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Female dewlap ornaments are evolutionarily labile and associated with increased diversification rates in *Anolis* lizards

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The evolution of costly signalling traits has largely focused on male ornaments. However, our understanding of ornament evolution is necessarily incomplete without investigating the causes and consequences of variation in female ornamentation. Here, we study the *Anolis* lizard dewlap, a trait extensively studied as a male secondary sexual characteristic but present in females of several species. We characterized female dewlaps for 339 species to test hypotheses about their evolution. Our results did not support the hypothesis that female dewlaps are selected against throughout the anole phylogeny. Rather, we found that female dewlaps were evolutionary labile. We also did not find support for the adaptive hypothesis that interspecific competition drove the evolution of female dewlaps. However, we did find support for the pleiotropy hypothesis as species with larger females and reduced sexual size dimorphism were more likely to possess female dewlaps. Lastly, we found that female dewlap presence influenced diversification rates in anoles, but only secondarily to a hidden state. Our results demonstrate that female ornamentation is widespread in anoles and the traditional hypothesis of divergent selection between the sexes does not fully explain their evolution. Instead, female ornamentation is likely to be subject to complex adaptive and non-adaptive evolutionary forces.

1. Introduction

The evolution of ornaments, conspicuous traits that function primarily as intraspecific signals, has garnered substantial interest. A substantive body of theoretical and empirical literature has focused on understanding how sexual selection can drive the evolution of male-biased ornaments in particular [1–5]. Yet, the focus on the evolution of traits exhibiting male-biased dimorphism obscures the fact that female ornaments are common in nature [6,7]. Many traits that are classically defined as male secondary sexual characteristics based on dimorphism are monomorphic or polymorphic in closely related species—for example, male-like plumage in female hummingbirds [8], spines and crests in female agamid lizards [9], and horns in female *Onthophagus* beetles [10]. Thus, sexual selection for male ornaments coupled with ecological selection against female ornaments may not be the dominant mechanism by which ornaments evolve [6–8,11]. Investigating the causes and consequences of variation in female ornamentation will build our understanding of the evolution of ornamental traits more broadly [6,7,11,12].

Table 1. Three hypotheses for the drivers of female dewlap evolution tested in this study, their associated predictions (P) for comparative and phylogenetic analyses, and whether predictions were met for the full tree (i.e. all *Anolis*), Greater Antillean (GA), *Dactyloa* clade and *Draconura* clade anoles.

	full tree	GA	*Dactyloa*	*Draconura*
genetic correlation hypothesis				
P1: the ancestral dewlap state is sexually monomorphic	no	no	no	no
P2: transition rates are biased towards dewlap loss in females	no	no	no	no
P3: female dewlaps are negatively associated with temperature	marginal	yes	no	no
pleiotropy hypothesis				
P1: female dewlap state is associated with larger body size	yes	yes	marginal	yes
P2: female dewlap state is negatively correlated with SSD	yes	no	no	yes
ecological selection hypothesis				
P1: female dewlaps are more common in more complex communities	no	no	no	no
P2: female dewlaps are positively associated with temperature (competition)	no	no	no	no

Anole dewlaps are extendable skin flap ornaments on the neck used in signalling displays. The literature has largely viewed dewlaps as only a male secondary sexual characteristic [13–15] (but see [16]). This view is predicated on the observation that in many species female dewlaps are lost or rudimentary, which conforms to the expectations of selection against female ornaments [3]. Additionally, larger dewlaps are probably costly as they increase predation rates and parasite load [17,18]. Yet females of several species retain a fully developed dewlap [16]. Females also exhibit dewlap display behaviour even in species where their dewlaps are highly reduced [19–22]. Beyond sexual signalling [23,24], dewlaps are used in intraspecific aggression in males [19,25] as well as females of at least one species [22]. These observations present the possibility that dewlaps did not solely evolve as a secondary sexual character favoured in males and disfavoured in females. Here, we describe phylogenetic patterns of sexual dewlap dimorphism across 339 species of *Anolis*, allowing us to leverage the variation in female dewlap ornaments to test two non-adaptive hypotheses (genetic correlation and pleiotropy) and one adaptive hypothesis (ecological selection) regarding their evolution. Reduced female dewlaps are particularly common among the adaptive radiations of Greater Antillean anoles [16] which have received the bulk of research attention [14]. Thus, we also investigate potential differences between Greater Antillean and other anoles by assessing our hypotheses separately for each radiation. Finally, we examined the potential downstream role of female ornament variation in driving the diversification of anoles through signal partitioning, the divergence of traits to reduce competition between signals.

Because sexes largely share a common genome, female ornaments are commonly hypothesized to be byproducts of sexual selection on males—the genetic correlation hypothesis [3]. Under the genetic correlation model, initial selection for showy males must be strong enough to compensate for the fitness cost not only to males, but also to females that retain the trait. Subsequently, differential selection between sexes should select for reduced ornaments in females when phenotypes become decoupled either through sex-specific genetic architecture or differential regulation of shared genetic architecture [3]. Yet, evidence for the genetic correlation hypothesis is surprisingly ambiguous across animal taxa [7]. Previous work on anoles demonstrated that male and female dewlap size is not correlated across species [16], as would be predicted prior to the trait being decoupled between sexes [3]. However, selection against female dewlaps has not been tested. Female dewlaps may be selected against due to predation because dewlaps increase conspicuousness [18] or due to parasitism because dewlaps are a favoured attachment site and thereby increase ectoparasite load [17]. Thus, differences in predation or parasitism may drive patterns of female dewlap evolution. Several sources have put forth the idea that biotic interactions are stronger at lower latitudes and elevations [26,27] but this remains controversial [28–33]. Yet, evidence suggests that climate, specifically temperature, may better predict global variation in predation intensity [34,35] and parasite load [33] than latitude or elevation. Therefore, we predict that if selection against female dewlaps due to predation or parasitism varies across species, temperature will be inversely related to female dewlap state (table 1). Additionally, the genetic correlation model predicts that once female ornamentation is lost, reversals to mutual ornamentation should not occur. Thus, the ancestral state of sexual ornaments should be monomorphic, existing until a compensatory mechanism in females arises allowing for divergent selection between the sexes (table 1).

Alternatively, the pleiotropy hypothesis states that female ornamentation evolves as a byproduct of selection on 'male-like' traits other than the ornament itself because of genetic or developmental integration [7,10]. In this scenario, female dewlaps may arise from selection on a linked trait, such as body size, despite being neutral or costly in isolation. In many species, sex-specific body size is regulated by hormones such as testosterone [36] that also trigger the development of exaggerated secondary sexual characters [12,37–40]. To test this, we use sexual size dimorphism (SSD) as a measure of overall morphological similarity between males and females. Because SSD is usually male-biased in anoles and testosterone is known to generate larger body size [36,40,41], we also use female body size as a proxy andromorphic trait assuming larger females are more 'male-like'. Under the pleiotropy hypothesis, we predict that larger bodied females should be more likely to possess dewlaps and the species with lower SSD should be more likely to have female dewlaps (table 1).

We also examined an adaptive hypothesis that ecological selection from interspecific interactions drives the gain of female dewlaps. Male anoles sometimes perform displays at predators [42] and as aggression during interspecific competition

[43,44]. If dewlaps serve similar function in females, stronger and more frequent biotic interactions may select for their presence. Female ornaments may also be driven by selection favouring conspecific mate recognition in more diverse communities—the species recognition sub-hypothesis [45]. Thus, we predict that female dewlaps should be more common in communities with more congeners due to increased interspecific competition. Assuming temperature is a proxy for the intensity of interspecific interactions beyond predation, we also predict that warmer temperatures will be positively associated with female dewlap presence (table 1).

Finally, we tested whether the evolution of a female ornament has downstream consequences for diversification rates. Ornamental traits are hypothesized to drive diversification by promoting the evolution of prezygotic reproductive barriers [46,47]. However, previous studies found mixed support for this hypothesis across traits and taxa potentially because traits are subject to both sexual and ecological selection [48–52]. Alternatively, the lack of signal may be due to studies often using sexual dimorphism as a proxy for the strength of sexual selection with mixed results [50,52,53]. If selection favours the same trait in both males and females, mutually ornamented species may appear less dimorphic than predicted by sexual selection on males alone. The presence of female ornamentation, particularly if aspects of signalling are decoupled between sexes, theoretically allows species to access novel signalling space. Opportunities for prezygotic barriers may therefore be higher in these clades as they can theoretically arise in either direction. Yet, studies have largely ignored the potential relationship between female ornamentation and diversification rates. By reassessing a 'classic' secondary sexual characteristic, we highlight the potentially complex and overlooked selective forces shaping trait evolution.

2. Methods

(a) Data collection

We compiled phenotypic data on male and female anole dewlaps for 339 species (approx. 89% of all *Anolis* species; [54]). For each species, we classified both the male and female dewlap as absent, rudimentary or fully developed (electronic supplementary material, table S1; see electronic supplementary material, methods). We compiled maximum snout-vent length (SVL) for sexes of each species from the literature (electronic supplementary material, table S1). We then calculated SSD as (male SVL/female SVL) − 1, so that negative values indicate female-biased SSD and positive values male-biased SSD. Finally, we downloaded the most recent comprehensive dated, molecular tree of anoles [54] and pruned it to include only our focal taxa (figure 1*a*). We performed downstream comparative analyses on the subset of 293 species (approx. 77% of *Anolis* species) for which we had both phenotypic and phylogenetic data.

(b) Determining community composition and environment

To compute community richness and range overlap between anole species, we used the Global Assessment of Reptile Distributions (GARD) dataset [55] (electronic supplementary material, figure S1; see electronic supplementary material, methods). We calculated range overlap for each species against every other as a proportion of the focal species' total range size using the 'intersect' function in the *raster* R package [56]. We then calculated how many other species co-occur with each species based on a threshold of 20% range overlap [57,58]. As a secondary approach, we also calculated species co-occurrence for each species as the cumulative proportion of range overlap with all other species.

To quantify how temperature (as a proxy for interspecific interactions) may influence female dewlaps, we downloaded bioclimatic data at a resolution of 2.5 arc minutes from the WorldClim database [59]. For each species, we extracted values for annual mean temperature (AMT; BIO1) across their GARD polygon range. From range-wide values, we computed mean, minimum, and maximum values for hypothesis testing.

(c) Comparative analyses

To asses phylogenetic signal, we calculated Bloomberg's K, the ratio of observed to expected phenotypic variance under Brownian motion [60], for all variables. We then fit phylogenetic generalized least-squares (PGLS) models to test the associations of body size and SSD with female dewlap state. We also used PGLS to test the relationship between female dewlap state and, separately, the number of sympatric congeners per species and cumulative range overlap. We then fit PGLS models for range-wide mean and minimum AMT with female dewlap state. Maximum range-wide AMT was excluded because of collinearity with mean range-wide AMT. We repeated analyses for male dewlaps and tested if female and male dewlaps were correlated by fitting hidden Markov models in *corHMM* [61]. We performed other comparative analyses using the packages *phytools* [62] and *nlme* [63] in R.

(d) Ancestral state reconstruction

We performed maximum-likelihood ancestral state reconstruction and transition rates (q) estimation for male and female dewlap states separately using the 'ace' function in the R package *ape* [64]. We conducted ancestral state reconstructions using the equal rates, symmetrical and all rates different model, then compared models using AICs and pairwise-likelihood tests. Because maximum-likelihood methods do not provide estimates of the number of transitions between states, we also performed stochastic character mapping using SIMMAP [65]. We performed 999 simulations and averaged the number of transitions across all simulations. To compare with our maximum-likelihood ancestral state reconstruction, we also calculated the posterior probability of each ancestral state by summarizing across simulations.

(e) Hidden state speciation and extinction

To test for state-dependent shifts in diversification rates associated with female dewlaps, we fit hidden state speciation and extinction (HiSSE) models to our data [66]. Because HiSSE can only handle binary trait data, we performed two analyses. First, we binned absent and rudimentary female dewlaps and, second, we binned rudimentary and developed female dewlaps. We constructed four models. First, our null model set all rates equal for speciation (λ), extinction (μ) and transitions (q) and did not include hidden states. Second, our 'hidden state' model included two hidden states and allowed λ and μ to vary as functions of the unobserved states only. Third, our 'dewlap' model allowed all three parameters to vary with female dewlap state. Fourth, our 'dewlap + hidden' model allowed all three parameters to vary with female dewlap state as well as a two hidden states. All models were fit using the *hisse* package [66] in R. We did not perform HiSSE analyses on males because the method is not robust to high skew of tip states [67].

(f) Greater Antillean versus other anoles

To examine whether and how the evolution of female dewlaps varies across anole faunas, we also conducted comparative

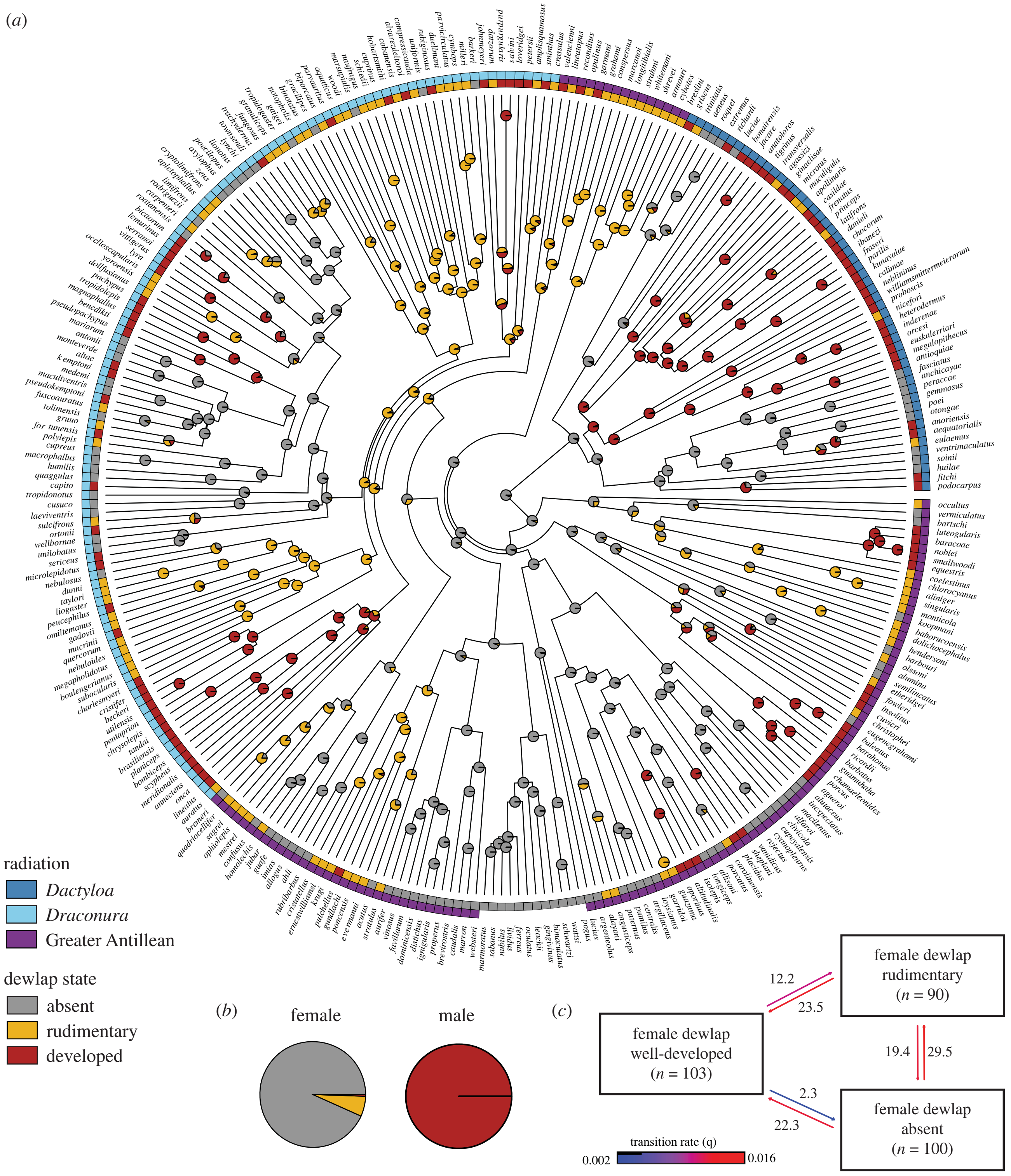

Figure 1. (*a*) Phylogeny of *Anolis* with tip labels for female dewlap character states. Subset radiations of anoles (Greater Antillean, *Dactyloa* and *Draconura*) examined in this study are also labelled. Maximum-likelihood ancestral character estimations for female dewlap state are shown. (*b*) Pie chart of the scaled likelihoods for the ancestral state of female and male dewlaps in the most recent common ancestor of crown group anoles. (*c*) Transition rates between female dewlap states. Arrows are coloured by transition rate and labelled with estimated mean number of transitions Number of analysed species in each character state is noted. (Online version in colour.)

analyses and transition rate estimation separately for Greater Antillean anoles and two non-Greater Antillean clades in females: *Dactyloa* and *Draconura* (figure 1). *Dactyloa* is sister to all other anoles and *Draconura* represents a back-colonization of the mainland Americas nested within the Greater Antillean radiation [54]. Due to the large number of PGLS analyses for female dewlaps, we adjusted these *p*-values using the Benjamini–Hochberg procedure. We did not divide male analyses by clade as they were often fixed for a character state. We also tested for differences in female dewlap presence between Greater Antillean and non-Greater Antillean anoles (*Dactyloa* and *Draconura* clades) by fitting hidden Markov models in *corHMM* [61].

3. Results

(a) Comparative analyses

In total, female anoles in 34.2% of species studied (116 of 339 species) had well-developed dewlaps compared to 30.4% (103 species) with rudimentary and 35.4% (120 species) with

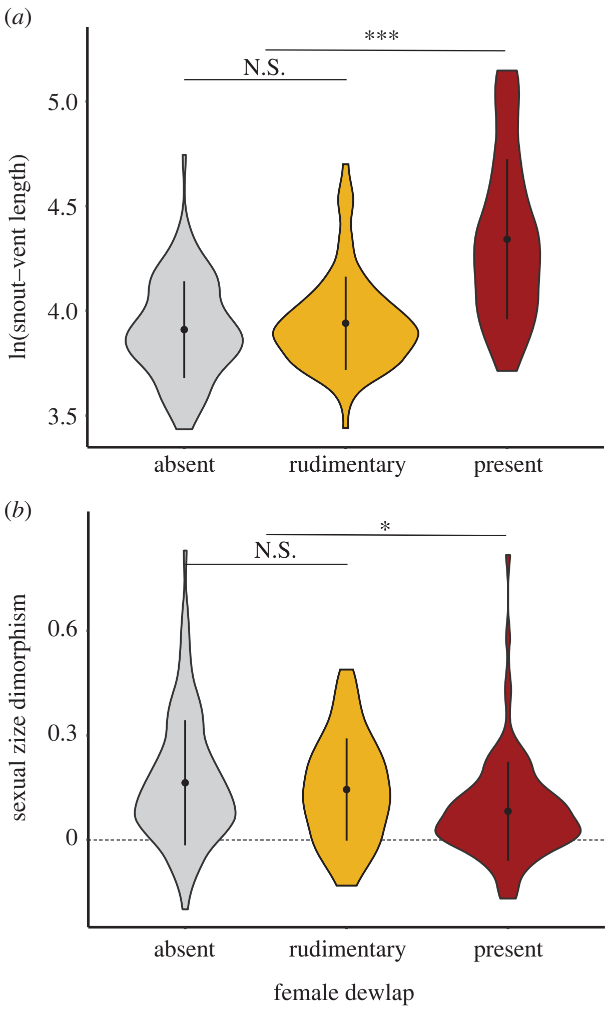

Figure 2. Violin plots of (*a*) ln female SVL and (*b*) SSD for species with absent ($n = 98$), rudimentary ($n = 88$) and developed ($n = 100$) female dewlaps. Mean and s.d. are shown. Positive SSD values (i.e. above the dashed line) denote male-biased dimorphism and negative values denote female-biased dimorphism. Significantly different groups are denoted by asterisks: $^{*}p < 0.05$ and $^{***}p < 0.001$. (Online version in colour.)

absent dewlaps. We detected significant phylogenetic signal for female dewlap state, body size and SSD (all $p < 0.001$; see electronic supplementary material, results). We recovered a significant association between female dewlap state and SSD ($F_{2,283} = 4.36$, $p = 0.047$) where species with well-developed female dewlaps had significantly lower SSD than species with rudimentary or no female dewlap (figure 2). Female body size was also significantly associated with dewlap state ($F_{2,283} = 24.14$, $p < 0.001$). Our body size results were consistent among anole faunas for SVL but not SSD (table 1; electronic supplementary material, figure S2 and results).

We found a marginally negative relationships between female dewlaps states and average range-wide AMT ($F_{2,277} = 3.93$, $p = 0.053$; electronic supplementary material, figure S3). Species with female dewlaps experienced marginally lower temperatures than those with absent or rudimentary dewlaps. Female dewlap states did not predict range-wide minimum AMT ($F_{2,277} = 1.00$, $p = 0.492$). Within anole faunas, we found female dewlaps only significantly predicted average range-wide AMT in Greater Antillean anoles ($F_{2,101} = 5.51$, $p = 0.020$). In Greater Antillean anoles, average range-wide AMT was lower in species with both rudimentary and developed female dewlaps relative to those without female dewlaps. We did not recover any relationship between AMT and female dewlaps in mainland anoles (all $p > 0.05$; electronic supplementary material, figure S4). The number of co-occurring congeners did not predict female dewlap state (all $p > 0.05$; electronic supplementary material, figure S1). Because cumulative range overlap and number of congeners produced consistent results, we report results only for number of congeners. All tests using male dewlaps were not significant (all $p > 0.05$; see electronic supplementary material, results)

We found that although developed female dewlaps were more common in non-Greater Antillean species than Greater Antillean species (figure 2; chi-squared: $\chi^2 = 20.31$, $p < 0.001$), female dewlap states were not correlated with anole faunas across the phylogeny ($\text{AIC}_{\text{independent}} = 558.5$, $\text{AIC}_{\text{correlated}} = 571.8$, $\Delta_{\text{AIC}} = -13.3$). In total, 19% (27 species) of Greater Antillean anoles had well-developed female dewlaps compared with 46% (89 species) of non-Greater Antillean species. Comparing male and female dewlaps, our best-fit model was no association ($\text{AIC}_{\text{independent}} = 611.8$, $\text{AIC}_{\text{correlated}} = 666.9$, $\Delta_{\text{AIC}} = -55.9$).

(b) Ancestral state reconstruction

For female dewlaps, our best-fit model was the all rates different model for our whole dataset (figure 1; electronic supplementary material, table S2). We recovered no evidence of biased transition rates towards loss of dewlaps in females (figure 1*c*). Stochastic character mapping recovered 29.54 ± 0.15 absent to rudimentary, 22.27 ± 0.11 absent to developed, 23.50 ± 0.12 rudimentary to developed, 19.41 ± 0.14 rudimentary to absent, 2.29 ± 0.04 developed to absent and 12.20 ± 0.09 developed to rudimentary dewlap transitions in female anoles (figure 1*c*). Our estimated ancestral state for crown group anoles was females without dewlaps (scaled likelihood = 0.93; posterior probability = 0.91; figure 1). For our subsetted data, our best-fit model was symmetrical for the Greater Antilles and all rates different for *Dactyloa* and *Draconura* (electronic supplementary material, table S2). Our estimated ancestral state was no female dewlap for both Greater Antillean (scaled likelihood = 0.95; posterior probability = 0.91) and *Dactyloa* anoles (scaled likelihood = 0.93; posterior probability = 0.90), but rudimentary for *Draconura* anoles (scaled likelihood = 0.85; posterior probability = 0.80). The best-fit model for male dewlaps was equal rates and the estimated ancestral state was a fully developed male dewlap (scaled likelihood = 1.00; posterior probability = 1.00; electronic supplementary material, table S3; see electronic supplementary material, results). Thus, the ancestral anole lineage had a sexually dimorphic dewlap.

(c) Hidden state speciation and extinction

The best-fit model for our HiSSE analyses binning rudimentary and developed dewlaps (i.e. absent versus present) was the 'dewlap + hidden' model (table 2). Thus, our data suggest that female dewlap presence is associated with greater speciation rates, but that the effect is secondary to an unmeasured hidden state. Our parameter estimates support heterogeneous transition rates consistent with our other analyses (electronic supplementary material, table S4). We found the best-fit model when binning rudimentary and absent dewlaps (i.e. 'reduced' versus developed) was

Table 2. HiSSE model selection comparing absent and present (rudimentary and developed) dewlaps and parameter estimate results, including log-likelihoods, AIC, difference in AIC with minimum value (Δ_{AIC}) and parameter estimates for speciation rate dewlap absent (λ_0), dewlap present (λ_1) and with hidden states (λ_A and λ_B). Other parameter estimates are not shown as they were not relevant to the goals of this study.

model	log-likelihood	AIC	Δ_{AIC}	λ_{0A}	λ_{1A}	λ_{0B}	λ_{1B}
null	−1266.97	2539.94	30.28	0.058	0.058	—	—
hidden state	−1259.41	2528.82	19.16	0.005	0.005	0.066	0.066
dewlap	−1266.26	2544.53	34.87	0.051	0.060	—	—
dewlap + hidden	−1238.83	2509.66	0	0.003	0.036	0.065	0.097

hidden state only model (electronic supplementary material, table S5; see electronic supplementary material, results).

4. Discussion

(a) The genetic correlation hypothesis

Our results suggest that the evolution of anole dewlaps is not dominated by sex-biased selection against female ornamentation. We found no evidence for biased transitions towards female dewlap loss as predicted under the genetic correlation hypothesis (table 1). Rather, female dewlaps are widespread throughout the anole phylogeny, are evolutionarily labile and exhibit a transition bias towards the gain of dewlaps (figure 1; electronic supplementary material, figure S2 and table S2). Our results are consistent with work on a smaller dataset that found biased transitions from dewlap size dimorphism to monomorphism [16]. Our results also indicate that the ancestral anole did not possess a developed female dewlap (figure 1*b*) clarifying the previously ambiguous ancestral state [16]. Because the ancestral male was inferred to possess a fully developed dewlap, the trait was probably already decoupled between sexes in the ancestral anole rather than genetically correlated. Still, our results do not mean that runaway selection does not operate locally in specific clades or species. Certainly, there is ample evidence that male dewlaps are involved in sexual signalling [23–25] and male dewlap loss is rare. Nevertheless, our data demonstrate that microevolutionary processes that shape trait evolution for any given species are not necessarily generalizable as explanations for macroevolutionary patterns.

We found some marginal support for predation and parasitism potentially driving the lack of female dewlaps, but not for interspecific competition driving the gain of female dewlaps (table 1). Female dewlaps were more common in cooler compared to warmer environments at least in Greater Antillean anoles. This effect is also marginally significant across all anoles and the trend is in the predicted direction (electronic supplementary material, figure S3). This is theoretically consistent with the role of biological interactions. Still, we urge caution when interpreting these results. Because we did not directly measure predation or parasitism, we also cannot differentiate between these mechanisms with our data, nor are these processes mutually exclusive. Both processes appear to constrain dewlap size in at least some species [17,18]. Nevertheless, we posit that selective pressures against dewlaps might be sufficiently weaker in cooler environments to allow female dewlaps to be regained. Variation in the relative fitness of female dewlaps across environments is consistent with our inability to recover a bias towards female dewlap loss across anole diversity. Although weaker predation and parasite pressure may facilitate the evolution of female dewlaps, probably by lowering their relative fitness costs, it remains unclear when selection would favour female dewlaps.

(b) The ecological selection hypothesis

Our results do not support interspecific competition selecting for female dewlaps (table 1). Whether competition is actually stronger in the tropics is controversial [30]. Regardless, we also did not find support for this hypothesis in our analyses of sympatric congeners consistent with previous work suggesting female dewlap were not more common in solitary species [16] and that male anoles do not partition dewlap colour in more complex communities [13]. Thus, interspecific competition driving the evolution of female dewlaps is not supported.

(c) The pleiotropy hypothesis

We observed an apparent threshold effect where females above 120 mm SVL uniformly possess well-developed dewlaps. Overall, females possessing dewlaps were on average larger and had less male-biased SSD than species with rudimentary or absent female dewlaps (figure 2). Thus, our results support the pleiotropy hypothesis that female body size or related traits are integrated with female dewlaps. Although a similar pattern could be generated via correlative selection [68], experimental work has demonstrated shared regulatory pathways for body size and ornaments in both anoles and other taxa [10]. For example, supplemental testosterone led to increases in body and dewlap size in female *A. sagrei* [40,41]. Similarly, changes in body size and blue ventral patches can be induced in female fence lizards, *Sceloporus undulatus*, through supplemental testosterone [69]. Sufficiently strong selection on non-dewlap traits such as body size may outweigh the potential cost of female dewlaps in some species. However, causality may also be reversed with selection on female dewlaps generating larger bodied females. Either way, this mechanism does not account for the repeated evolution of female dewlaps in smaller bodied and highly size dimorphic species. Thus, multiple forces likely contribute to shaping macroevolutionary patterns for female dewlap ornaments. Nevertheless, our results suggest a role of pleiotropy in shaping the macroevolutionary patterns of female dewlaps. Given evidence that pleiotropy influences female ornament evolution in several taxa [10,69], we highlight the need for developmental and ecological data in a broader range of species to better understand the evolution of ornaments.

(d) The untested social selection hypothesis

An alternative hypothesis for the evolution of female ornaments is social selection, under which female ornaments are adaptive as intraspecific signalling traits [11,70]. Because social selection incorporates varying selective pressures, detecting its operation requires testing specific hypotheses relating to social interactions known to a given taxon. For example, female ornaments may arise due to direct sexual selection on females through male choice [71,72] or due to selection for signals of social status or competitive advantage that indirectly influence fecundity [11,70,73]. There is some evidence that female dewlaps, even when rudimentary, may play a role in courtship in *A. sagrei* [74] and female–female aggression in *A. carolinensis* [22]. Thus, social selection hypotheses should provide fruitful avenues for future research.

Previous work suggested that a negative correlation between female dewlap size and SSD supported the social selection hypothesis [16]. Although our results are consistent with this pattern, we believe that they support the pleiotropy hypothesis better than social selection. Still, we cannot definitively rule out either hypothesis. Greater male–male competition is associated with greater SSD in lizards [75,76], but the effects of female–female competition have not been tested to our knowledge. By contrast, developmental integration between body and dewlap size has been shown in anoles [40,41]. Thus, for now, we interpret lower SSD to more likely reflect less male–male competition and call on future studies to examine the relationship between female–female competition and SSD.

(e) Diversification and female ornamentation

Although signalling traits are often thought to provide opportunities for the evolution of prezygotic barriers, the hypothesis that stronger sexual selection on males increases diversification rates has mixed support [48–52]. Mutual ornamentation should allow species to access novel signalling interactions not available to single-sex ornamented species. Indeed, we recovered evidence that female dewlaps did influence speciation rates (table 2). This was only true when rudimentary dewlaps were binned with developed dewlaps suggesting that the presence of a female ornament, not whether it is reduced relative to the male, is associated with increased speciation rates. This is in line with the observation that female dewlaps are used as signals even when rudimentary [20,22,74]. Still, the influence of female ornamentation was secondary with most variation in speciation rates explained by a hidden state. Nevertheless, our results are consistent with previous evidence that dimorphism itself is not associated with diversification rates and may be a poor proxy for processes which are [52,53]. Furthermore, although we cannot rule out sexual selection on females as the driver of dewlap evolution, our results open up the possibility that ornaments drive diversification through mechanisms other than sexual selection. This possibility warrants further investigation particularly as mounting evidence suggests that the strength of sexual selection does not itself influence diversification rates [49,52,53].

5. Conclusion

Our results support a growing body of literature demonstrating that the male-biased sexual selection framework, in which ornaments are selected against in females, is often not sufficient to explain the evolution of ornamental traits [7,11,12]. Across the anole phylogeny there is a bias towards regaining well-developed dewlaps in females. This pattern is potentially driven by multiple evolutionary forces including variable costliness, pleiotropy and lineage-specific selection. We also find that female ornaments can increase speciation rates, though secondarily in this case, to an unmeasured state. Thus, ornaments themselves, rather than dimorphism or strength of sexual selection, appear to play a role in diversification rates [53,77]. Our results highlight the potential of anoles for studying complex sexual and ecological drivers of ornament evolution, and call for revisiting commonly held assumptions about the evolution of ornamentation.

Data accessibility. All data and code used in this study are available from the Dryad Digital Repository: https://doi.org/10.6078/D11Q63 [78].

Additional text, tables and figures are provided in the electronic supplementary material [79].

Authors' contributions. M.L.Y.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, validation, visualization and writing—original draft; E.P.W.: formal analysis, investigation, methodology, validation, visualization and writing—original draft; G.O.U.W.: investigation, methodology and writing—review and editing; I.J.W.: funding acquisition, investigation, methodology, resources, supervision and writing—review and editing.

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