regarding the ability of *A. aquaticus* to perceive ultraviolet colors, anoles utilizing heavily shaded habitats, such as *A. aquaticus* (100% of 103 surveyed individuals were located in shade; unpublished data), are less likely to use ultraviolet signals (Fleishman *et al.* 1993). Even so, we conservatively interpret our findings as solely quantifying individual variation in the 3 human-visible color channels (red, green and blue).

To photograph lizards, we positioned each male *A. aquaticus* on its right side and used forceps to gently pull the ceratobranchial forward to maximally extend the dewlap (Bels 1990). Dewlaps were perpendicular with the camera lens, and lizards were photographed against a white background and next to a ruler for scale, exactly 20 cm from the camera. The camera (Sony NEX-3, Sony, Thailand) was manually set to an ISO of 800, shutter speed of 30, and aperture of F22. All photographs were saved as RAW files to prevent loss of information (Stevens *et al.* 2007). Photographs were taken in the shade, using the camera flash to standardize the lighting conditions (as per Calisi & Hews 2007).

### Digital measurements

Dewlap size and color were quantified using Adobe Photoshop (version CS6, Adobe Systems). RAW files were converted to uncompressed TIFF files (RGB full color). Dewlap area was measured by tracing the outer edge of the entire dewlap using the quick selection tool, and calculating the area after setting the scale using the ruler placed next to the lizard in the photograph. This measurement process was repeated 3 times, and the average of the 3 dewlap area measurements was used in subsequent analyses. Area measurements were highly repeatable, corresponding to previous findings (Vanhooydonck *et al.* 2005a).

Prior to obtaining color measurements from photos, the total brightness of each photo was adjusted with the background as a standard (Calisi & Hews 2007) using the curves adjustment function in Adobe Photoshop to eliminate any differences in ambient lighting (Ng *et al.* 2013). We outlined the colored area of the dewlap and used the average blur function to obtain the average color of the dewlap area (Langkilde & Boronow 2012). We then used the color picker tool to obtain the RGB (red, green, and blue) values of the averaged color area.

### Statistical methods

All morphological variables were log-10 transformed prior to analysis, except where noted. Because mass increases linearly with the cube of body length (Stamps *et al.* 1994), we took the cube-root of mass before log-10 transformation to make this body condition proxy comparable to other linear morphological measures (Losos 1990b). To correct for size, we used the residuals of a linear regression of SVL and each log-10 transformed morphological variable (head length, width and height; tail length, width and height; limb length; cube-root of mass). The residuals of the regression of SVL and the cube-root of mass were used as our “condition” variable (Losos 1990b). We reduced the dimensionality of 3 separate groups of morphological variables by conducting principal components analyses (PCA; using the covariance matrix) for (1) head dimensions (length, width and height), (2) tail dimensions (length, width and height) and (3) dewlap RGB values. From each PCA, we retained the first 2 principal components (PC1 and PC2), which explained at least 90% of the variance (see Results). PCs were used in place of head, tail, and dewlap color measurements in subsequent analyses (hereafter referred to as PC<sub>H</sub>, PC<sub>T</sub> and PC<sub>COL</sub>, respectively). Using PCs allowed us to utilize all measured variables in our models while maintaining low variance inflation factors (VIF, a measure of multicollinearity). We tested the relationships of dewlap area and dewlap color (PC1<sub>COL</sub> and PC2<sub>COL</sub>) with fitness-relevant morphological traits (SVL, mass, PC1<sub>H</sub>, PC2<sub>H</sub>, PC1<sub>T</sub>, PC2<sub>T</sub> and limb length) using linear models.

To test for sexual dimorphism, we used a generalized linear model (family = binomial) with sex as the response and SVL and 6 size-corrected traits (mass, PC1<sub>H</sub>, PC2<sub>H</sub>, PC1<sub>T</sub>, PC2<sub>T</sub> and limb length) as the predictors. We then tested whether the scaling relationships of traits differed between sexes using standardized major axis (SMA, also known as reduced major axis) regression. Unlike ordinary least squares, SMA regression assumes measurement error in both X and Y and is, therefore, widely considered to more accurately estimate true allometric slopes (McArdle 1988; Bonduriansky 2007). We calculated the scaling exponent,  $b$ , which is the slope of the relationship of two log-transformed variables (e.g. SVL and limb length) in SMA regression. Proportionality (“isometry”) of linear traits (limb length, and the lengths, widths and heights of the head and tail) versus SVL is defined as  $b = 1$ . Positive allometry is defined as  $b > 1$ , such that lizards with larger SVLs have proportionally larger (linear) traits than expected under isome-

try. Because mass is a three-dimensional measurement, the scenario in which SVL and mass scale isometrically is indicated by  $b = 3$ . SVL was the predictor in each of these SMA regressions.

For males, we also used SMA regression to determine the scaling relationship of male SVL (predictor) and dewlap area (response). As dewlap area is a two-dimensional variable, isometry was indicated at  $b = 2$ .

All analyses were performed using R (v. 3.2.1, R Foundation for Statistical Computing, Vienna, Austria). Multicollinearity in our models was low ( $VIF < 2$ ), falling within acceptable levels for observational data (Zuur *et al.* 2010). We used the “smatr” package with method = SMA to test for allometric relationships, using a robust method (Huber’s  $M$  estimation) to minimize the effect of any potential outliers (Warton *et al.* 2012). An alpha of 0.05 indicated significance in all tests.

## RESULTS

Of 47 males, 3 were excluded only from the dewlap area analyses because their head position in the photographs did not meet our inclusion criterion (i.e. the entire dewlap area was not completely parallel with the background). Because of irregular lighting in some photographs, 6 of 47 males were excluded only from our analyses of dewlap color.

### Interpretation of principal components

The PCA on size-adjusted head length, head width and head height provided two overall measures of head shape,  $PC1_H$  and  $PC2_H$ .  $PC1_H$  (smallness) accounted for 78.5% of all variance, and  $PC2_H$  (longness) accounted for 13% of variance. Head traits loadings had varying signs and magnitudes; for  $PC1_H$ : head length =  $-0.707$ , head width =  $-0.164$ , head height =  $-0.688$  and for  $PC2_H$ : head length =  $0.703$ , head width  $< 0.001$ , head height =  $-0.708$ . A PCA on size-adjusted tail length, tail width and tail height also produced two overall measures of tail shape:  $PC1_T$  (longness) and  $PC2_T$  (narrowness) explained 81.9% and 13.7% of overall variance, respectively. Tail trait loadings varied in sign and magnitude ( $PC1_T$ : tail length =  $0.998$ , tail width  $< 0.001$ , tail height  $< 0.001$ ;  $PC2_T$ : tail length  $< 0.001$ , tail height =  $-0.836$ , tail width =  $-0.547$ ).

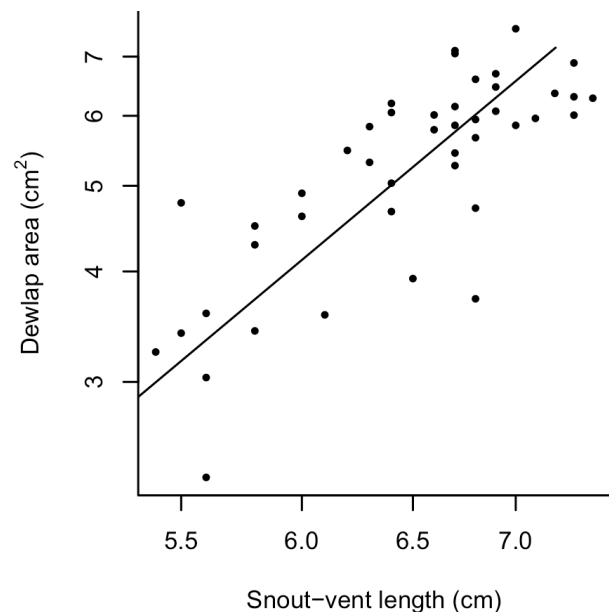
Finally, our PCA on dewlap red, green and blue values provided two generalized measures of these color channels:  $PC1_{COL}$  (larger blue : red ratio, 68.7% of variance) and  $PC2_{COL}$  (redness, 28% of variance). Loadings for the dewlap color PCA are as follows: for  $PC1_{COL}$ , red

=  $0.178$ , green =  $0.349$ , blue =  $0.920$ ; for  $PC2_{COL}$ , red =  $0.840$ , green =  $0.434$ , blue =  $-0.327$ . Large values of  $PC1_{COL}$  corresponded to greater blue : red ratios of the dewlap (i.e. lower red intensity when accounting for the other color channels); those dewlaps with relatively higher blue channel values appear brown to the human eye, and those with lower blue channel values appear red.  $PC2_{COL}$  primarily represented the relative brightness of the red color channel of the dewlap.

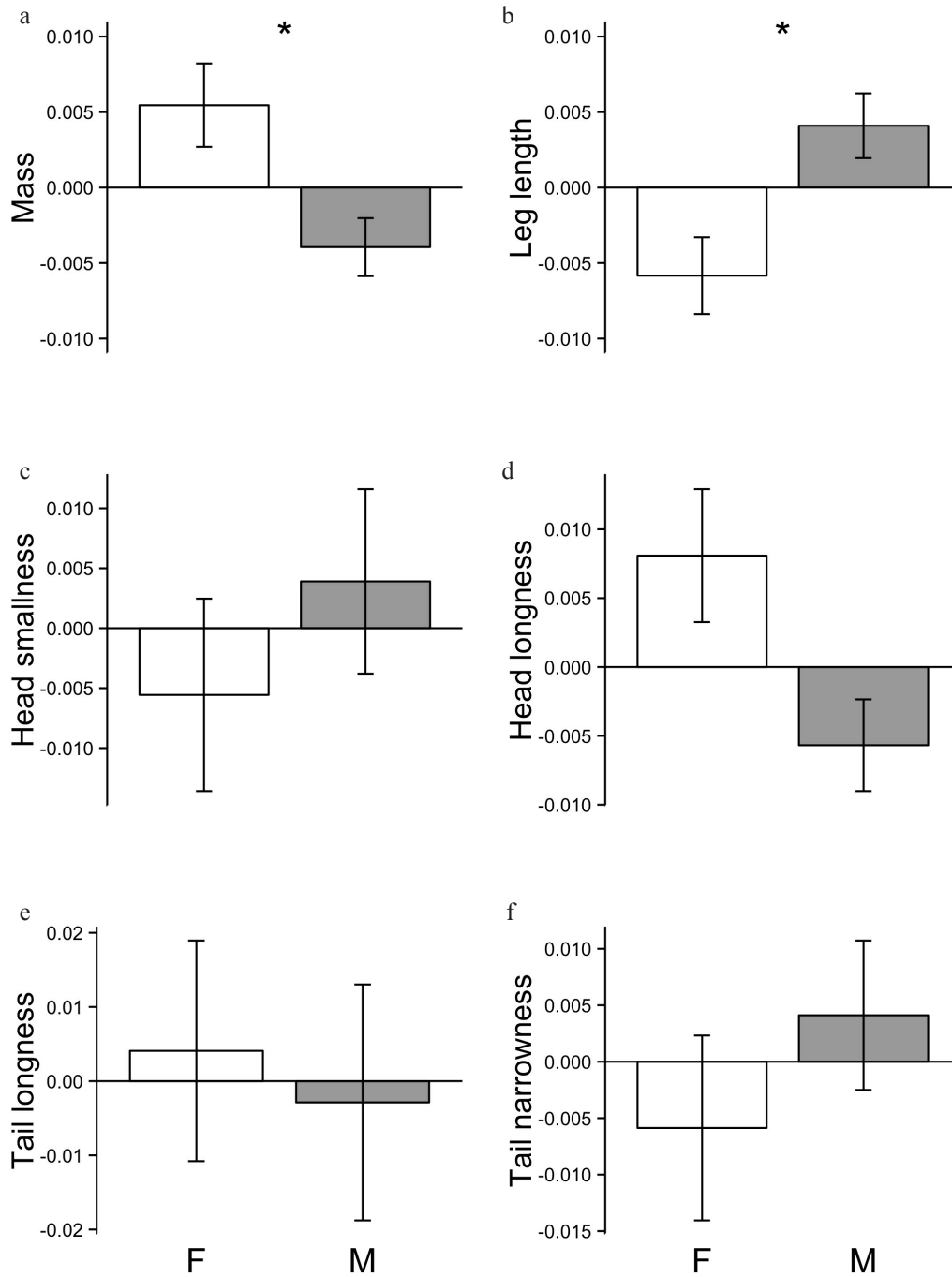
### Relationship of male morphology with dewlap parameters

Sexually mature males in our study ranged between 54 and 74 mm in SVL. Dewlap area was positively related to SVL ( $F_{1,36} = 58.660$ ,  $P < 0.001$ ) and exhibited positive allometric scaling with SVL ( $b = 3.024$ ;  $r = 0.561$ , degrees of freedom [df] = 42,  $P < 0.001$ ; Fig. 1). Dewlap area was not correlated with any other size-corrected trait measured (all  $P > 0.395$ ).

Our results indicate that larger males had relatively redder dewlaps. A negative relationship existed between dewlap  $PC1_{COL}$  and SVL ( $F_{1,33} = 5.281$ ,  $P = 0.028$ ) such that high values of SVL corresponded to negative blue : red ratio values of the dewlap. Relative dewlap redness was also greater in males with overall larg-



**Figure 1** Allometric relationship of snout-vent length (SVL) and dewlap area in male *Anolis aquaticus*. Axes are log scaled.



**Figure 2** Average *Anolis aquaticus* female (open bars) and male (shaded bars) measurements for size-corrected: (a) mass, (b) leg length, (c) head smallness (PC1<sub>H</sub>), (d) head longness (PC2<sub>H</sub>), (e) tail longness (PC1<sub>T</sub>) and (f) tail narrowness (PC1<sub>T</sub>). Head shape variables (head smallness and longness) were the first two principal components (PC1<sub>H</sub> and PC2<sub>H</sub>, respectively) of a principal components analysis (PCA) of head length, width and height. Tail shape variables (tail longness and narrowness) were the first two principal components (PC1<sub>T</sub> and PC1<sub>T</sub>, respectively) of a PCA of tail length, width and height. Variables were size corrected by obtaining the residuals of a regression of each trait against snout–vent length; residuals were used in subsequent analyses. Bars represent  $\pm 1$  standard error. Asterisks (\*) indicate significant differences.

**Table 1** Comparison of scaling relationships between male and female *Anolis aquaticus*

Trait	Sex differences		Male allometry				Female allometry			
	LRS	<i>P</i>	<i>b</i>	<i>r</i>	df	<i>P</i>	<i>b</i>	<i>r</i>	df	<i>P</i>
Mass	4.11	0.043	2.97	-0.03	45	0.877	3.77	0.46	32	<0.001
Limb length	3.94	0.047	0.83	-0.40	45	0.012	1.10	0.18	31	0.429
Head length	8.56	0.003	1.47	0.49	45	0.001	2.58	0.80	31	<0.001
Head height	1.77	0.183	1.27	0.29	45	0.068	1.65	0.60	31	0.002
Head width	1.30	0.254	1.07	0.16	45	0.358	1.25	0.44	31	0.047
Tail length	0.56	0.453	2.99	0.84	45	<0.001	3.61	0.87	31	<0.001
Tail height	2.12	0.146	1.74	0.71	45	<0.001	2.31	0.79	31	<0.001
Tail width	2.08	0.150	1.47	0.57	45	<0.001	1.92	0.66	31	<0.001

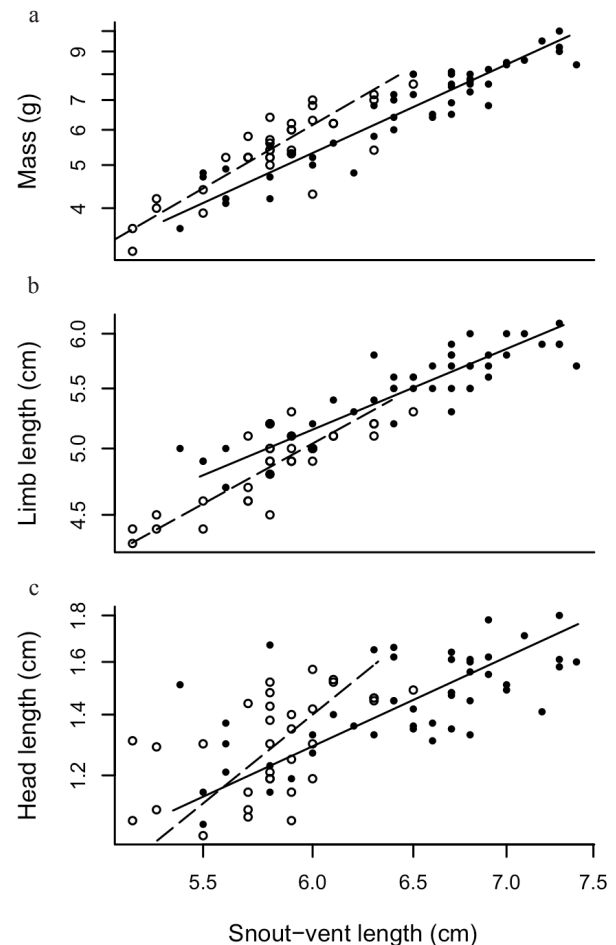
For all variables except for mass, isometry is indicated at  $b = 1$ ; isometry of mass is indicated at  $b = 3$ . Traits that scale with values of  $b$  significantly below  $b_{\text{isometry}}$  are negatively allometric, whereas those that scale with values of  $b$  significantly above  $b_{\text{isometry}}$  are positively allometric. Sexual divergence in scaling relationships is evidenced when the test for slope sexual divergence is less than 0.05. All degrees of freedom (df) = 1 for sexual differences.

er and longer heads. PC1<sub>COL</sub> was positively correlated with PC1<sub>H</sub> ( $F_{1,33} = 4.805$ ,  $P = 0.037$ ) and negatively correlated with PC2<sub>H</sub> ( $F_{1,33} = 5.588$ ,  $P = 0.024$ ). Condition, hind limb length and tail shape did not relate significantly to PC1<sub>COL</sub> (all  $P > 0.317$ ). The model relating PC2<sub>COL</sub> and the other morphological traits was not a better fit than the intercept-only model ( $F_{7,33} = 0.437$ ,  $P = 0.872$ ). Dewlap RGB differences in this species are, therefore, primarily due to variation in the ratio of the blue to red color channels.

### Sexual dimorphism and sexually divergent scaling relationships

Males had greater SVL ( $\chi^2_1 = 17.665$ ,  $P < 0.001$ ) but lower condition ( $\chi^2_1 = 8.427$ ,  $P = 0.004$ ) than females (Fig. 2a). Size-corrected hind limb length was greater in males than females ( $\chi^2_1 = 6.066$ ,  $P = 0.014$ ; Fig. 2b). There was a trend (though non-significant) for PC2<sub>H</sub> to be lower in males than females ( $\chi^2_1 = 3.474$ ,  $P = 0.062$ ), suggesting sexual dimorphism in head shape; for a given size, males had somewhat thicker and shorter heads than females (Fig. 2d). None of the other measured, size-corrected traits differed between the sexes (all  $P > 0.224$ ; Fig. 2).

Sexual divergence was evident in scaling relationships (Table 1). Allometric slopes differed between males and females for mass, limb length and head length. Females, but not males, had a positive scaling relationship of mass with SVL (Fig. 3a). Male hind limb length scaled negatively with SVL, whereas female limb length was isometric (Fig. 3b). Head length had positive



**Figure 3** Allometric relationships of snout-vent length (SVL) and (a) mass, (b) leg length and (c) head length for male (closed dots, solid line) and female (open dots, dashed line) *Anolis aquaticus*. Axes are log scaled.

allometry in both sexes; however, females had a significantly greater allometric slope than males (Fig. 3c). Head height allometric slopes did not differ between the sexes, and the pooled slope of this scaling relationship indicates positive allometry (LRS = 19.39,  $df = 2$ ,  $P < 0.001$ ). By contrast, head width did not differ between the sexes and exhibited isometry (LRS = 4.78,  $df = 2$ ,  $P = 0.091$ ). Male and female tail size scaling relationships did not differ; all tail dimensions had positive allometry with SVL after pooling the sexes (tail length: LRS = 111.90,  $df = 2$ ,  $P < 0.001$ ; tail height: LRS = 61.17,  $df = 2$ ,  $P < 0.001$ ; tail width: LRS = 30.47,  $df = 2$ ,  $P < 0.001$ ).

## DISCUSSION

To examine the roles of allometric scaling in sexual signaling and sexual dimorphism, we used *A. aquaticus*, a lizard with an exaggerated secondary sexual trait, the dewlap. In terms of the potential information content of this sexual trait, we found that *A. aquaticus* dewlap area positively correlated with body size, and that dewlap color was an indicator of body and head sizes. Furthermore, a positive allometric scaling relationship suggests that the dewlap may have a “super-honest” signaling capacity: larger individuals had disproportionately large sexual signals. Sexual dimorphism was apparent, as males were larger, with relatively longer legs and lower condition than females. Males also trended toward having relatively thicker, shorter heads. Contrary to the prediction that positive allometry is a hallmark of sexual selection, both sexually selected and non-sexually selected traits deviated from isometry in both sexes. Allometric patterns of traits were, instead, suggestive of physiological constraints, intralocus sexual conflict or ecological selection. These results broadly agree with predictions that deviations from isometry occur when fitness is determined by the interaction of a trait and body size, rather than trait size alone (Bonduriansky & Day 2003; Bonduriansky 2007).

### The super-honest information content of a widespread sexual trait

To our knowledge, this is one of the first studies to report that the *Anolis* dewlap exhibits positive allometry (see also Driessens *et al.* 2015). Until recently, understanding of this genus-wide sexual ornament was based on a study by Echelle *et al.* (1978). Echelle *et al.* (1978) report that *Anolis* dewlaps exhibit intraspecific positive allometry at small-to-medium body sizes (which we interpret as ontogenetic allometry) and an asymptot-

ing of the allometric slope at large body sizes (presumably indicating negative static allometry, although not explicitly stated). These authors propose that there is an optimal dewlap size for each species and that ecological selection (e.g. enhanced risk of predation) may ultimately limit the size of this sexual ornament in large individuals (Echelle *et al.* 1978), a suggestion echoed by Vanhooydonck *et al.* (2005b). Our results, and those of Driessens *et al.* (2015), contradict the idea that dewlap size approaches an asymptote. Male *A. aquaticus* and *A. sagrei* dewlaps had allometric slopes ( $b = 3.02$  and  $3.42$ , respectively) derived from reduced major axis regression analyses that substantially deviated from isometry (this study; Driessens *et al.* 2015). Whether males of other *Anolis* species also bear a super-honest dewlap remains unexplored. Interspecific variability in dewlap information content and allometry within the *Anolis* genus is a topic ripe for investigation.

Our results also indicate that males with larger SVLs and larger, longer heads (low  $PC1_H$  and high  $PC2_H$ ) had dewlaps that were relatively redder (low  $PC1_{COL}$ ). Across lizard species, head size positively correlates with bite force (Herrel *et al.* 1999, 2001, 2006; Verwaijen *et al.* 2002; Herrel & O'Reilly 2006) and influences the outcome of male contests (Huyghe *et al.* 2005). Taken together, these results suggest that dewlap color not only conveys information about body size (perhaps to amplify variation; Wallace 1987) but also bite force: individuals with brighter, redder dewlaps have head sizes that can potentially inflict more damage during male–male contests (Lailvaux *et al.* 2004). We are unaware of any other *Anolis* species in which dewlap coloration has been found to correspond to head size or bite force. As a species, *A. aquaticus* has a tall head shape and a correspondingly high bite force (Muñoz *et al.* 2015), and its high degree of sexual dimorphism suggests that males frequently engage in biting-based intrasexual contests (Lailvaux & Irschick 2007). Males of this species may, therefore, particularly benefit from such a conspicuous signal of weapon size.

It is curious that dewlap area was not indicative of male condition, as most sexual traits with positive allometry tend to be condition-dependent (e.g. Rodriguez *et al.* 2015). Despite this, the cube root of size-corrected mass was not correlated with SVL or the dewlap, indicating that males with larger dewlaps did not necessarily possess relatively greater fat reserves. Indeed, the isometric scaling relationship of male mass and SVL suggests that mass increased proportionally with SVL throughout post-maturation growth. However, large



males with disproportionately large sexual traits may pay a physiological cost, either (i) the result of mobilizing stored energy for the production and maintenance of large sexual traits or (ii) a consequence of an energetically-intensive behavioral strategy associated with bearing a large sexual trait (e.g. enhanced dewlap display rate; Johnson *et al.* 2011). If true, then the isometric relationship of mass and dewlap size may itself indicate that males with larger dewlaps are of higher quality, as they can maintain proportional energy reserves despite a disproportionate energetic demand.

Similarly, we found no correlation between the red-orange *A. aquaticus* dewlap brightness (PC1<sub>COL</sub> or PC2<sub>COL</sub>) and male condition. By contrast, Driessens *et al.* (2015) found that the brightness of the red and yellow regions of the *A. sagrei* dewlap correlated with body condition but, as a different body condition proxy (size-corrected mass) was used, direct comparisons with our condition proxy are not possible. Red, orange and yellow dewlap colors are produced by a combination of pterin and carotenoid pigments (Ortiz *et al.* 1963; Steffen & McGraw 2007; Alfonso *et al.* 2013). Red colors in the dewlap are almost exclusively the product of pterin (particularly drosoperin) pigments that, unlike carotenoid pigments, are not obtained from dietary sources (Macedonia *et al.* 2000; Steffen & McGraw 2009; Steffen *et al.* 2010). *A. aquaticus* dewlap color variation is, therefore, unlikely to be the result of dietary quality differences among individuals and may, instead, be determined by genetics (Ng *et al.* 2013), hormonal changes (Cox *et al.* 2015) and/or the health status of individuals (Cook *et al.* 2013).

### Allometric patterns of sexual and non-sexual traits

Comparing the allometric slopes of sexual (dewlap, male head size and female condition) versus non-sexual (leg length and tail size of both sexes) traits suggested that emergent allometric patterns are poor indicators of past sexual selection. Many, but not all, of the traits we classified as sexual (based on the existing literature) scaled positively with size: male dewlap area, male head length and female mass. Male head width and height, considered to be sexually selected components of male weaponry (Herrel & O'Reilly 2006), did not deviate from isometry. Other traits exhibited positive allometry, but were not considered to be sexual traits; in particular, tail length, width and height strongly exhibited positive allometry in both sexes. Our results broadly agree with a recent reassessment of our understanding of sex-

ual selection and allometry (Bonduriansky 2007). We found that positive allometry alone did not necessarily correspond to sexually selected traits. Instead, a diversity of allometric slopes of sexual traits was possible, and positive allometry was not a hallmark of sexual traits.

We note the unexpected finding that male and female tail dimensions (length, height and width) all exhibited large, positively allometric slopes ( $b = 1.47$  to  $3.61$ ). Although diversity in the static allometries of sexual traits is becoming more widely acknowledged, it is nevertheless uncommon for non-sexual traits to rival exaggerated sexual traits in allometric slope (Bonduriansky 2007), and we are unaware of a precedent. It could be possible that tail length actually represents a sexual trait in *A. aquaticus*, although this seems unlikely.

Instead, we propose two alternative interpretations of positive tail allometry that rely on an interpretation of tail size as a non-sexual trait. First, it may be possible that ecological selection interacts with sexual selection such that the allometric slopes of tail size, while not sexually selected *per se*, are indirectly driven by the sexual selection of other traits. For example, directional sexual selection on a conspicuous trait (e.g. the dewlap) may disproportionately generate predation pressure on more conspicuous individuals, as signals are often perceived, even by predators, on exponential scales (Green & Marler 1979; Shepard 1987). If predation pressure is disproportionate for large individuals with large dewlaps, then large males (and females, if selection is correlated; Lande 1980; Cox & Calsbeek 2009) could be predicted to have disproportionately larger predator-escape structures (i.e. pre-autotomized tail length [Medel *et al.* 1988] or the ability to swim faster facilitated by greater tail area [Brossman *et al.* 2013]). Second, we also note that a similar, but not as steep, positive allometric slope was found for tail size in the newt *Triturus vulgaris*, a species in which tail shape plays a role in mate choice (Green 1992). In addition to an explanation based on sexual selection, Green (1992) suggests that positive allometry in tail shape may be an adaptation to counter the disproportionately greater need for propulsive force when very large individuals swim. This explanation could certainly likewise apply to *A. aquaticus*, and further examination of the morphological determinants of swim speed in aquatic lizards would contribute to our ability to explain this unusual allometric pattern. Whether or not tail shape allometry is driven by either of these proposed mechanisms, it is clear that there is greater allometric diversity of non-sexual traits than previously thought.

Limb length, like tail size, was also considered to be a non-sexual trait in *A. aquaticus*. Unlike tail size, limb length allometric slopes differed between the sexes: males exhibited negative allometry in limb length, whereas female limb length was isometric. Although male limb length became proportionally shorter as male SVL increases, males had significantly longer size-corrected limb length overall (i.e. had a greater intercept of their allometric equation) than did females, in agreement with Irschick *et al.* (2005). As males spend more time in exposed habitat than females (Eifler & Eifler 2010), they may encounter greater predation risk and, consequently, enhanced selective pressure for greater sprint speeds overall (Irschick & Losos 1998, 1999). However, the sexual differences in limb length allometry require further discussion and may be explained in multiple ways. First, it is notable that female limb length in our study did not exceed approximately 53 mm, whereas maximum male limb length was greater than 60 mm (Fig. 3b). It is plausible that limbs that scale proportionally with SVL provide the optimal morphological strategy for *A. aquaticus* that climb and run on broad surfaces like vertical banks and boulders, but only to a point: males with very long limbs and large body sizes may fare particularly poorly if they encounter any narrow surfaces in their heterogeneous environments (Irschick & Losos 1999; Calsbeek & Irschick 2007), causing selection for proportionally smaller limb length with body size in males larger than approximately 65 mm SVL. Alternatively, large males may divert resources during post-maturation growth from limb length to sexual traits, as larger males have disproportionately larger dewlaps but shorter limbs. As a final explanation, or perhaps as a consequence of either the first two explanations, the observed sexual difference in limb length scaling relationships could be related to the existence of alternative male morphs in the population (Moore 1991; Lailvaux *et al.* 2004). This possibility is further discussed below.

We found that sexual differences in the relative allometric scaling of head traits may produce head shape sexual dimorphism. There was a trend (although non-significant) for male head shape (PC<sub>2H</sub>) to differ from that of females. Males tended to have proportionally shorter, thicker heads than females; female head shape was flatter and longer after size correction. Although head length and height in both sexes scale with positive allometry, female head length had a significantly higher allometric slope than male head length. Consequently, males have an increasingly smaller head length:

height ratio than females as body size increases; male head shape remains block-like, whereas female head shape elongates. This sexual divergence in head shape allometry could potentially produce the head shape dimorphism suggested by our results.

The relative allometric scaling relationships of male leg and head dimensions support the idea of “plastic” alternative male morphs (Moore 1991) in this genus and that a switch in male competitive strategies may occur within the lifetimes of *A. aquaticus* males. Lailvaux *et al.* (2004) found that sexually mature *A. carolinensis* males fall into one of two life-stage morphs with respective phenotypic optima: either “heavyweight” (larger, with relatively larger heads for their body size and greater bite force) or “lightweight” (smaller, with relatively longer limbs for their body size and enhanced jumping capacities). As anoles have indeterminate growth, lightweights that survive the high-mortality pinch-point at the lightweight/heavyweight transition are hypothesized to develop into testosterone-rich heavyweights (Lailvaux *et al.* 2004; Vanhooydonck *et al.* 2005b; Husak *et al.* 2007).

Although our size distribution of male *A. aquaticus* was unimodal (Hartigan’s dip test:  $N = 48$ , dip statistic = 0.053,  $P = 0.395$ ; Hartigan & Hartigan 1985), allometric scaling relationships nevertheless suggest that a similar separation may occur among *A. aquaticus* males. Sexually mature *A. aquaticus* males not only exhibit positive allometry in head size but also exhibit negative allometry in hind limb length (female *A. aquaticus* are isometric, by comparison). Therefore, large *A. aquaticus* males have relatively larger heads and shorter limbs for their body size. The reverse is true for small *A. aquaticus* males, with relatively smaller heads and longer limbs. Further work is needed to determine how limb length and head size influence performance and, thus, fitness of large versus small males in the field, particularly with respect to limb length, as *A. aquaticus* morphology is thought to be optimized for climbing on bare rock (Muñoz *et al.* 2015). Our results suggest that sexually mature males of this species could switch between two alternative plastic morphs as they grow, although the functional significance of the traits differing between these morphs is unknown.

Dewlap allometry in *A. aquaticus* further supports the prediction of alternative male morphs. Small sexually mature males have disproportionately small dewlaps in addition to relatively longer limbs and smaller weapons (i.e. the biting apparatus). In lieu of defending territories, small *A. aquaticus* males may use a sneaky copu-

lation tactic facilitated by their small, fast-moving body shape; such a size- or stage-dependent conditional strategy is widely represented across taxa, including invertebrates (Dennenmoser & Thiel 2008), amphibians (Arak 1988), birds (Jiguet & Bretagnolle 2001), reptiles (Madsen *et al.* 1993), fish (Taborsky *et al.* 1987) and mammals (Schradin *et al.* 2009). Over time, as males attain larger SVL and disproportionate increases in sexual trait and weapon sizes, they may switch their behavioral tactic to one of territory defense and mate guarding (corresponding to observations by Trivers 1976). By synthesizing information from the allometric scaling relationships of multiple traits, we can identify the morphological changes that may accompany this type of shift in behavioral tactics.

## CONCLUSIONS

Allometric relationships involved in producing alternative male morphs, as described here, support Bonduriansky's (2007) model of optimal allometry, which states that a trait's allometric pattern is actually dependent on the unique selective pressures placed on two different traits (body size and a secondary sexual trait). We extend this understanding by noting that the interactions of the allometric relationships of multiple traits (in our example: body size, an ornament, a weapon and a non-sexual trait) are likely to influence optimal allometry after taking into account whole-organism performance. This study provides empirical evidence of the complexities of the underlying processes that produce allometric patterns, and it demonstrates the unreliability of using emergent properties as indicators of past selective regimes (Bonduriansky and Day 2003; Eberhard *et al.* 2009).

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