Loss of pigments in females is associated with sexual dichromatism in an ornamental trait

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Abstract

Sexual dichromatism is thought to evolve primarily as a function of sexual selection, especially female choice. However other forces, from sex-specific environmental conditions to social signaling in females, can also generate color differences between sexes. We studied dewlap dichromatism across 292 species of *Anolis* lizards. Dewlaps are colorful throat ornaments found on males of most anole species but are also present in females in many species. Although male and female dewlaps often have similar coloration, in some species they are strikingly dichromatic. We found that ornament color is labile and that dichromatism results from the loss of costly pigments in females. This pattern could indicate a shift towards signal loss in females; however, the secondary gains of female dewlaps across the phylogeny suggest a potential advantageous function. Possible mechanisms for female dewlap coloration include social selection, non-sexual signaling, or detectability in different microhabitats (e.g., sensory drive). Female dewlap color overlap between co-occurring species is both less than expected by chance overall and reduced in species-rich communities, suggesting that dichromatism could be driven by competition. Our results highlight that selection on females drives the observed pattern of dichromatism, suggesting a potentially adaptive role for female ornaments and emphasizing the need for additional work to understand female ornament evolution.

Keywords: Anolis, anole, dewlap, macroevolution, comparative biology, sexual dimorphism

Introduction

Sexual dichromatism, a form of dimorphism in which the sexes differ in their coloration, is common across a wide range of animals and has been the focus of extensive study in frogs (Bell and Zamudio 2012), birds (Badyaev and Hill 2003), fishes (Kodric-Brown 1998), and butterflies (Allen et al. 2011). As with most forms of sexual dimorphism, sexual selection is thought to be the primary mechanism by which sexual dichromatism evolves—particularly in ornamental traits. Specifically, the dominant model is one in which more costly character states are favored in one sex due to mate choice by the other (Lande 1980), and there is abundant evidence that female choice is a major driver of the evolution of male-biased sexual dimorphism (Amundsen and Forsgren 2001; Stuart–Fox and Ord 2004; Chen et al. 2012). However, many systems also exhibit patterns inconsistent with sexual selection as the evolutionary mechanism (Irwin 1994; Tobias et al. 2012; Yuan et al. 2022). Examination of such systems can bring important perspectives to our understanding of the evolution of dimorphism in general.

Beyond sexual selection, environmental factors can also drive patterns of dichromatism. Differences in habitat (Bossu and Near 2015; Medina et al. 2017), diet (McGraw et al. 2002), and anti-predator strategies, such as crypsis or aposematism (Taylor et al. 2019; Ramírez-Delgado and Cueva del Castillo 2020), between sexes can all lead to differences in coloration. Interspecific interactions can also drive the evolution of dichromatism. For example, coloration is used in species recognition in many systems (Losos 1985; Couldridge and Alexander 2002), and, within species, sex-specific coloration can be useful for identifying mating opportunities and defending sex-specific resources (Grether et al. 2015). Females might experience selection to display divergent signals from those of males to avoid harassment associated with mating (Xu and Fincke 2011; Khan 2020) or to defend territory from other, rival females (Tobias et al. 2012).

The tendency toward studies of only dimorphic species can also cloud our interpretation of general patterns. For example, ornamental traits which are dimorphic and therefore thought to be secondary sexual characteristics in one species may be monomorphic in closely-related species (Emlen et al. 2005; Bell and Zamudio 2012; Yuan et al. 2022), and the dynamics of ornament evolution when the trait is promoted in both sexes are not well understood. Even if ornaments are favorable in females, they may be under different selective regimes than in males (LeBas 2006; Kraaijeveld et al. 2007; Tobias et al. 2012). For example, it may not be advantageous for females to produce an 'honest' signal of quality by diverting costly resources to ornaments because they invest more in offspring, thereby shifting the relative tradeoffs with signal efficiency (Chenoweth et al. 2006; Potti et al. 2013). Thus, the signaling function in females may not explicitly advertise fitness. Even if the signaling trait itself is selected for in both sexes, the components of the signal may change between males and females as a function of differential selection.

Here, we studied the evolution of color in *Anolis* dewlap ornaments, extensible skin flaps on the neck used in communicative displays. Although conventionally understood as a male secondary sexual characteristic lost in females (Nicholson et al. 2007), many species have regained fully developed female dewlaps (Harrison and Poe 2012; Yuan et al. 2022), and evidence does not support the hypothesis that female dewlaps are universally costly across the anole phylogeny (Yuan et al. 2022). Furthermore, dewlaps are often sexually dichromatic when present in both sexes (e.g., White et al. 2019). While selection on males for colorful dewlap ornaments and a correlated evolutionary response in females would ultimately result in monochromatism, the observed pattern of dichromatic dewlaps in so many species suggests additional mechanisms at play. Thus, *Anolis* lizards present an opportunity to study macroevolutionary patterns of sexual dichromatism in an ornamental trait and to test hypotheses about their evolution. We focused on the evolution of red, orange, and yellow displays, because these colors often represent honest signals of individual quality (Weaver et al. 2017; Andrade and Carneiro 2021). These colors are generated in animals through a combination of dietarily-acquired carotenoids and metabolically-produced pterins (Bagnara and Hadley 1973; Weaver et al. 2017; Andrade and Carneiro 2021). These pigments may represent honest signals of individual quality in animals either because of the cost of acquiring and diverting resources to coloration or because they are indexed to vital metabolic pathways (Hill 1992, 2011; Weaver et al. 2017; Andrade and Carneiro 2021). Evidence generally supports the role of carotenoids as an honest signal in vertebrate systems (Hill 1992; Weaver et al. 2018). While evidence for pterin pigments as honest signals is more mixed (Andrade and Carneiro 2021), there is evidence pterins can be honest signals in at least some squamate (Weiss et al. 2011, 2012) and bird systems (Nolan et al. 2006).

We tested a series of hypotheses regarding the evolution of dichromatism in dewlap ornaments across the *Anolis* radiation that fall into two major categories: evolutionary constraints and adaptation. To examine constraints on dewlap dichromatism, we tested whether dewlap color evolution is correlated between the sexes. A strong pattern of correlation between male and female colors suggests that genetic linkage is likely a major factor in determining patterns of dewlap color diversity (Lande 1980). Next, we examined evidence for a pleiotropy effect under which species with less sexual size dimorphism are predicted to exhibit monochromatic dewlap ornaments (i.e. more size dimorphism is associated with more dewlap dichromatism). Testosterone, an androgen, is associated with body size as well as color signals in iguanian lizards (Cox et al. 2015; Pollock et al. 2017). Under this scenario, female dewlap color is linked to other andromorphic traits that may constrain the ability of dichromatism to evolve. To investigate adaptive drivers of female dewlap color evolution, we examined whether the loss of costly pigments (e.g., carotenoids and pterins) in females, specifically, leads to dewlap dichromatism. This pattern would suggest that male color is more highly constrained or that selection on females — either to be less conspicuous in their ornaments or to differentiate their signals from males — results in dewlap dichromatism. Finally, we tested whether dichromatism could result from competition for signaling space with co-occurring species by examining whether female anoles are less likely to co-occur with species with shared dewlap color elements than expected by chance and whether they exhibit less overlap in dewlap coloration in species-rich communities. Simultaneously examining multiple potential drivers of sexual dichromatism can provide novel insights into the evolution of complex traits.

Methods

Data Collection

We collected color data for both male and female anole dewlaps from 292 species. We determined dewlap color by searching the literature, field guides, and photographic records from Anole Annals (www.anoleannals.org), iNaturalist (www.inaturalist.org) and Anolekey (www.stevenpoe.net/anole-key-and-collecting-guide.html). We assigned dewlap color using all primary colors (red, yellow, blue) and secondary colors (purple, orange, green), plus black, white (including gray), and brown. All of these colors occur in both male and female dewlaps. For dewlaps with patterns containing multiple colors, we included all colors in the species record. We binned dewlap colors into major color classes because for most species color is only known from generalized descriptions in the literature or other species accounts. We then characterized a species as dichromatic if any mismatch occurred between the colors observed in male and female dewlaps. For species with known dewlap color polymorphism, we recorded all observed colors. We characterized polymorphic species as dichromatic only if there was no color overlap across all morph color elements between the sexes. We noted which species have sexually size dimorphic dewlaps and species which reportedly lack a female dewlap entirely. Because existing records may not fully characterize dewlap polymorphisms and have historically focused less on dewlap traits in females than males there is likely to be some degree of noise in this dataset.

However, dewlaps are a highly conspicuous and well-studied trait in anoles, and we have no reason to expect that any imperfect dewlap descriptions represent a source of systematic bias that would impact our results.

For each sex and species, we classified colors as either containing ‘costly’ pigments (i.e., carotenoids and pterins) or not based on our current understanding of color generation in squamates. Specifically, red, yellow, and orange colors are known to be produced from dietary carotenoids or metabolically generated pterins (Bagnara and Hadley 1973; Andrade et al. 2019). Green is generated through a combination of structural iridophores and carotenoid or pterin pigments (Rohrlich and Porter 1972; Saenko et al. 2013). To the best of our knowledge, red and yellow colors in anole dewlaps are produced by both carotenoids and pterins interactively (Steffen and McGraw 2007; Alfonso et al. 2013). We classified carotenoids and pterins as present if at least one color was predicted to require them (i.e. red, yellow, orange, and green colors). Although we have not performed a molecular analysis to confirm the presence of these pigments across all the species that express these colors, previous studies have consistently detected the presence of both classes of dewlap pigments in the limited number of species in which they have been studied (Ortiz et al. 1963; Macedonia et al. 2000; Steffen and McGraw 2007; Alfonso et al. 2013).

To characterize species co-occurrence, we used the Global Assessment of Reptile Distributions (GARD) dataset (Roll et al. 2017) and the *rangebuilder* package (Davis Rabosky et al. 2016) in R v.4.2.1. We calculated range overlap for each pair of species in our dataset based on GARD polygons. From this, we calculated for each species the number of congeneric species with which it overlaps in at least 20% of its range (hererafter ‘number of congeners’) (Pigot and Tobias 2013; Shi et al. 2018). We used this metric of co-occurring species as a proxy for competition (e.g., *Anolis cristatellus* overlaps with 7 species in more than 20% of its range, and therefore its ‘number of congeners’ is 7). For each species, we also computed the cumulative proportion of its range that overlaps with the ranges of other species (hereafter ‘cumulative range overlap’; Yuan et al. 2022). We compiled body size data, measured as snout-vent length (SVL), and sexual size dimorphism (SSD) as described in Yuan et al. (2022). Finally, we downloaded the most comprehensive available molecular tree of anoles (Poe et al. 2017).

Evolutionary constraints

We quantified phylogenetic signal for our focal traits (dewlap dichromatism, costly female pigments, and costly male pigments) using the δ statistic approach (Borges et al. 2019). Previous work has shown that SSD and SVL exhibit phylogenetic signal in anoles (Velasco et al. 2020; Yuan et al. 2022), which we confirmed for our dataset before proceeding with additional analyses. We tested for correlations between male and female costly pigments, between dichromatism and male costly pigments, and between dichromatism and female costly pigments by fitting independent and correlated trait evolution models using the R package *corHMM* (Boyko and Beaulieu 2021). We fit both standard single-rate models and hidden Markov models allowing for rate heterogeneity. The inclusion of hidden Markov models should reduce the potential for spurious correlations generated by a few transitions in deep time (Boyko and Beaulieu 2023). We identified the best-fit model by comparing AIC scores. We then fit phylogenetic generalized least squares (PGLS) models to test the associations of dichromatism with female SVL and SSD to test our pleiotropy hypothesis using the R package *phytools* (Revell 2012). For significant models, we performed *post hoc* pairwise tests to quantify the relationships between pairs of variables in our dataset. As an alternative non-phylogenetic approach, we also tested correlations using χ^2-tests. Because the evolutionary dynamics of female dewlaps (Yuan et al. 2022), along with several other traits (Patton et al. 2021), vary between mainland anoles (i.e., Draconura and Dactyloa clades) and the Greater Antillean adaptive radiations, we also tested for correlated evolution between dichromatism and region of origin (e.g., mainland versus island).

Adaptive hypotheses

To examine whether the loss of costly pigments (e.g., carotenoids and pterins) in females, drives transitions to dewlap dichromatism, we inferred ancestral states and the number of transitions between states for carotenoid-pterin pigment presence in each sex and for dichromatism using stochastic character mapping in SIMMAP (Bollback 2006). We coded states as monochromatic, dichromatic, or dewlap absent in at least one sex. Similarly, we coded carotenoid-pterin pigment traits as no dewlap, absent, or present. We fit equal rates, symmetric, and all rates different models and then compared models using AIC. For our best-fit model, we calculated the posterior probability of each ancestral state and mean parameter estimates through 999 simulations.

To assess the hypothesis that dewlap dichromatism is influenced by competition, we fit phylogenetic generalized least squares (PGLS) models to test for associations of dichromatism with co-occurrence, given by number of congeners and cumulative range overlap, using the R package *phytools* (Revell 2012). Next, we ran permutation tests to assess whether co-occurring species overlap in female dewlap color less than expected by chance, which would suggest they partition signaling space. Specifically, for each species we identified the species with which it co-occurs in >20% of its range and then calculated how many of those species shared at least one color element with the focal species. We stored this as a proportion of the total number of species with which it overlaps (number of co-occurring species with shared color elements/number of total co-occurring species). We then shuffled color assignmets across all species 1,000 times and re-calculated this metric for each species. Finally, we compared how often the means of the permuted distributions of color overlap were less than that of the true distribution and divided by 1,000 to obtain a p-value. We repeated this test examining costly pigment overlap as well.

We then calculated the number of species with costly pigments in female dewlaps that co-occur divided by the total number of species present, across communities. To do this, we constructed rasters of (1) the proportion of species with costly pigments in females and (2) species richness (for species with female dewlaps only) at 5-arc minute resolution using the

‘RangeRichness’ function in the R package *rangeBuilder* (Davis Rabosky et al. 2016). As we are primarily interested in the effect of co-occurrence on costly pigment overlap, we excluded cells in which only a single species occurs. We then performed a spatial linear regression of female costly pigment proportion on species richness; if the strength of competition influences dichromatism, we should observe decreasing overlap in female dewlap color with increasing species richness, indicated by a negative regression coefficient.

Results

Data

In total, we sampled 68 dichromatic species, 125 monochromatic species, and 99 species without a reported female dewlap. For carotenoids and pterins, we found that 137 species exhibited colors with these pigments in females and 247 species in males. Comparatively, 56 species lacked these pigments in females and 43 species in males.

Evolutionary constraint hypotheses

We recovered a significant phylogenetic signal for all three focal traits (dichromatism: $\delta = 5.10$, $P < 0.001$; female costly pigments: $\delta = 2.88$, $P < 0.001$; male costly pigments: $\delta = 3.69$, $P < 0.001$). We found support for our first evolutionary constraint hypothesis that the presence of male and female pigments was correlated across the phylogeny ($\chi^2 = 51.87$, $d.f. = 4$, $P < 0.001$; Table 1). We also found that dichromatism was correlated with the loss of female costly pigment (pigments not present, $\chi^2 = 347.67$, $d.f. = 4$, $P < 0.001$) but not the presence of male costly pigments ($\chi^2 = 7.62$, $d.f. = 4$, $P = 0.107$; Table 1). Specifically, female dewlaps without carotenoid or pterin pigments were significantly more common in dichromatic species compared to monochromatic species (55.9% v 14.4%; Fig. 1). For island versus mainland comparisons, we found that dichromatism was more common in mainland species when not accounting for phylogeny ($\chi^2 = 36.63$, $d.f. = 2$, $P < 0.001$; Fig. 2). However, we found only ambiguous support for the correlated model over the hidden Markov independent model

(ΔAICc = 1.5). These results were consistent when we excluded species without female dewlaps; hence, we only discuss results of our full dataset here.

We found that female SVL significantly predicted dewlap dichromatism ($F_{2,282} = 4.96$, $P = 0.008$), but SSD did not ($F_{2,282} = 1.86$, $P = 0.158$). However, *post hoc* pairwise tests revealed no SVL differences between species with monochromatic and dichromatic dewlaps (all $P > 0.05$). Rather, overall PGLS results were driven by SVL differences between species with and without female dewlaps (all $P < 0.05$; Fig. S1). Thus, our pleiotropy hypothesis was not supported for dewlap color.

Adaptive hypotheses

Our stochastic character mapping analyses indicated that dewlap dichromatism is evolutionarily labile (Fig. 2). We inferred 36.36 ± 0.19 transitions from no dewlap to monochromatism, 70.05 ± 0.23 transitions from monochromatism to dichromatism, 34.50 ± 0.22 transitions from dichromatism to monochromatism, and 35.71 ± 0.20 transitions from dichromatism to no dewlap. We inferred no transitions from no dewlap to dichromatism nor from monochromatism to no dewlap.

From our analysis of male carotenoid and pterin pigments, we inferred 1.04 ± 0.01 transitions from pigments absent to dewlap absent, 51.67 ± 0.38 transitions from pigments absent to present, 46.79 ± 0.19 transitions from pigments present to absent. For female carotenoids and pterins, we inferred 23.59 ± 0.13 transitions from dewlap absent to pigments absent, 29.95 ± 0.16 transitions from dewlap absent to pigments present, 18.73 ± 0.12 transitions from pigments present to dewlap absent, 57.33 ± 0.31 transitions from pigments absent to present, and 45.46 ± 0.20 transitions from pigments present to absent. All other transitions for male and female pigment were estimated to be zero. Our stochastic character mapping inferred a root state of no female dewlap (dichromatism: posterior probability = 0.97; female pigment: posterior probability = 0.61) and a male dewlap without costly pigments (posterior probability = 0.72) (Figs 1 and 2).

Number of congeners ($F_{2,272} = 1.54$, $P = 0.217$) was not significantly associated with dichromatism nor was cumulative range overlap ($F_{2, 272} = 1.859$, $P = 0.173$). However, we found that females were significantly less likely to share dewlap colors with other species with which they co-occur than expected by chance($p = 0.011$). Species were also significantly less likely to share costly pigments with the species with which they co-occur than expected by chance ($p = 0.001$). Our raster regression of female costly pigment proportion on species richness (for species with female dewlaps) was significant ($F_{1,153131} = 2.07e^{5}$, $P = 2.2e^{-16}$, $R^2 = 0.568$, $\beta = -0.049$) and had a negative regression coefficient, indicating decreasing color overlap with increasing species richness.

Discussion

Dewlap color is correlated, but females drive dichromatism

Our results support general findings that ornaments are frequently evolutionarily labile despite often being complex structures (Badyaev and Hill 2003). Our results suggest that both adaptation and evolutionary constraint played some role in the evolution of sexual dichromatism in anole dewlaps. We found support for correlated dewlap color evolution between the sexes (evolutionary constraint) and for dewlap dichromatism largely driven by the loss of carotenoid and pterin pigments in females rather than males (adaptation); Table 1. Although males similarly exhibit repeated transitions between the presence and absence of carotenoids and pterins, unlike in females these transitions were not correlated with transitions between dichromatism and monochromatism. It has been hypothesized that signal evolution should be driven by males due to the role of signal ornaments in courtship, increasing pressure to partition signal space (Darwin 1871; Badyaev and Hill 2003). However, several studies have demonstrated that females can be the more evolutionarily labile sex and drive the evolution of sexual dimorphism and dichromatism (Irwin 1994; Badyaev and Hill 2003; Price and Eaton 2014; Dale et al. 2015; Diamant et al. 2021; Yuan et al. 2022). Males may be more constrained by sexual selection to maintain a smaller range of colors that can act as honest signals or have high detectability in the anole system as evidenced by their bias toward carotenoid and pterin pigments (85.3% of species). These pressures are conceivably lessened in females, which may use their dewlaps for non-sexual signaling or not at all, or may be selected against in females of some species but not others (West-Eberhard 1983; Tobias et al. 2012). Indeed, natural selection, including selection on the use of dewlaps for non-sexual signaling, should impose other, potentially competing evolutionary pressures on ornament evolution. Studies considering additional signaling components such as color patterns, color diversity, and brightness and contrast will provide further insights about the lability and function of colorful ornaments.

Why do we observe loss of costly pigments in females, manifesting in sexual dichromatism across *Anolis* lizards? It is possible that the loss of costly pigments represents a step toward the loss of female dewlaps entirely. That is, females initially shift away from costly pigments rather than the loss of the whole structure. Although this is somewhat supported by unidirectional transitions from dichromatism to loss of the female dewlap, we do not observe transitions from females without costly pigments to the absence of a female dewlap. Instead, we might interpret this to suggest that structure loss and pigment loss are alternative mechanisms to compensate for a costly structure in females. However, this interpretation is also challenged by the repeated regain of female dewlaps inconsistent with such ornaments being a costly consequence of sexual selection on males (Yuan et al. 2022). Indeed, a growing body of literature has demonstrated that female ornaments can be advantageous (Tobias et al. 2012). Given the lack of compelling evidence that female dewlaps are broadly selected against across anoles, we should consider alternative explanations for the observed pattern of sexual dichromatism.

Dewlap color is not pleiotropic

We do not find evidence for pleiotropy between dewlap color and female size. Less sexually size dimorphic species were not more likely to have monochromatic dewlaps, nor were species with larger females. This contrasts with the pattern observed in the dewlap structure itself where species with larger-bodied females and lower sexual size dimorphism were more likely to exhibit large female dewlaps (Yuan et al. 2022). Androgens do increase female ornamental color intensity in *Anolis sagrei* (Cox et al. 2015) and *Sceloporus undulatus* (Pollock et al. 2017). However, this process appears to involve increased color expression rather than a shift in color entirely as would be required in many ornamentally dichromatic anole species. Thus, while androgen expression can drive the structural development and overall saturation of female dewlaps, it does not appear to readily influence expression of alternative pigments.

Evidence for signal partitioning

We found evidence that females are less likely to co-occur with species with shared color elements and with shared costly pigments than expected by chance, and we found that female costly pigment overlap decreased in areas with higher species richness, supporting our competition hypothesis. This may suggest intraspecific sex discrimination in mutually ornamented species. For instance, aggressive displays may be sex-specific with females competing for ecological resources to maximize fecundity (Tobias et. al 2012) and mating opportunities. Such signals are most effective when they differ between true competitors and non-competitors (Bradbury and Vehrencamp 1998); thus, partitioning signal space may also allow females to improve signal efficacy by reducing competing information overlapping with male signaling. Alternatively, partitioning signal space with males may also reduce conflict with males (Xu and Fincke 2011; Khan 2020). Although we observe a pattern of signal partitioning, the underlying mechanism remains unclear as the pattern is consistent with several evolutionary processes.

We might expect that if female dewlap color is driven by male mate choice that it should also serve as an indicator of fitness (Tobias et al. 2012; Nolazco et al. 2022). There is some evidence that investment in dewlap color is a fitness signal in male anoles (Cook et al. 2013). Yet, mutual mate choice does not necessitate the signal be sexually dichromatic, nor would it predict transitions away from costly pigments in only one sex (although in some circumstances iridophores and melanin can also advertise fitness; McGraw 2008; Assis et al. 2018). It is also possible that female anoles have coopted dewlaps for non-sexual signaling (Amundsen 2000). This encompasses a range of potential mechanisms that can be grouped broadly under social selection (West-Eberhard 1983) – i.e. intraspecific interactions not directly related to mate choice. In some cases, we might still expect an honest signal, such as for female-female aggression (e.g., Bywater et al. 2008; Berglund and Rosenqvist 2009). Certainly, there are many sexually monochromatic dewlaps across anoles. Whether dewlap monochromatism is a consequence of genetic correlation or because both sexes are signaling greater fitness or social dominance requires further investigation. Under other scenarios, such as conspecific recognition in species inhabiting complex communities or with low population densities, honest signals may be irrelevant. These latter cases may select for costly pigment loss in females and subsequent sexual dichromatism.

In many animal systems, light availability influences visual perception and even color preference (Goyret and Yuan 2015). Thus, a potentially compelling hypothesis for future explorations is the sensory drive hypothesis (Endler 1992), in which sexual dichromatism reflects optimization for detectability in different microhabitats as female anoles tend to occupy less exposed microhabitats than males (Andrews 1971; Butler et al. 2000). Here, we should assume that female dewlaps have some signaling function but can be agnostic as to exactly what that function is. Whether detectability is related to dewlap hue is controversial. Some studies suggest that male dewlaps do not vary in relative detectability across habitats (Fleishman et al. 2009; Macedonia et al. 2014), but these results may be due to averaging effects across variable light patches. Indeed, others have shown slightly greater detectability in white and blue relative to red dewlaps in lower light environments (Macedonia 2001; Fleishman et al. 2022). White dewlaps in males are also more common in species that occupy dimmer, closed-habitat environments (Fitch and Hillis 1984; Fleishman 1992). The improved detectability of white under low light environments has been observed in other animal systems as well. For example, white is often selected for in nocturnally-pollinated flowers due to improved detectability to insects (Kelber et al. 2003; Borges et al. 2016). Therefore, the abundance of white and blue female dewlaps potentially optimizes signal efficiency without the need for costly pigments. Further work directly tackling these hypotheses will be fruitful for our understanding of sex-specific signaling evolution.

Future directions

A caveat to our conclusions is that we cannot assess the role of UV color in dichromatism. Some anole dewlaps are reflective in the UV spectrum (Steffen & McGraw, 2009),) and anoles are tetrachromatic with UV visual perception (Loew et al. 2002). Unfortunately, the data on UV coloration is limited to a small subset of species and almost strictly males (Macedonia 2001; Leal & Fleishman 2004; Steffen & McGraw, 2009; Ng et al. 2013; Driessens et al. 2017). Thus, it is not currently possible to compile a comparative dataset on sexual differences in UV reflectance across anoles. Nevertheless, even if UV color experiences different evolutionary dynamics, it does not negate our findings regarding visual spectrum dichromatism. Anoles certainly perceive and respond to visual spectrum color differences irrespective of UV (Sigmund 1983; Losos 1985). Furthermore, there appears to be a tradeoff between UV and red spectrum coloration in at least some anoles (Steffen & McGraw, 2009; Driessens et al. 2017). Drosopterin pigment is a dominant driver of coloration in *A. sagrei* dewlaps that are red-orange reflective and UV absorptive (Steffen & McGraw, 2009). Thus, our results may indirectly capture some degree of UV variation. Given the bias toward red-orange coloration in male dewlaps (Fig. 1), it is likely that UV reflectance is generally low across males. This raises the possibility that female dewlaps, which tend to lack pterin-based coloration, generally reflect more strongly in the UV spectrum.

Despite the ability to perceive UV color, how anoles use these signals remains unclear and understudied. For example, studies have found conflicting results regarding the relationship between UV reflectance and environmental conditions. Although Ng et al. (2013) found that canopy cover and rainfall predicted red color in *A. distichus* male dewlaps, they were unable to explain variation in UV color. Other studies found conflicting results, with one study supporting greater UV reflectance in low light, mesic environments for *A. cristatellus* (Leal & Fleishman 2004) and another in high light, xeric environments for *A. sagrei* (Driessens et al. 2017). Because the limited number of existing studies present no consistent pattern, it is difficult to predict how UV may factor into our hypotheses about the evolution of sexual dichromatism. Thus, characterization of the UV component of dewlaps is an important avenue for future research not only for understanding the evolution of dichromatism but also for signal ecology in this system more generally.

Conclusions

Overall, our data support loss of pterin and carotenoid colors in females as the primary driver of transitions to dewlap dichromatism. We also find support for competition as a compelling potential driver of sexual dichromatism in the anole system. However, the precise mechanism underlying female signal partitioning, whether social selection or sensory drive, remains to be demonstrated. These mechanisms are not mutually exclusive, and different selective regimes may operate in different species. It is difficult to assess most hypotheses relating to why females drove transitions to dewlap dichromatism without knowledge of how dewlaps are used in female anoles, and, unfortunately, our functional understanding of female signaling in anoles is limited. It appears that females perform dewlap displays less than males (Johnson and Wade 2010), yet females of several species do perform dewlap displays in field and experimental settings (Jenssen et al. 2000; Johnson and Wade 2010). The few studies that have addressed the function of female dewlaps suggest possible use in female-female interactions in *A. carolinensis* (Greenberg and Noble 1944; Jenssen et al. 2000) and *A. sagrei* (Driessens et al. 2014). In any case, substantive focus on female dewlap function and behavior is necessary for a more complete understanding of ornamental evolution in anoles. Beyond anoles, we have limited information on the function, ecology, and evolution of female ornaments in general (Ah-King 2022). Thus, a broader focus on female ornament evolution across taxa is warranted to more fully understand ornamental trait evolution.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data associated with this study is available at Dryad: DOI: 10.5061/dryad.05qfttfds (Westeen *et al.* 2025).

Author contributions

MLY conceived of the study. All authors further developed the study, collected the data, and edited the manuscript. EPW and MLY analyzed the data and wrote the manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

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Table 1 Log-likelihoods, AIC, ΔAIC for models testing correlations between two categorical variables. For each test, we fit four models: independent, hidden Markov independent, correlated, and hidden Markov correlated. The best-fit models (ΔAIC = 0) are bolded.

Model	Log-Likelihood	AIC	ΔAIC
I. Male pigment v. female pigment			
Independent	-516.8	1057.6	271.4
Hidden Markov independent	-377.1	806.2	20.0
Correlated	**-357.1**	**786.2**	**0**
Hidden Markov correlated	-341.2	830.3	44.1
II. Dichromatism v. female pigment			
Independent	-411.6	847.1	52.7
Hidden Markov independent	-376.2	804.3	9.9
Correlated	**-361.2**	**794.4**	**0**
Hidden Markov correlated	-351.5	851.1	56.7
III. Dichromatism v. male pigment			
Independent	-511.8	1047.7	199.7
Hidden Markov independent	**-398.0**	**848.0**	**0**
Correlated	-389.1	850.2	2.2
Hidden Markov correlated	-374.3	896.7	48.7

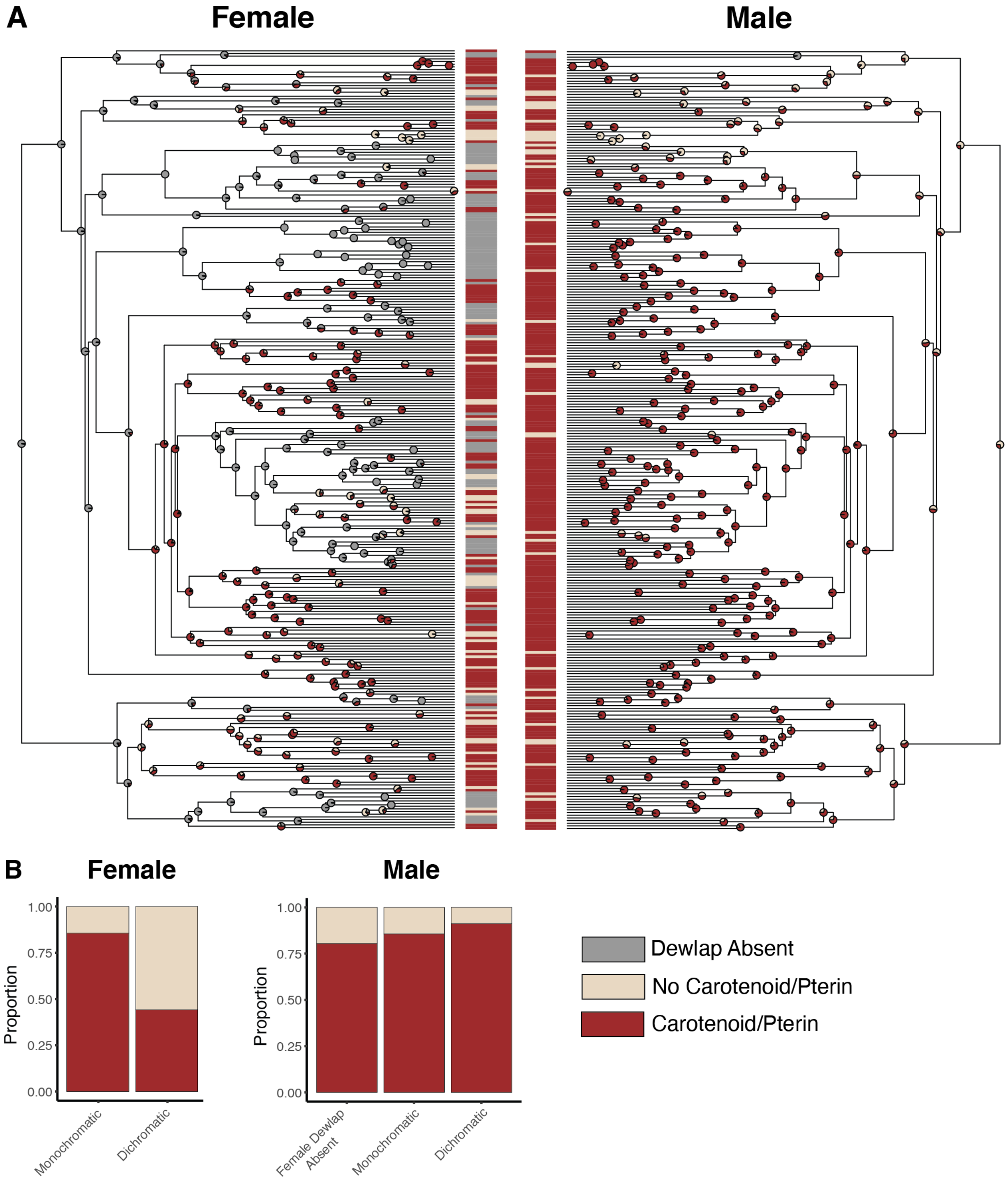
Figures

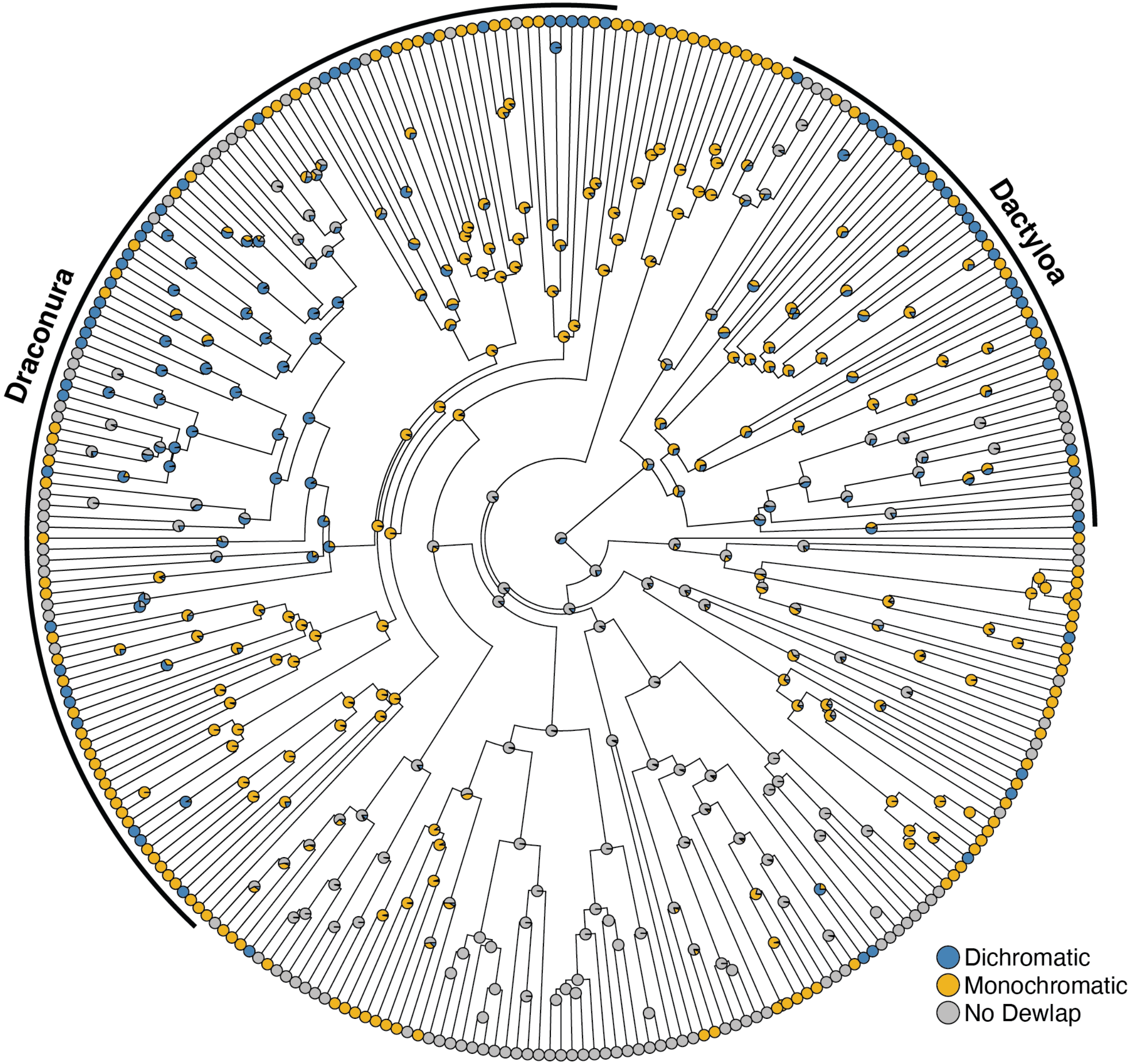
Figure 1 (A) Ancestral character estimation based on stochastic character mapping of the presence of 'costly' carotenoid and pterin pigments for females (left) and males (right). Pie charts represent the posterior probabilities for each state at the corresponding node. Tip states are shown in the center. (B) Bar charts depicting the proportion of species in each character state for the presence of carotenoids and pterins. Species are divided by dichromatism state: female dewlap absent, monochromatic, and dichromatic. Female dewlap absent is not shown for females because this category is necessarily fixed.

ALT TEXT: Phylogeny and bar charts showing the presence of dewlap ornaments and costly pigments across *Anolis* species and sexes, with subfigures A and B.

Figure 2 Ancestral character estimation based on stochastic character mapping of dichromatism state in anoles. Pie charts represent the posterior probabilities for each state at the corresponding node. The major mainland clades of anoles (Dactyloa and Draconura) are labeled.

ALT TEXT: A fan phylogeny showing dewlap color state (dichromatic, monochromatic, or no dewlap) of extant *Anolis* species and their ancestors.


A
Female
Male
B
Female
Male
Proportion
0.00
0.25
0.50
0.75
1.00
Monochromatic
Dichromatic
Female Dewlap Absent
Monochromatic
Dichromatic
Dewlap Absent
No Carotenoid/Pterin
Carotenoid/Pterin


Draconura
Dactyloa
Dichromatic
Monochromatic
No Dewlap