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Multivariate genetic architecture of the *Anolis* dewlap reveals both shared and sex-specific features of a sexually dimorphic ornament

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Abstract

Darwin viewed the ornamentation of females as an indirect consequence of sexual selection on males and the transmission of male phenotypes to females via the 'laws of inheritance'. Although a number of studies have supported this view by demonstrating substantial between-sex genetic covariance for ornament expression, the majority of this work has focused on avian plumage. Moreover, few studies have considered the genetic basis of ornaments from a multivariate perspective, which may be crucial for understanding the evolution of sex differences in general, and of complex ornaments in particular. Here, we provide a multivariate, quantitative-genetic analysis of a sexually dimorphic ornament that has figured prominently in studies of sexual selection: the brightly coloured dewlap of *Anolis* lizards. Using data from a paternal half-sibling breeding experiment in brown anoles (*Anolis sagrei*), we show that multiple aspects of dewlap size and colour exhibit significant heritability and a genetic variance–covariance structure (**G**) that is broadly similar in males ($\mathbf{G}_m$) and females ($\mathbf{G}_f$). Whereas sexually monomorphic aspects of the dewlap, such as hue, exhibit significant between-sex genetic correlations (r_{mf}), sexually dimorphic features, such as area and brightness, exhibit reduced r_{mf} values that do not differ from zero. Using a modified random skewers analysis, we show that the between-sex genetic variance–covariance matrix (**B**) should not strongly constrain the independent responses of males and females to sexually antagonistic selection. Our microevolutionary analysis is in broad agreement with macroevolutionary perspectives indicating considerable scope for the independent evolution of coloration and ornamentation in males and females.

Introduction

In support of his theory of sexual selection, Darwin (1871) amassed an extensive catalogue of examples in which males display elaborate ornaments that are often reduced or absent in females. Despite the ensuing tendency for studies of sexual selection to focus on the evolution of ornamentation in males, recent research has increasingly sought to explain why females also express ornaments and other costly or conspicuous displays (Amundsen, 2000; Rubenstein & Lovette, 2009; Rosvall, 2011; Harrison & Poe, 2012; Tobias *et al.*, 2012; Dale *et al.*, 2015). Although Darwin recognized sex-role reversal as an adaptive explanation for some situations in which females are conspicuously ornamented (e.g. Amundsen & Forsgren, 2001; Berglund & Rosenqvist, 2001; Forsgren *et al.*, 2004), he generally viewed the ornamentation of females as an indirect consequence of sexual selection on males and the transmission of male phenotypes to females via the 'laws of inheritance' (Amundsen, 2000; Tobias *et al.*, 2012). However, the extent to which the constraints of shared inheritance contribute to the expression and coevolution of ornaments in both sexes remains largely uncertain (Kraaijeveld *et al.*, 2007; Potti & Canal, 2011; Tobias *et al.*, 2012; Kraaijeveld, 2014).

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From a macroevolutionary perspective, patterns of ornamentation in males and females tend to be positively correlated across species, suggesting some degree of genetic constraint (Ord & Stuart-Fox, 2006; Cardoso & Mota, 2010; Dale *et al.*, 2015). Nonetheless, many comparative analyses also reveal considerable independence in the evolution of ornaments by males and females, suggesting that these genetic constraints can be overcome (Wiens, 1999; Ord & Stuart-Fox, 2006; Harrison & Poe, 2012; Dale *et al.*, 2015). Although illustrative of broad evolutionary patterns, comparative analyses do not quantify the genetic variances and covariances that shape a population's response to selection. Hence, they cannot directly address the extent to which a shared genetic architecture is likely to influence the evolution of males and females over shorter, microevolutionary timescales. Unfortunately, most studies of the genetic architecture underlying ornaments have either focused exclusively on males, as is common for highly dimorphic or sex-limited ornaments (Moller, 1991; David *et al.*, 2000; Brooks & Endler, 2001), or have combined data from males and females without explicitly comparing their respective genetic architectures, as is common for monomorphic or weakly dimorphic traits expressed by both sexes (Evans & Sheldon, 2012, 2015; Hubbard *et al.*, 2015). Only a handful of studies have directly quantified the extent to which males and females share a genetic architecture for ornaments, the majority of which have focused on avian coloration and plumage (Moller, 1993; Price & Burley, 1993; Roulin *et al.*, 2001; McGlothlin *et al.*, 2005; Potti & Canal, 2011). It is therefore difficult to assess the generality with which shared inheritance influences the evolution of sexual ornaments (Kraaijeveld *et al.*, 2007; Kraaijeveld & Reumer, 2008; Tobias *et al.*, 2012).

From a quantitative-genetic perspective, shared inheritance can be operationally defined by the between-sex genetic correlation (r_{mf}), which describes the extent to which heritable variation in a given trait is correlated between males and females (Lande, 1980, 1987). Across a variety of traits and taxa, estimates of r_{mf} tend towards high values approaching 1 for sexually monomorphic traits and towards low values approaching 0 for highly dimorphic traits, suggesting that the evolution of sexual dimorphism often proceeds by reducing genetic correlations between the sexes (Poissant *et al.*, 2010). The limited data available for sexual ornaments yield fairly high and significant estimates of between-sex genetic correlations ($0.79 < r_{mf} < 0.97$) for aspects of plumage and coloration in birds (Price & Burley, 1993; Roulin *et al.*, 2001; McGlothlin *et al.*, 2005; Potti & Canal, 2011), although tail length in barn swallows ($r_{mf} = 0.54$), eyestalk length in stalk-eyed flies ($r_{mf} = 0.29$) and levels of various hydrocarbon pheromones in fruit flies ($-0.15 < r_{mf} < 0.85$) exhibit more substantial reductions in shared inheritance (Moller, 1993; Wilkinson, 1993; Chenoweth & Blows, 2003; Kraaijeveld *et al.*, 2007). This univariate perspective is highly intuitive, but many ornaments are inherently complex and comprised of multiple signals that may be better represented by multivariate approaches (Brooks & Endler, 2001; Blows *et al.*, 2003). Likewise, quantitative-genetic analyses deriving multitrait matrices within each sex (i.e. sex-specific genetic variance–covariance matrices, $\mathbf{G}_m$ and $\mathbf{G}_f$) and between sexes (i.e. between-sex genetic variance–covariance matrices, $\mathbf{B}$) often provide greater insight into the complex nature of intersexual genetic constraints than can be gleaned from univariate measures of r_{mf} alone (Steven *et al.*, 2007; Lewis *et al.*, 2011; Gosden *et al.*, 2012; Wyman *et al.*, 2013). However, few studies have explored sex differences in the quantitative-genetic architecture of sexual ornaments from this multivariate perspective (Gosden *et al.*, 2012; Gosden & Chenoweth, 2014).

We present a multivariate analysis of the quantitative-genetic architecture underlying a sexually dimorphic ornament that has figured prominently in studies of behavioural ecology and sexual selection – the colourful dewlap of *Anolis* lizards. Most of the approximately 400 species in the genus *Anolis* communicate visually using a dewlap, an extensible flap of brightly coloured skin located on the throat (Nicholson *et al.*, 2007; Losos, 2009; Harrison & Poe, 2012). In the majority of *Anolis* species, females possess a dewlap that is similarly coloured but greatly reduced in size (or absent entirely) relative to conspecific males, although females of some species exhibit dewlaps of comparable size (Fitch & Hillis, 1984; Harrison & Poe, 2012) or with dramatically different patterning and coloration relative to conspecific males (Losos, 2009; Harrison & Poe, 2012). Males display their dewlaps in a variety of contexts related to courtship, male–male aggression, species recognition and predator deterrence (Sigmund, 1983; Losos, 1985, 2009; Leal & Rodriguez-Robles, 1997; Nicholson *et al.*, 2007; Vanhooydonck *et al.*, 2009). Less is known about the functional significance of the dewlap in females, although it is used in female–female displays by several species (Orrell & Jenssen, 1998, 2003). Phylogenetic analyses reveal that dewlap size is uncorrelated between males and females across *Anolis* species (Harrison & Poe, 2012), but the extent to which the sexes of any species share a genetic basis for dewlap size or colouration is unknown.

We addressed this question using a paternal half-sibling breeding experiment on the brown anole (*Anolis sagrei*), a species in which adult males possess dewlaps roughly an order of magnitude larger than those of females. Dewlap colouration varies from bright red, orange and yellow to dull brown among populations of *A. sagrei* and is sexually monomorphic in some aspects, but dimorphic in others (Vanhooydonck *et al.*, 2009; Cox *et al.*, 2015). Both sexes display the dewlap in social interactions, but these displays are more frequent

and elaborate in males (Partan *et al.*, 2011; Driessens *et al.*, 2014, 2015). Although the size and colour of the dewlap may convey information about sex and individual quality (Driessens *et al.*, 2014, 2015) and predict the outcome of male–male contests (Steffen & Guyer, 2014), no study to date has linked dewlap phenotypes to reproductive success in *A. sagrei* (Tokarz, 2002; Tokarz *et al.*, 2005). By quantifying genetic variances and covariances between multiple aspects of dewlap size and colour within each sex, we first tested whether and how the genetic architecture of the dewlap in males ($\mathbf{G}_m$) differs from that in females ($\mathbf{G}_f$). Next, we tested the extent to which heritable variation in males is correlated with that in females by estimating between-sex genetic correlations (r_{mf}) for individual dewlap traits and deriving a between-sex genetic variance–covariance matrix (**B**) for the dewlap. Finally, we simulated the evolutionary response to both random and sexually antagonistic selection vectors to test the extent to which **B** is likely to constrain the further independent evolution of the dewlap in *A. sagrei* males and females.

Materials and methods

Breeding design

The brown anole, *Anolis* (*Norops*) *sagrei* (Duméril & Bibron, 1837), is a small, sexually dimorphic and semi-arboreal lizard native to Cuba and islands throughout the Bahamas. We collected *A. sagrei* adults from Great Exuma in the Commonwealth of the Bahamas (23°29′N, 75°45′W) and imported them to the University of Virginia, where they were housed individually in plastic cages (males: 40 × 23 × 32 cm; females: 30 × 20 × 20 cm; Lee's Kritter Keeper, San Marcos, CA) containing a carpet substrate, a potted plant for oviposition, PVC pipe for perching and hiding and a strip of fibreglass screen for basking. We placed each cage beneath two ReptiSun 10.0 UVB bulbs (ZooMed, San Luis Obispo, CA) and maintained constant diurnal temperature (29 °C), relative humidity (65%) and photoperiod (12-h L:12-h D during simulated winter or 13-h L:11-h D during the breeding season). Adult anoles were fed crickets (*Gryllus assimilis* and *Gryllodes sigillatus*; Ghann's Cricket Farm, Augusta, GA) dusted weekly with Fluker's Reptile Vitamin and Calcium supplements (Fluker's Cricket Farms, Port Allen, LA). We sprayed cage walls and potted plants twice daily with deionized water for drinking and to maintain a humid microenvironment.

For breeding, we introduced a female into the cage of a male and allowed the pair to mate for 14 days before returning the female to her own cage. To generate paternal half-siblings, we repeated this procedure by introducing a second female into the cage of the same male 7 days after removal of the first female. Anoles lay single eggs every 7–14 days and produce viable eggs from stored sperm for several months following a single mating (Cox & Calsbeek, 2010), so we recreated each pairing every 4–6 months to prevent sperm limitation. After they had mated, we housed females in isolation and checked the potted plant in each female's cage once per week for freshly laid eggs. We transplanted each new egg to an individual plastic container filled with moist vermiculite (1:1 deionized water to vermiculite by mass) and then incubated these containers at 28 °C, 80% relative humidity and 12-h L:12-h D photoperiod in a Percival Intellus 136VL. New hatchlings were sexed, massed, assigned a toe clip for permanent identification and housed individually in cages identical to those of adult females. We raised hatchlings on pinhead crickets (*Acheta domestica*, bred from adults from Fluker's Cricket Farms; dusted daily with Fluker's Reptile Vitamin and Calcium) until they reached 3 months of age, at which point we fed them increasingly larger sizes of *Gryllodes sigillatus* crickets as they grew, dusting the crickets weekly with vitamins and minerals (see Cox *et al.*, 2017 for details).

Dewlap phenotypes

We quantified the dewlap phenotypes of 301 male and 334 female progeny of 47 sires (mean size of paternal half-sibling families = 13.4, range 2–27 progeny) and 86 dams (mean size of maternal full-sibling families = 7.3, range 1–22 progeny). Progeny were bred in two successive years (2012, 2013) from the same sire–dam pairs, and because they were consequently measured at different time points (2014, 2015), we included cohort as an effect in most analyses. At the point when dewlap phenotypes were quantified, all progeny had grown to adults between 22 and 32 months of age (mean ± SD = 27.1 ± 2.2 months), well after the attainment of sexual maturity (estimated to have occurred between 10–16 months based on body size; Cox & Calsbeek, 2011) and close to the attainment of asymptotic body size (Cox *et al.*, 2017). Due to the range of adult ages at measurement, we included body size (snout–vent length, SVL) as a covariate in most analyses. We quantified dewlap phenotypes using two different methods.

First, we extended the dewlap with forceps over a piece of white graph paper alongside a colour standard (Kodak Gray Scale and Color Control Patches) and took a digital photograph (Canon EOS Rebel T3i with 100-mm macrolens) while standardizing lighting (FE30050-10 28W fluorescent photography bulbs in reflecting hoods) and distance from the camera lens. We imported digital files to ImageJ (Schneider *et al.*, 2012), set the scale using the dimensions of the grids on the graph paper, circumscribed the dewlap from its anterior and posterior points of contact with the body using the 'Freehand' tool and then calculated the area of the

dewlap (mm^2). To quantify dewlap colour, we used the 'Oval' tool to sample a circle with a diameter of 2 mm (females) or 5 mm (males) in the centre of the dewlap (as in Fig. 1a; sex differences in sampled diameters are due to sex differences in dewlap size) and then used the 'RGB Measure' plugin tool to calculate the mean red, green and blue values for all pixels within the circumscribed area. We converted RGB values to hue (primary colour reflected, measured on a 360° colour wheel), saturation (purity of the colour, 0% = grey, 100% = fully saturated) and brightness (lightness of the colour, 0% = black, 100% = white) for analysis. As context for our genetic analyses, we quantified sexual dimorphism in dewlap phenotypes using univariate analyses with each dewlap trait as a dependent variable, sex as a main effect and age or body size (SVL) as a covariate. Dewlap area and SVL were ln-transformed prior to analysis.

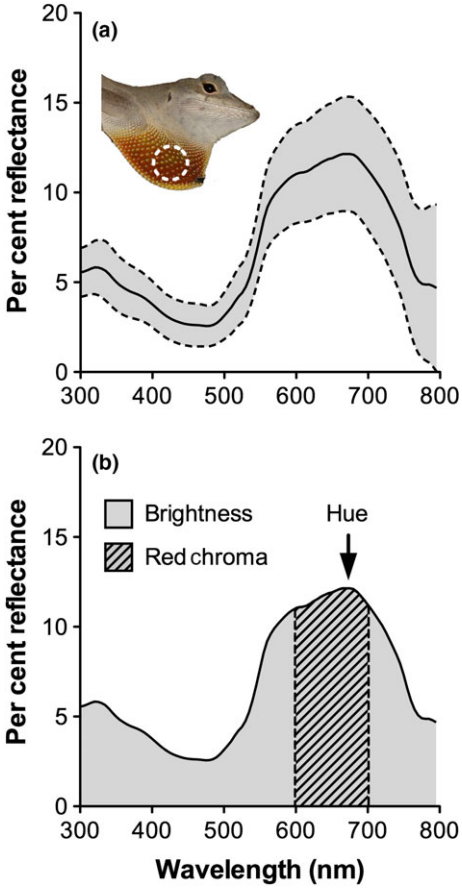

Fig. 1 (a) Mean (solid line) ±SD (dashed lines) reflectance spectrum for the centre of the dewlap (indicated by the dashed circle in the inset image) of *Anolis sagrei* males. (b) Illustration of traits calculated from the reflectance spectrum, including brightness (total area under the curve), red chroma (cross-hatched area divided by total area under the curve) and hue (wavelength of maximal reflectance). [Colour figure can be viewed at wileyonlinelibrary.com]

As a complementary method, we used a spectrometer to characterize the reflectance spectra of dewlaps in males, an approach that provides a more detailed and holistic summary of reflectance across ultraviolet, visible and infrared wavelengths (Evans & Sheldon, 2012, 2015). We could not obtain accurate measures of reflectance spectra for females using this method due to the small size of the dewlap relative to the spectrometer probe. Therefore, we analysed reflectance spectra from males primarily to assess whether we could detect significant and similar genetic variance and covariance using either method (photographs and spectra). We first extended the dewlap with forceps over a flat black background and then placed the probe of the spectrometer (USB 4000 with DH-2000 deuterium and halogen light source, QR600-7-SR-125F fibre, Ocean Optics, Dunedin, FL) on the centre of the dewlap (Fig. 1a), using a custom fitting on the probe to block ambient light. We generated three replicate reflectance spectra between 300 and 700 nm for the dewlap of each male, calibrating the spectrometer to black (velvet cloth) and white standards (USRS-099-010 Certified Reflectance Standard, Labsphere, North Sutton, NH) every five animals or 15 spectra. We generated an average reflectance curve from the three replicates per male and then calculated brightness (total area under the reflectance curve), red chroma (area under the curve between 605 and 700 nm as a proportion of total brightness) and hue (wavelength with maximal reflectance) for each male (Fig. 1b). We selected red chroma because it encompasses the most reflective portion of the spectrum in the dewlap (Fig. 1). Although both of our approaches for quantifying male dewlaps generated measures of 'hue' and 'brightness', these measures are not directly comparable between methods (see descriptions of how each was calculated, above) and may therefore capture different dimensions of phenotypic variation.

Quantitative genetics

We estimated both phenotypic (**P**) and genetic (**G**, including $\mathbf{G}_m$, $\mathbf{G}_f$ and **B**) variance–covariance matrices for dewlap traits using animal models in ASReml 4.1 (Gilmour *et al.*, 2015). Following Lande (1980), **G** can be written as the symmetrical matrix

$$\begin{pmatrix} \mathbf{G}_m & \mathbf{B} \\ \mathbf{B}^T & \mathbf{G}_f \end{pmatrix}$$

where T indicates matrix transposition. The evolutionary response to selection on each sex depends on the genetic variances and covariances of traits within each sex ($\mathbf{G}_m$ and $\mathbf{G}_f$) and the genetic variances and covariances of traits between sexes (**B**). Following exploratory

univariate analyses, we fit two multivariate models to derive these matrices. The first model included the four traits measured from photographs in each sex: dewlap area (ln-transformed), hue, saturation and brightness. Each trait was modelled separately for each sex, resulting in a total of eight traits in the model. This analysis allowed us to estimate $\mathbf{G}_m$, $\mathbf{G}_f$ and $\mathbf{B}$ for dewlap traits measured from photographs. The second model was fit using only the data from males and included the same four traits as above, as well as total brightness and red chroma from reflectance spectra. Hue as measured from reflectance spectra had zero additive genetic variance in univariate models and was therefore excluded from the multivariate analysis. This second model allowed us to assess whether the two methods for quantifying dewlap colour (reflectance spectra and photographs) captured similar information about genetic variance in males. Our goal in this analysis was not to test for equivalence of particular phenotypes (e.g. hue or brightness) across methods *per se*, but to broadly assess the extent to which these two methods captured common dimensions of genetic variance and covariance. Both models included snout–vent length (SVL, ln-transformed) as a covariate and cohort (2012 or 2013) as a fixed effect. Heritability estimates (h^2) and genetic correlations (r_g, r_{mf}), along with their approximate standard errors, were calculated in ASReml. We conservatively interpreted statistical significance as parameter estimates > 2 SE above zero.

We used two methods to compare $\mathbf{G}_m$ and $\mathbf{G}_f$, which can be conceptualized as a test of the extent to which the genetic architecture of the dewlap (i.e. genetic variances for individual traits and genetic covariances between traits) is similar in each sex. First, we used common principal components analysis to characterize structural similarity of these matrices (Phillips & Arnold, 1999; Steven *et al.*, 2007; Campbell *et al.*, 2011). This method evaluates several nested models for matrix similarity, ranging from unrelated (sharing no common principal components), to sharing one or more principal components (CPC1 to full CPC), to proportional (sharing all CPC but differing in total genetic variance) and equal (sharing all CPC and total genetic variance). We chose the best-fitting model using the Flury hierarchy and an information theoretic (AIC) approach (Phillips & Arnold, 1999). Although the Flury hierarchy is straightforward, it has been criticized for its reliance on orthogonal vectors and its disconnect with evolutionary theory (Steppan *et al.*, 2002; Aguirre *et al.*, 2014). Therefore, we also compared $\mathbf{G}_m$ and $\mathbf{G}_f$ using the random skewers method (Cheverud, 1996; Cheverud & Marroig, 2007; Roff *et al.*, 2012), which uses the multivariate breeder's equation (eqn. 1 from Lande, 1979) to estimate the predicted evolutionary response of each matrix to a set of random selection vectors. The correlation in predicted response vectors between $\mathbf{G}_m$ and $\mathbf{G}_f$ (null hypothesis = no correlation) reflects their similarity in a way that is potentially relevant to evolutionary change, although with the caveat that we did not include elements of between-sex genetic covariance ($\mathbf{B}$) in this analysis. Hence, this analysis is useful as a heuristic for assessing the congruence of within-sex genetic architectures, which are important components of the response to selection in each sex, but not for projecting sex-specific evolution, which also depends upon patterns of between-sex genetic covariance. We implemented this analysis in Skewers (Revell, 2007) by applying 10 000 random skewers to each within-sex matrix.

To assess the potential for genetic correlations between the sexes to constrain sex-specific evolution, we used a modification of the random skewers approach in which we compared the predicted response to selection using our empirically derived $\mathbf{B}$ matrix to the responses predicted using two artificially constructed matrices. In the first artificial matrix ($\mathbf{B}_0$), we simulated a hypothetical scenario in which the sexes were free to evolve independently by setting all elements of $\mathbf{B}_0$ to zero (Lewis *et al.*, 2011). In the second ($\mathbf{B}_1$), we simulated a hypothetical scenario in which the sexes were completely constrained from evolving independently ($r_{mf} = 1$) by setting the diagonal elements of $\mathbf{B}_1$ to the geometric mean of the two sex-specific genetic variances and the off-diagonal elements of $\mathbf{B}_1$ to be proportional to those of $\mathbf{G}_m$ and $\mathbf{G}_f$. Because elements in $\mathbf{G}_m$ differed from those in $\mathbf{G}_f$, the latter was accomplished by multiplying the average within-sex genetic correlation for each trait by the geometric mean of the appropriate genetic variances, making the cross-trait between-sex covariances in $\mathbf{B}_1$ as similar as possible to their within-sex counterparts in $\mathbf{G}_m$ and $\mathbf{G}_f$. All three resulting $\mathbf{G}$ matrices included our empirical estimates of $\mathbf{G}_m$ and $\mathbf{G}_f$ and differed only in whether they contained our empirical estimates of between-sex covariance ($\mathbf{B}$), or hypothetical values representing no between-sex covariance ($\mathbf{B}_0$) or perfect between-sex covariance ($\mathbf{B}_1$). We compared these three matrices using two different random skewers analyses. First, we chose skewers from a random uniform distribution in all possible directions, as usual. Second, we constrained the skewers to contain only sexually antagonistic elements favouring increased sexual dimorphism for each trait. That is, when the male phenotypic mean was larger than the female mean, only positive selection gradients were allowed for males and negative selection gradients were allowed for females. The *P*-values for each comparison indicate whether the two matrices produce similar evolutionary responses (null hypotheses = no correlation), although our primary goal in these comparisons was not to test for similarity *per se*, but to compare the magnitudes of the matrix correlations (r) from each analysis to determine whether the predicted response to selection using our empirically estimated $\mathbf{B}$ was more similar to a situation in which

the sexes were completely genetically constrained ($\mathbf{B}_1$) or completely unconstrained ($\mathbf{B}_0$). By conducting this analysis using both random and sexually antagonistic selection vectors, we further tested whether the extent of the constraint inferred from our estimated **B** was dependent on the type of selection.

Results

Reflectance spectra for male dewlaps

Spectra for male dewlaps exhibited a pronounced peak in reflectance from 550 to 750 nm, with maximal reflectance centred between 605 and 700 nm, the range that we used to quantify red chroma (Fig. 1). Brightness measured from reflectance spectra was phenotypically correlated with hue and brightness measured from photographs, but was neither heritable nor genetically correlated with other dewlap traits (Table 1). Red chroma measured from reflectance spectra was strongly phenotypically correlated with hue, saturation and brightness measured from photographs (Table 1). Red chroma also exhibited significant heritability ($h^2 = 0.53$) and was strongly genetically correlated with both hue and saturation measured from photographs (Table 1), suggesting that each of our methods for quantifying phenotypes captured similar properties of the genetic architecture of male dewlaps.

Sexual dimorphism in dewlap phenotypes

With the exception of dewlap area and brightness, most dewlap traits were phenotypically correlated with one another ($0.13 < r < 0.63$). Overall patterns of phenotypic correlation were broadly similar in each sex, although dewlap hue and brightness were only correlated in females, and dewlap saturation and brightness were strongly positively correlated in males, but negatively correlated in females (Table 2). Dewlap area increased with body size (SVL, both variables ln-transformed) in both sexes (ln SVL: $F_{1,623} = 20.05$; $P < 0.0001$; sex × ln SVL: $F_{1,623} = 1.83$; $P = 0.18$). Dewlap brightness increased with body size in females, but decreased with body size in males (ln SVL: $F_{1,623} = 1.10$; $P = 0.30$; sex × ln SVL: $F_{1,623} = 12.3$; $P = 0.0005$). Dewlap hue and saturation were unrelated to body size in either sex. We found extreme sexual dimorphism in dewlap area (10-fold larger in males in absolute size; eight-fold larger for a given SVL; sex: $F_{1,624} = 1326$; $P < 0.0001$), pronounced sexual dimorphism in dewlap brightness (two-fold brighter in females; sex: $F_{1,624} = 169.63$; $P < 0.0001$), modest sexual dimorphism in dewlap saturation (9% more saturated in males; sex: $F_{1,624} = 23.27$; $P < 0.0001$) and no sexual dimorphism in dewlap hue (sex: $F_{1,624} = 0.19$; $P = 0.66$).

Table 1 Phenotypic and genetic covariance (left) and correlation (right) matrices for dewlap traits measured from photographs (P) or reflectance spectra (S). Values in A-B are variances for each trait (diagonal) and covariances between traits (off-diagonal). Values in C are correlations between traits. Values in D are heritabilities for each trait (diagonal) and genetic correlations between traits (off-diagonal). Parameters were estimated in ASReml from models including body size (lnSVL) and cohort (2012, 2013) as effects. Standard errors are given in parentheses beside each estimate. Statistically significant estimates are indicated in bold and estimates with borderline significance are indicated in italics.

	$Area_P$	Hue_P	Sat_P	$Bright_P$	$Bright_S$	$Chroma_S$	$Area_P$	Hue_P	Sat_P	$Bright_P$	$Bright_S$	$Chroma_S$
	(A) Phenotypic variance–covariance matrix (**P**)						(C) Phenotypic correlation matrix					
$Area_P$	**0.0438 (0.004)**											
Hue_P	**−0.118 (0.054)**	**15.73 (1.47)**					**−0.142 (0.063)**					
Sat_P	**0.210 (0.086)**	**−12.73 (1.82)**	**43.71 (3.77)**				**0.152 (0.060)**	**−0.486 (0.048)**				
$Bright_P$	0.0581 (0.096)	−0.342 (1.910)	**30.57 (3.51)**	**54.90 (4.79)**			0.037 (0.062)	−0.012 (0.065)	**0.624 (0.038)**			
$Bright_S$	1.90 (1.60)	**73.08 (32.88)**	40.24 (47.77)	**157.3 (55.62)**	**18539 (1505)**		0.067 (0.055)	**0.135 (0.059)**	0.045 (0.053)	**0.156 (0.053)**		
$Chroma_S$	0.0009 (0.001)	**−0.111 (0.013)**	**0.148 (0.021)**	**0.0872 (0.021)**	−0.588 (0.360)	**0.00194 (0.00017)**	0.092 (0.063)	**−0.633 (0.038)**	**0.508 (0.046)**	**0.267 (0.059)**	−0.098 (0.059)	
	(B) Genetic variance–covariance matrix (**G**)						(D) Heritability/genetic correlation matrix					
$Area_P$	**0.014 (0.006)**						**0.315 (0.127)**					
Hue_P	−0.114 (0.083)	**14.17 (2.24)**					−0.257 (0.180)	**0.901 (0.080)**				
Sat_P	0.021 (0.112)	**−7.72 (2.47)**	**12.40 (4.38)**				0.051 (0.272)	**−0.582 (0.143)**	**0.284 (0.087)**			
$Bright_P$	−0.101 (0.146)	0.387 (2.98)	7.30 (4.40)	**19.13 (7.03)**			−0.196 (0.277)	0.024 (0.177)	**0.474 (0.186)**	**0.348 (0.113)**		
$Bright_S$	**3.64 (1.60)**	−1.14 (37.96)	−20.62 (47.95)	52.62 (55.39)	1758 (1515)		*0.738 (0.382)*	−0.007 (0.208)	−0.140 (0.328)	0.287 (0.311)	0.095 (0.081)	
$Chroma_S$	*0.0010 (0.001)*	**−0.0993 (0.013)**	**0.0951 (0.0205)**	0.0290 (0.215)	0.0341 (0.426)	**0.00103 (0.00021)**	*0.265 (0.157)*	**−0.822 (0.064)**	**0.842 (0.118)**	0.207 (0.146)	0.025 (0.312)	**0.531 (0.079)**

Sex differences in genetic architecture of the dewlap

In both sexes, the area of the dewlap was moderately and significantly heritable (h^2 = 0.31–0.35) and the hue of the dewlap was strongly and significantly heritable (h^2 = 0.67–0.92; Table 3). Saturation and brightness were both moderately and significantly heritable in males (h^2 = 0.25–0.36), but were not significantly heritable in females (h^2 = 0.14–0.18; Table 3). In all but one case, genetic correlations between dewlap traits were of the same sign in each sex, although the degree of correlation often differed substantially between males and females (Table 3). For example, whereas dewlap brightness was genetically independent of hue in males (Fig. 2a), these traits were strongly positively correlated in females (Fig. 2b). Conversely, whereas dewlap saturation and hue were strongly negatively correlated in males (Fig. 2c), this same genetic correlation was weak and nonsignificant in females (Fig. 2d). Likewise, dewlap saturation and brightness were positively correlated in males (Fig. 2e), but not in females (Fig. 2f). Consequently, values of heritability and the signs of genetic correlations were broadly congruent between the sexes (Fig. 3a), but the magnitudes of genetic correlations often differed somewhat between the sexes (Fig. 3b).

A similar pattern was evident from common principal components analysis of $\mathbf{G}_m$ and $\mathbf{G}_f$ using the Flury hierarchy, which favoured a model in which males and females share one of four possible eigenvectors (Table 4). This common principal component (loading positive for hue and brightness, negative for area and saturation) represents the major axis of genetic variation ($\mathbf{g}_{max}$) in females (66% of total variance in $\mathbf{G}_f$) and the secondary axis of genetic variation in males (39% of total variance in $\mathbf{G}_m$). Perhaps as a consequence of this shared axis of genetic variation, random skewers analysis indicated a high and significant correlation between the average predicted responses to selection acting through $\mathbf{G}_m$ and $\mathbf{G}_f$ (r = 0.85, P = 0.03).

Between-sex genetic correlations and covariances

The between-sex genetic correlation was strong and highly significant for dewlap hue (r_{mf} = 0.70; Fig. 4c-d), the trait that displayed the highest heritability in each sex (Table 3). Between-sex genetic correlations were moderate, but not significantly different from zero, for dewlap area (r_{mf} = 0.41; Fig. 4a-b) and brightness (r_{mf} = 0.39; Fig. 4e-f), and effectively zero for dewlap saturation (Table 3). Patterns of intersexual genetic covariance and correlation between pairs of traits in **B** were generally weak (r < 0.42; Table 3) and nonsignificant, with the exception of a positive genetic correlation between female brightness and male hue (r = 0.54) and a negative genetic correlation between female hue and male saturation (r = −0.48). Using the standard random skewers approach, we found that the average response to random selection vectors using the observed **B** matrix was significantly correlated with both the average response from a hypothetical matrix in which the sexes were completely genetically independent ($\mathbf{B}_0$; r = 0.87; P < 0.001) and with the average response from a hypothetical matrix in which the sexes were completely genetically constrained ($\mathbf{B}_1$; r = 0.84; P = 0.002). Thus, when we considered random selection vectors in all possible directions, the observed matrix was only slightly more akin to an unconstrained matrix than to a constrained matrix. However, when we considered only sexually antagonistic selection vectors acting in the direction of observed sexual dimorphism (i.e. selection favouring an elaboration of existing sexual dimorphism), the response predicted from the observed **B** matrix was much more similar to the response predicted from $\mathbf{B}_0$ (r = 0.93; P < 0.001) than to the response predicted from $\mathbf{B}_1$ (r = 0.61;

Table 2 Phenotypic covariance (left) and correlation (right) matrices for dewlap traits in males (top) and females (bottom). Values in A-B are phenotypic variances (diagonal) and covariances between traits (off-diagonal). Values in C-D are phenotypic correlations between traits. Parameters were estimated in ASReml from models including body size (lnSVL) and cohort (2012, 2013) as effects. Standard errors are given in parentheses beside each estimate. Statistically significant estimates are indicated in bold.

	Area	Hue	Saturation	Brightness	Area	Hue	Saturation
	(A) Phenotypic variance–covariance matrix for males ($\mathbf{P}_m$)				(C) Phenotypic correlation matrix for males		
Area	**0.044 (0.004)**						
Hue	**−0.112 (0.056)**	**15.90 (1.73)**			**−0.134 (0.065)**		
Saturation	**0.207 (0.085)**	**−12.76 (1.93)**	**43.51 (3.73)**		**0.150 (0.060)**	**−0.485 (0.049)**	
Brightness	0.057 (0.096)	−0.209 (1.991)	**30.48 (3.52)**	**55.09 (4.84)**	0.037 (0.062)	−0.007 (0.067)	**0.623 (0.038)**
	(B) Phenotypic variance–covariance matrix for females ($\mathbf{P}_f$)				(D) Phenotypic correlation matrix for females		
Area	**0.070 (0.006)**						
Hue	**−0.197 (0.069)**	**17.16 (1.63)**			**−0.179 (0.061)**		
Saturation	**0.530 (0.098)**	**−12.18 (1.65)**	**37.67 (3.01)**		**0.326 (0.051)**	**−0.479 (0.048)**	
Brightness	−0.019 (0.138)	**14.48 (2.40)**	**−15.86 (3.27)**	**83.64 (6.60)**	−0.008 (0.057)	**0.382 (0.050)**	**−0.283 (0.052)**

Table 3 Within- and between-sex genetic covariance (left) and correlation (right) matrices for dewlap traits. Values in A-B are additive genetic variances for each trait (diagonal) and covariances between traits (off-diagonal). Values in C are between-sex genetic covariances for each trait (diagonal) or pair of traits (off-diagonal). The lower-left quadrant of **G** (**B**^{T}) is shown. Values in D-E are heritability for each trait (diagonal) and genetic correlations between traits (off-diagonal). Values in F are between-sex genetic correlations for each trait (diagonal) or pair of traits (off-diagonal). Parameters were estimated in ASReml from models including body size (lnSVL) and cohort (2012, 2013) as effects. Standard errors are given in parentheses beside each estimate. Statistically significant estimates are indicated in bold and estimates with borderline significance are indicated in italics.

	Area	Hue	Saturation	Brightness	Area	Hue	Saturation	Brightness
	(A) Genetic variance–covariance matrix for males ($\mathbf{G}_m$)				(D) Heritability/genetic correlation matrix for males			
Area	**0.014 (0.006)**				**0.315 (0.129)**			
Hue	−0.094 (0.102)	**14.61 (3.32)**			−0.210 (0.217)	**0.919 (0.129)**		
Saturation	−0.003 (0.133)	**−7.90 (3.42)**	**11.06 (5.45)**		−0.007 (0.334)	**−0.621 (0.161)**	**0.254 (0.117)**	
Brightness	−0.109 (0.151)	0.574 (3.59)	6.70 (5.20)	**19.60 (7.57)**	−0.210 (0.289)	0.034 (0.212)	**0.455 (0.230)**	**0.356 (0.123)**
	(B) Genetic variance–covariance matrix for females ($\mathbf{G}_f$)				(E) Heritability/genetic correlation matrix for females			
Area	**0.024 (0.009)**				**0.346 (0.117)**			
Hue	−0.056 (0.117)	**11.66 (2.95)**			−0.106 (0.217)	**0.679 (0.127)**		
Saturation	0.178 (0.146)	−1.49 (2.57)	6.51 (4.15)		0.449 (0.292)	−0.171 (0.269)	0.173 (0.106)	
Brightness	−0.039 (0.194)	**8.53 (3.83)**	2.61 (4.14)	11.74 (8.09)	−0.072 (0.363)	**0.729 (0.243)**	0.298 (0.528)	0.140 (0.094)
f / m	(C) Between-sex genetic covariance matrix (**B**^{T})				(F) Between-sex genetic correlation matrix			
Area	0.008 (0.005)	−0.021 (0.122)	−0.177 (0.158)	−0.164 (0.187)	0.414 (0.275)	−0.035 (0.206)	−0.342 (0.298)	−0.238 (0.262)
Hue	−0.023 (0.095)	**9.14 (2.45)**	*−5.49 (2.94)*	3.42 (3.42)	−0.057 (0.238)	**0.700 (0.115)**	**−0.484 (0.230)**	0.226 (0.220)
Saturation	0.131 (0.112)	−1.36 (2.56)	−0.022 (2.19)	−4.08 (3.92)	0.437 (0.365)	−0.139 (0.262)	−0.003 (0.390)	−0.361 (0.336)
Brightness	0.009 (0.154)	*7.05 (3.85)*	−1.24 (4.94)	5.85 (5.79)	0.023 (0.408)	*0.539 (0.288)*	−0.108 (0.432)	0.386 (0.381)

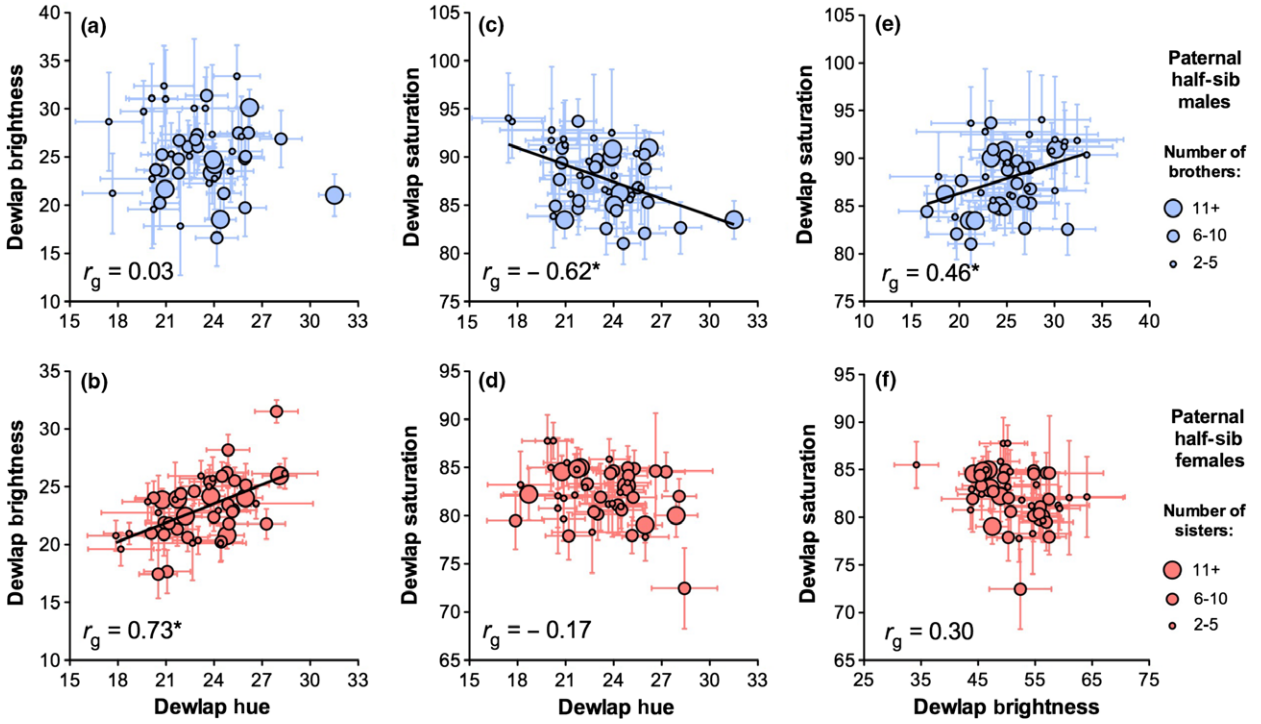

Fig. 2 Sex-specific genetic correlations (r_g) between dewlap traits, as illustrated by plots of paternal half-sib family means (± SE) of each trait for males (top panels) and females (bottom panels). Symbol sizes correspond to the number of total progeny in each family, as indicated to the right of the panels. Regression lines are for illustrative purposes and do not account for effects of size, age or cohort. Values of r_g in each panel were derived from animal models including these effects, as presented in Table 3D-E. Asterisks indicate significant genetic correlations. [Colour figure can be viewed at wileyonlinelibrary.com]

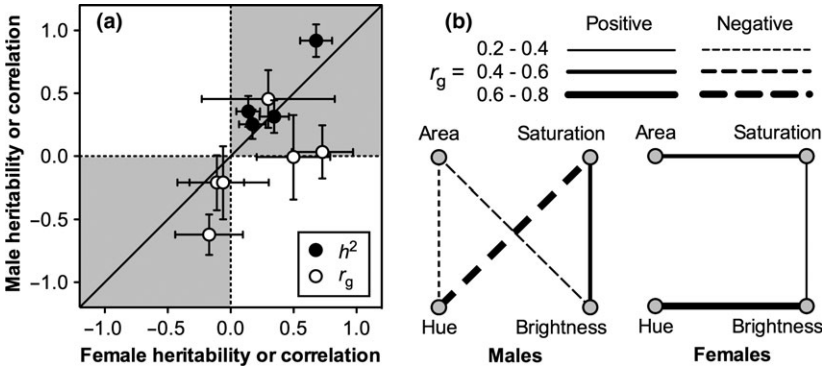

Fig. 3 (a) Estimates (± SE) of heritability (h^2) and genetic correlation (r_g) in males as a function of the same estimates in females for dewlap area, hue, saturation and brightness. The solid diagonal line indicates congruence in genetic architecture between the sexes. Correlations often vary in magnitude between the sexes, but not in direction, as indicated by their restriction to quadrants I and III in grey. (b) Schematic illustrating different patterns of genetic correlation in each sex, with line weight and style corresponding to the magnitude and direction of each correlation, as indicated in the legend. Traits are not connected for absolute values of $r_g < 0.2$.

Table 4 Comparison of within-sex genetic covariance matrices ($\mathbf{G}_m$ and $\mathbf{G}_f$) using the Flury hierarchy. The preferred model, which was chosen by minimizing the value of AIC, is indicated in bold and corresponds to one principal component shared between $\mathbf{G}_m$ and $\mathbf{G}_f$.

Hierarchy					
Higher	Lower	Chi-square	d.f.	*P*	AIC
Equality	Proportionality	3.79	1	0.0516	49.00
Proportionality	Full CPC	13.44	3	0.0038	47.22
Full CPC	CPC (2)	11.71	1	0.0006	39.79
CPC (2)	**CPC (1)**	16.19	2	0.0003	30.08
CPC (1)	Unrelated	3.89	3	0.2735	**17.89**
Unrelated	—				20.00

$P = 0.04$). This implies that our observed **B** should not strongly constrain an evolutionary response to selection for increased sexual dimorphism in the *A. sagrei* dewlap.

Discussion

We found significant heritability in multiple components of the *Anolis* dewlap, a sexually dimorphic ornament that has been studied extensively with respect to its behavioural ecology and evolutionary diversification. The two most sexually dimorphic aspects of the dewlap in our analysis were its size (eight-fold larger in males even after accounting for sex differences in body size) and its brightness (two-fold brighter in females). For each of these traits, the between-sex genetic correlation was modest and not statistically different from zero ($r_{mf} = 0.39$–0.41). By contrast, males and females were nearly identical in dewlap hue, a trait that exhibited a high and significant between-sex genetic correlation ($r_{mf} = 0.70$). This negative association between the degree of phenotypic sexual dimorphism and the magnitude of r_{mf} agrees with the general pattern across other traits and taxa (Ashman, 2003; Bonduriansky & Rowe, 2005; McDaniel, 2005; Poissant *et al.*, 2010), supporting the idea that the evolution of sexual dimorphism is often accompanied by a reduction in r_{mf} (Lande, 1980; Poissant *et al.*, 2010; Delph *et al.*, 2011). The modest values of r_{mf} (and other elements of **B**) that we observed are broadly consistent with the interpretation that although males and females share some of the genetic architecture for dewlap size and colour, this shared inheritance is unlikely to act as a strong constraint on sex-specific evolution. In this sense, our microevolutionary analyses of quantitative genetics agree with the conclusions of macroevolutionary studies indicating considerable scope for the independent evolution of coloration and ornamentation in males and females of *Anolis* and other vertebrates (Wiens, 1999; Ord & Stuart-Fox, 2006; Harrison & Poe, 2012; Dale *et al.*, 2015).

Dewlap traits with high levels of additive genetic variance in males tended to exhibit high levels in females (Table 3; Fig. 3), broadly similar to patterns observed in other species (Lande, 1980, 1987; Fairbairn & Roff, 2006). However, the heritability of dewlap traits also tended to differ subtly between males and females (Table 3), similar to other studies reporting sex differences in heritability or additive genetic variance for shared traits (Arnold & Phillips, 1999; Jensen *et al.*, 2003; Sakai *et al.*, 2008; Wyman & Rowe, 2014; Cox *et al.*, 2017). Although genetic correlations between dewlap traits were never opposite in sign between males and females, they were often strong and significant in one sex, but weak and nonsignificant in the other (Table 2; Figs 2 and 3). These element-by-element comparisons support the general conclusion that patterns of genetic covariance differ subtly between

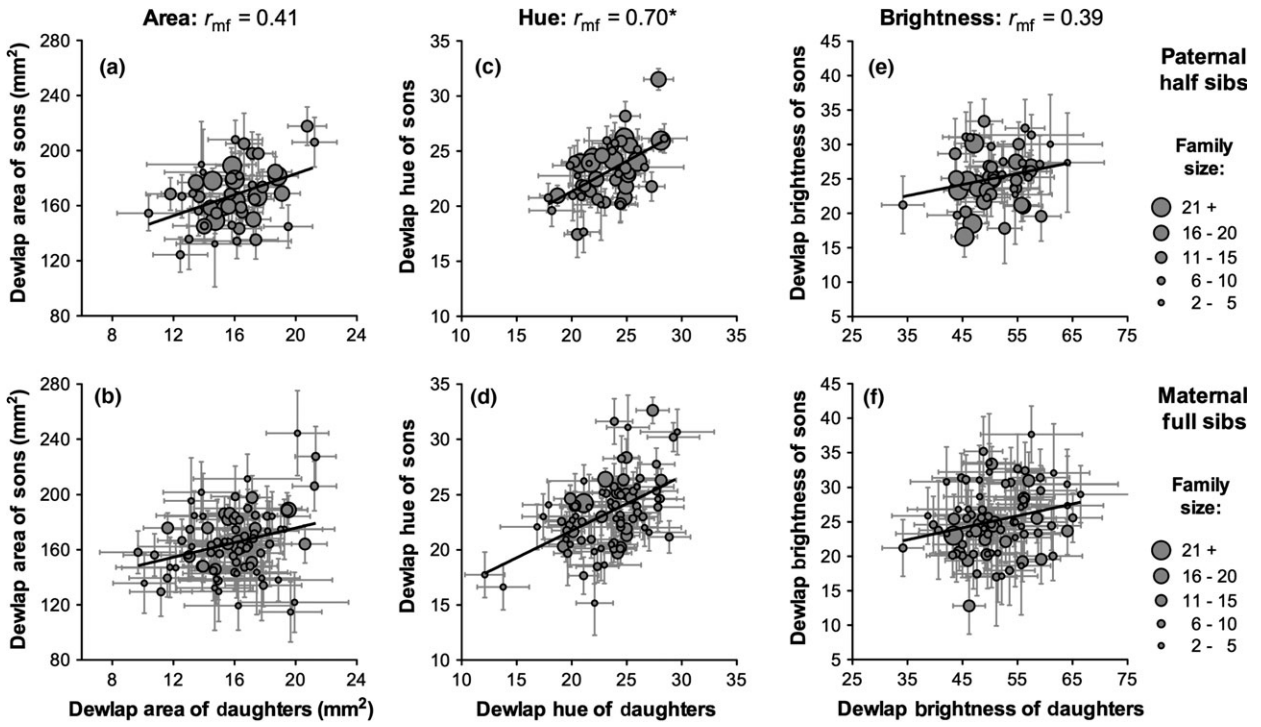

Fig. 4 Between-sex genetic correlations for dewlap area, hue and brightness, as illustrated by plots of family means (± SE) for sons versus those for daughters, based on 47 families comprised of paternal half-siblings (top row) or 80 families comprised of maternal full siblings (bottom row, seven maternal families are omitted because they only contained progeny of one sex). Symbol size corresponds to the number of total progeny in each family, as indicated in the figure legend. Regression lines are for illustrative purposes and do not account for effects of size, age or cohort. Values of r_{mf} at the top of each column were derived from animal models including these effects, as presented in Table 3F.

males and females, as observed across a diverse array of plants (Ashman, 2003; Steven *et al.*, 2007; Sakai *et al.*, 2008; Campbell *et al.*, 2011) and animals (Holloway *et al.*, 1993; Guntrip *et al.*, 1997; Jensen *et al.*, 2003; Rolff *et al.*, 2005; McGuigan & Blows, 2007; Dmitriew *et al.*, 2010; Lewis *et al.*, 2011).

Multivariate comparisons of $\mathbf{G}_m$ and $\mathbf{G}_f$ in other species indicate that males and females tend to share a similar orientation of **G** (common principal components or eigenvectors), but usually differ in its size and shape (different proportions and eigenvalues) (Ashman, 2003; Arnold *et al.*, 2008; Barker *et al.*, 2010; Campbell *et al.*, 2011; Wyman *et al.*, 2013). However, several studies have documented even more pronounced differences in $\mathbf{G}_m$ and $\mathbf{G}_f$ that include highly divergent orientations of their major axes of genetic variation (Jensen *et al.*, 2003; Steven *et al.*, 2007). Our results are intermediate between these two scenarios, indicating that $\mathbf{G}_m$ and $\mathbf{G}_f$ for the anole dewlap share only one of four possible eigenvectors, representing the major axis of genetic variation ($\mathbf{g}_{max}$) in females (66% of total variance in $\mathbf{G}_f$) and the secondary axis of genetic variation in males (39% of total variance in $\mathbf{G}_m$). Given the large proportion of overall variance in **G** explained by this common principal component, it is not surprising that the predicted evolutionary responses to random selection vectors were highly correlated between $\mathbf{G}_m$ and $\mathbf{G}_f$, despite differences in their overall structure. Because this comparison does not include the between-sex covariances in **B**, it is only useful as a heuristic for assessing the congruence of within-sex genetic architectures, not as an assessment of the potential for sex-specific evolution, which is influenced by both within- and between-sex genetic covariances.

Between-sex genetic covariances in **B** were generally modest and nonsignificant (Table 3) and did not strongly alter the predicted responses to selection on male and female dewlaps, particularly when considering only sexually antagonistic selection gradients that would favour increased sexual dimorphism. In fact, the average response to sexually antagonistic selection vectors using the observed **B** matrix was highly correlated with the response observed under a hypothetical scenario in which males and females were genetically independent of one another ($\mathbf{B}_0$). Although methodological differences preclude direct comparisons, this conclusion stands in contrast to several recent studies demonstrating that **B** should strongly alter the

predicted response to selection in males and females (Steven *et al.*, 2007; Lewis *et al.*, 2011; Gosden *et al.*, 2012). This discrepancy likely reflects the relatively weak between-sex genetic correlations that characterize the anole dewlap (mean $r_{mf} = 0.38$), relative to values observed for floral traits in dioecious *Silene latifolia* (mean $r_{mf} = 0.72$; Steven *et al.*, 2007) and gynodioecious *Schiedea adamantis* (mean $r_{mf} = 0.51$; Campbell *et al.*, 2011), or cuticular hydrocarbons in *Drosophila serrata* (mean $r_{mf} = 0.59$; Gosden *et al.*, 2012). Similar to previous studies, we also found asymmetries in the above- and below-diagonal elements in **B**, such that male-to-female patterns of genetic covariance were not always closely aligned with corresponding female-to-male elements of the matrix (Steven *et al.*, 2007; Campbell *et al.*, 2011; Lewis *et al.*, 2011; Gosden *et al.*, 2012). The reasons for this apparently general pattern of asymmetry in **B** are not well understood, but may include prior effects of sex-specific selection in combination with mechanisms such as genomic imprinting, sex linkage and sex-biased expression of the genes underlying dimorphic phenotypes (Wyman *et al.*, 2013). Although our study does not directly address any of these potential mechanisms, previous experiments have shown that dewlap size and coloration are strongly responsive to testosterone in brown anoles (Cox *et al.*, 2009, 2015). Sex-biased modifiers of gene expression, such as testosterone, may contribute not only to the phenotypic expression of sexual dimorphism in dewlap size and colour, but also to the corresponding reduction of between-sex genetic correlations (Cox *et al.*, 2017) and the creation of sex-specific patterns of phenotypic and genetic integration (i.e. $\mathbf{G}_m$, $\mathbf{G}_f$, asymmetries in **B**) among dewlap traits (Cox *et al.*, 2016).

Our study provides one of the first multivariate investigations of the between-sex genetic architecture underlying any sexual ornament. Analyses of plumage and coloration in birds have generally yielded high and significant estimates of between-sex genetic correlations ($r_{mf} > 0.79$) for individual traits that act as ornaments or sexual signals (Price & Burley, 1993; Roulin *et al.*, 2001; McGlothlin *et al.*, 2005; Potti & Canal, 2011). Our analyses revealed a comparably high genetic correlation for dewlap hue, but all other aspects of dewlap colour and size had much lower values of r_{mf}, similar to those observed for highly dimorphic sexual ornaments such as tail length in barn swallows ($r_{mf} = 0.54$) or eyestalk length in stalk-eyed flies ($r_{mf} = 0.29$) (Moller, 1993; Wilkinson, 1993; Kraaijeveld *et al.*, 2007). In one of the few studies of the multivariate genetic architecture underlying a sexual ornament, the inclusion of the full matrix of covariances in **B** greatly reduced the extent to which male and female fruit flies were predicted to diverge in response to observed sex differences in selection on hydrocarbon pheromones (Gosden *et al.*, 2012). Likewise, **B** severely constrained the evolutionary response favoured by observed sexually antagonistic selection on life-history traits in the Indian meal moth (Lewis *et al.*, 2011). Although we do not know the actual form of sex-specific selection acting on multivariate dewlap phenotypes in *Anolis sagrei* (analyses of natural and sexual selection are presently underway in a wild population), our characterization of **B** using random sexually antagonistic selection vectors provides a counterpoint to these examples, suggesting that the multivariate genetic architecture of the dewlap is unlikely to impose such a strong constraint in this system.

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