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Author for correspondence:

Alejandro Rico-Guevara

e-mail: colibri@uw.edu

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The evolution of sexually dimorphic traits in ecological gradients: an interplay between natural and sexual selection in hummingbirds

Diego F. Beltrán¹, Marcelo Araya-Salas^{2,3}, Juan L. Parra⁴, F. Gary Stiles⁵ and Alejandro Rico-Guevara^{1,6}

¹Department of Biology, University of Washington, Seattle, WA 98195, USA

²Centro de Investigación en Neurociencias, Universidad de Costa Rica, San José, Costa Rica

³Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica

⁴Grupo de Ecología y Evolución de Vertebrados, Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

⁵Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia

⁶Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98105, USA

ID DFB, 0000-0002-6054-4216; MA-S, 0000-0003-3594-619X; JLP, 0000-0002-5689-1872; FGS, 0000-0003-2044-3733; AR-G, 0000-0003-4067-5312

Traits that exhibit differences between the sexes have been of special interest in the study of phenotypic evolution. Classic hypotheses explain sexually dimorphic traits via intra-sexual competition and mate selection, yet natural selection may also act differentially on the sexes to produce dimorphism. Natural selection can act either through physiological and ecological constraints on one of the sexes, or by modulating the strength of sexual/social selection. This predicts an association between the degree of dimorphism and variation in ecological environments. Here, we characterize the variation in hummingbird dimorphism across ecological gradients using rich databases of morphology, colouration and song. We show that morphological dimorphism decreases with elevation in the understory and increases with elevation in mixed habitats, that dichromatism increases at high altitudes in open and mixed habitats, and that song is less complex in mixed habitats. Our results are consistent with flight constraints, lower predation pressure at high elevations and with habitat effects on song transmission. We also show that dichromatism and song complexity are positively associated, while tail dimorphism and song complexity are negatively associated. Our results suggest that key ecological factors shape sexually dimorphic traits, and that different communication modalities do not always evolve in tandem.

1. Introduction

Evolutionary divergence of phenotypic traits and social signals is a proposed mechanism by which populations differentiate and new species are formed [1–3]. Traits that exhibit differences between sexes have been of special interest in studies of speciation via sexual selection and have been used as indicators of its intensity [4–6]. Nonetheless, the evolution of sexual differences can also be the product of natural selection, or of an interaction between the two [4,7]. Consequently, though the evolution of sexually dimorphic traits is the result of differential forces acting individually on either sex, the resulting difference provides valuable insight into the forces shaping trait evolution. One captivating example of sexually dimorphic traits evolving under both sexual and natural selection are avian bills shaped by plant–pollinator coevolution [8], while simultaneously used in physical combat as intrasexually selected weapons [7,9].

In birds, elevation and habitat structure are ecological factors proposed to be drivers of trait variation through natural selection, which in turn may either

promote sexual dimorphism or restrain trait divergence between sexes due to sexual selection. Examples of these potential effects include physiological and biomechanical constraints on flight performance [10,11] due to a reduction in oxygen availability and atmospheric pressure with elevation, which affect aerial agonistic [12] and display manoeuvres [13], as well as the potential cost of ornaments such as elongated tails [14]. Habitats may affect sexual dimorphism in feeding apparatus when there is differential resource distribution leading to divergence in foraging strategies [15] and food niche partitioning between sexes [8,16]. Habitat structure may also affect how songs are transmitted and perceived, yielding different optima for acoustic broadcasting [17–20]. Additionally, species richness and composition of assemblages vary with elevation [21–23], affecting inter- and intra-sexual acoustic competition [24–26] and visual communication [27,28]. Habitat structure also affects visual signals through changes in light availability and viewing geometry [29,30], which may alter how ornaments—like colourful plumage and elongated tails—are perceived. Given what is known about the effects of altitude and habitat structure on sexually dimorphic traits, it is important to evaluate how the interplay between these two environmental factors may affect the evolution of these traits (e.g. open habitats at high altitudes versus open habitats at low altitudes).

In addition, covariation of sexually dimorphic traits can help us understand the extent to which the same selective regimes may shape dimorphism across the main sensory modalities (e.g. acoustic and visual) that animals use to communicate [31,32]. Sexually dimorphic traits might also be affected by other selective pressures that covary with the environment [12,19,33]; for example, a mating preference for a conspicuous signal might differ between different light conditions [34]. Hence, by characterizing the association among sexually divergent traits and the way these associations change along environmental gradients, we can make inferences about the evolutionary mechanisms shaping sexual dimorphism.

Classic ideas suggest a trade-off between multiple signals, predicting a negative association between different sensory modalities—the transference hypothesis [35,36]. Alternatively, individuals may communicate different messages relying on each signal modality, in which case no association among traits is expected—the multiple message hypothesis [37]. Additionally, the redundant signal hypothesis states that assessing multiple signals of quality simultaneously is more reliable than using only one, predicting a positive correlation among signals [32,38]. Finally, the unreliable signals hypothesis states that many secondary sexual characters are dissociated from the individual condition, and thus are not expected to be selected for [39]. To differentiate these contrasting hypotheses, it is necessary to incorporate information from all signalling modalities to determine the existence and directionality of coevolution among sexually dimorphic traits.

Within birds, the hummingbirds (Trochilidae) are a morphologically, colourfully and acoustically diverse family, which are monophyletic [40], species-rich, and occur in many different environments across the Americas. In this family, several morphological and locomotion-related traits have been extensively studied, showing that wing, bill and tail traits are involved in intra- and inter-sexual interactions [14,41–43], but are also under natural selection for access to

resources through interference and exploitative competition [8,9,14,44]. Hummingbird coloration is highly diverse and has been associated with both sexual selection for mate attraction [45–47], selection for social dominance [27,48,49] and camouflage [45,46]; similarly, hummingbirds also display a wide range of diversity in song structure [50,51].

Here, we use hummingbirds to evaluate if ecological gradients shape morphological, visual and acoustic sexual dimorphisms, often attributed to sexual selection, and if these traits are correlated or evolve independently. We predict morphological dimorphism (MD) to be reduced in open habitats because of restricted resource partitioning between sexes, and thus reduced divergence of foraging strategies, due to lower resources [8] and at high elevations, as potentially costly morphological modifications (e.g. involved in expensive displays) would compromise the already tight energy budget at extreme conditions [10,52]. A particular MD presumed to be mostly under inter-sexual selection, tail length, should decrease with altitude, at any habitat structure, given augmented flight constraints, and in fact, high-elevation hummingbirds have been shown to have less elaborated tails [10,14]. Sexual dichromatism should decrease at higher elevations and open habitats, due to lower predation pressure on both sexes [53] and higher chance for visibility [29,33], which could result in both males and females becoming similarly colourful (i.e. monochromatic). We expect that song would be affected by elevation through the changes in species richness and acoustic competition [17,23], hence, species at mid-elevations, where species richness increases, should have lower song complexity than those in the two extremes given competition in the acoustic space [21]. We expect more complex songs in open environments because closed environments should negatively affect male song complexity, by increasing signal degradation as a result of higher vegetation density [18,20]. Finally, we expect these traits to negatively correlate under the transference hypothesis, because of high metabolic costs involved in the production and use of secondary sexual traits [35,36]. Nonetheless, because the costs of these traits may vary along elevational and habitat structure gradients, these associations could vary as well.

2. Methods

(a) Sexually dimorphic traits

(i) Morphological and tail dimorphism

We quantified dimorphism on 14 measurements taken from field captures including bill, wing and tail measurements (electronic supplementary material, table S1). We measured only adult individuals, of both sexes where available, for a total of 109 species with complete data for both sexes (three or more per sex) and included in the molecular phylogeny [40]. We scaled these 14 measurements to unit variance and performed a principal component analysis (PCA) keeping all PC axes (electronic supplementary material, table S1). We included body mass in the PCA to characterize sexual size differences that have been shown to be important for inter- and intra-specific interactions [54]. We then calculated MD as the Euclidean distance between males and females in the multidimensional space defined by the 14 PCs for each species (figure 1, electronic supplementary material, figure S1). We confirmed that this approach was appropriate to infer dimorphism in multidimensional space using simulations, and that it was consistent with weighting each PC

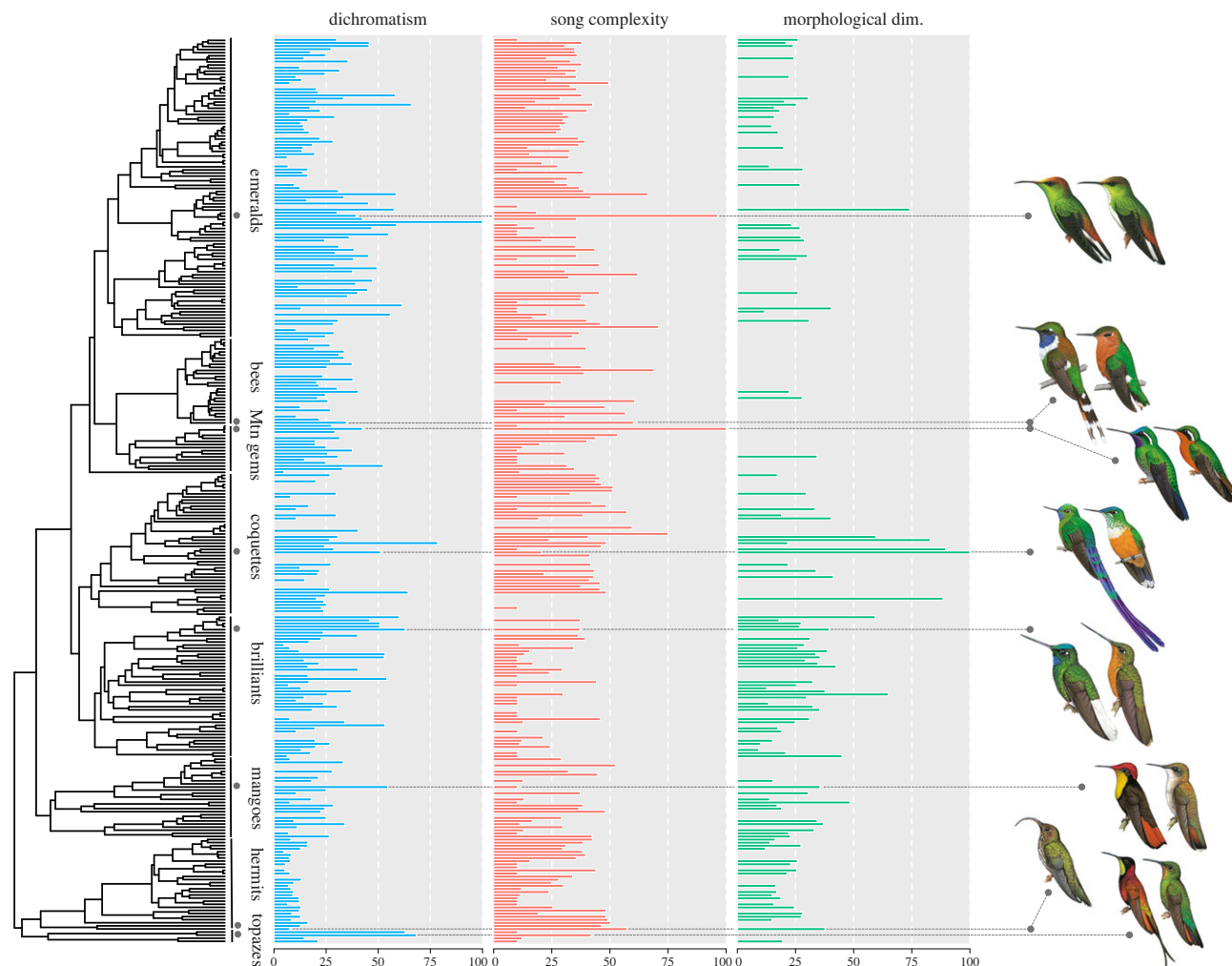


Figure 1. Scaled sexually dimorphic traits in hummingbirds. Tail length is included in MD. All traits were converted to percentages. On the left, the hummingbird phylogeny with 293 species [40]. On the right, barplots showing the magnitude of each dimorphic trait for each species. Dots next to the phylogeny and dotted lines connect to the species with the highest summed dimorphisms of each subclade. Bottom-up (male, left; female, right): topazes: *Topaza pella*, hermits: *Eutoxeres aquila* (monochromatic), mangoes: *Chrysolampis mosquitus*, brilliants: *Coeligena phalerata*, coquettes: *Agelaiocercus coelestis*, mountain (Mtn) gems: *Lampornis caloemelus*, bees: *Tilmatura dupontii*, emeralds: *Microchera cupreiceps*. Illustrations by Birds of the World | Cornell Lab of Ornithology. (Online version in colour.)

by its explained variance (see electronic supplementary material for details). To identify cases of male- or female-biased MD (e.g. one sex being predominantly larger than the other), we computed the log₁₀ difference between female and male values for each measurement and summed all differences for each species. This showed that MD was mostly male-biased (i.e. males larger; 107 species, 91.5%) while only 10 species (8.5%) were female-biased (electronic supplementary material, figure S2).

Next, we calculated tail length dimorphism (TLD) using the database from Clark [14], which includes the length for all rectrices for 332 species. Additionally, we used the Colwell [54] body mass database with additional values for missing species from various sources ([55–57]; D Plazas 2021, unpublished data; A Rico-Guevara 2021, unpublished data) for 244 species with weight data for both sexes. We then corrected for size by dividing average tail length of each sex by the square root of the corresponding average body mass of each sex, given that tail length allometry has been shown to be 0.5 in hummingbirds [14], and calculated tail dimorphism by subtracting the female value from the male value. We found that TLD using only the longest male rectrix was highly correlated with the TLD sum of all rectrices ($\rho = 0.91$, $p < 0.001$), so we calculated TLD of the longest male rectrix for simplicity (figure 1, electronic supplementary material, figure S1). This agrees with Clark [14], which states that typically just one tail-feather elongates in hummingbirds.

(ii) Sexual dichromatism

We used a reflectance dataset for hummingbirds that contains 237 species (two or more per sex) with colour data for five plumage patches [46]. For each of these species, we calculated the colour distance between sexes using the receptor-noise visual model [58,59]. This model quantifies the relative stimulation of each of the four cones in the avian visual system, corresponding to UV or violet, short, medium and long-sensitive wavelengths (i.e. quantum catches). Then, the model adds the effect of the quantum catches together while considering cone density and signal-to-noise ratio in the signal processing. We kept distances in the chromatic portion of the spectrum only [59,60]. Finally, we averaged the colour distances among patches to obtain a general measure of sexual dichromatism for each species (figure 1). All calculations were made in the R package *pavo* [61,62].

(iii) Song complexity

We focused on male song output since it has become a common indicator for the intensity of sexual selection [3]. Female song is rare in hummingbirds and has been observed only in a few species [35,63]. We collected recordings for 262 species from bioacoustics libraries and personal collections (see electronic supplementary material for sources). We excluded three species in which song has been reported as absent [35]. Only recordings

with at least two songs were analysed. A song was defined as a broadcast vocalization uttered repeatedly from a fixed position and that showed a regular pattern in the time spacing and/or the sequence of elements. Song elements, defined as continuous power spectral density traces in the spectrogram, were categorized within each recording based on visual inspection. A single acoustic space for all species was calculated as the first two principal components from a PCA on 26 acoustic features measured on elements, using the R package *warbleR* [64]. The acoustic features quantify the distribution of energy in the time and frequency domain, and the variation in dominant frequency across time (see electronic supplementary material, methods for details). Song acoustic space was quantified as the minimum spanning tree connecting all elements of the song in the overall acoustic space, using the R package *PhenotypeSpace* [65]. Four parameters describing song complexity were calculated for each song: element types, acoustic space, element transition diversity and between-song variation (electronic supplementary material, methods). To obtain a single measure of song complexity, we employed a PCA on all scaled parameters. PC1 (62.9% of total variance) loaded strongly and negatively on all properties except for element transition diversity, which loaded strongly on PC2 (8.8%). We kept PC1 as a measure of song complexity (figure 1; electronic supplementary material, table S2).

(iv) Altitude and habitat structure

We used the Rangel *et al.* [66] database, which contains values of minimum, medium and maximum altitude for 302 species of hummingbirds. We evaluated the correlation among these metrics and found that both minimum and maximum altitude were highly correlated with medium altitude ($\rho = 0.91$, $\rho = 0.95$; respectively), so we only kept medium altitude for further analyses. For habitat structure, we used the Parker *et al.* [67] database and gathered the type of habitat structure in which each species occurs based on the foraging stratum, grouped under three categories: understorey, mixed (i.e. species moving between shaded areas and gaps) and open (i.e. species which mostly use gaps and canopy). This approach does not recognize species that set courtship territories in strata different from their foraging stratum, but this information is lacking for most hummingbird species.

(b) Comparative analyses

(i) Effect of altitude and habitat

To evaluate the effect of altitude and habitat structure on each dimorphic trait, we employed Bayesian phylogenetic mixed-effect models (BPMs) in the R package *MCMCglmm* [68,69]. For each dimorphic trait as response variable, we ran a model with altitude, habitat structure and the interaction between the two as predictors. We selected the understorey as baseline habitat; thus, all the comparisons are relative to the understorey to aid interpretation. The baseline habitat was switched to evaluate if the relationship with altitude within each habitat was significantly different from zero as *post hoc* analyses. All continuous variables were scaled to unit variance prior to entering the models. To account for phylogenetic non-independence and uncertainty, we randomly sampled 100 phylogenetic trees from the posterior distribution [40] and ran a model with each tree as random effect, we then pooled together the posterior distributions of each parameter from all runs and computed the median and high-density interval (HDI) of the pooled posterior. We used flat, uninformative priors for the residuals and random effects covariance matrices. Each model was run for 500 000 generations, sampling every 300 generations with a burn-in of 10 000. We evaluated this configuration for convergence with a Gelman–Rubin diagnostic which was kept under 1.1 [70]. Each set of models included as many species as possible with

phylogenetic, altitude and habitat structure data: 224 species for dichromatism, 213 for song complexity, 107 for MD (figure 1) and 161 for TLD (figure S1).

(ii) Correlation between traits

To evaluate the relationship between dimorphic traits, we ran BPMs with all the possible pairwise combinations of traits setting one as response and the other as predictor. For the MD and TLD pair, since MD included tail length measurements, we recalculated MD in the same fashion but removed tail length to avoid circularity and to test for correlation between dimorphism of all other measurements and TLD. Furthermore, to test if associations between traits were dependent on altitude or existed only in a particular habitat type, we included altitude and habitat structure as interactions with the predictor in each model. For each pair of traits, we included as many species as possible; 106 for dichromatism and MD, 191 for dichromatism and song complexity, 143 for dichromatism and TLD, 96 for MD and song complexity, 147 for TLD and song complexity and 74 for MD and TLD.

3. Results

(a) Ecological effects on dimorphic traits

MD significantly decreased with elevation in the understorey (figure 2; posterior median = -0.59 , 95% HDI: -1.09 to -0.09 ; electronic supplementary material, table S3), in mixed habitats the relationship between MD and elevation was positive and significantly different from the understorey but not significantly different from zero, while in open habitats the relationship with MD was not significantly different than that of the understorey or from zero. To determine if the MD association was attributable to either body size or wing length, the two most often used size-related traits, we ran complementary lambda-estimated PGLS models between the log₁₀ sex differences in body size, wing length and folded wing length, and the same predictors as BPMs. We found only one significant effect of decreased wing length dimorphism with increased elevation, which is consistent with the general trend but did not fully account for the results obtained in the MD BPM (electronic supplementary material, table S4).

Dichromatism showed significant differences among elevation and habitat combinations (electronic supplementary material, table S3). Dichromatism increased with altitude in open and mixed habitats and these relationships were significantly different from that of the understorey, but not significantly different from zero. In the understorey, the relationship between dichromatism and elevation was negative and marginally significant (figure 2). To rule out that the associations with dichromatism were produced mainly by the conspicuous coloration of the crown or gorget (i.e. the most dichromatic patches), we ran five additional BPMs using only the dichromatism of each patch as response variable (electronic supplementary material, table S5). These models showed no significant associations for the crown or gorget, indicating that the association with altitude and habitat structure is not attributable to the most dichromatic patches. To determine if dichromatism at high altitudes could be reduced because of females becoming more colourful, we took the interpatch colour span data for each sex from [46] and found that at high altitudes, regardless of habitat, dichromatism derives mostly from males with complex

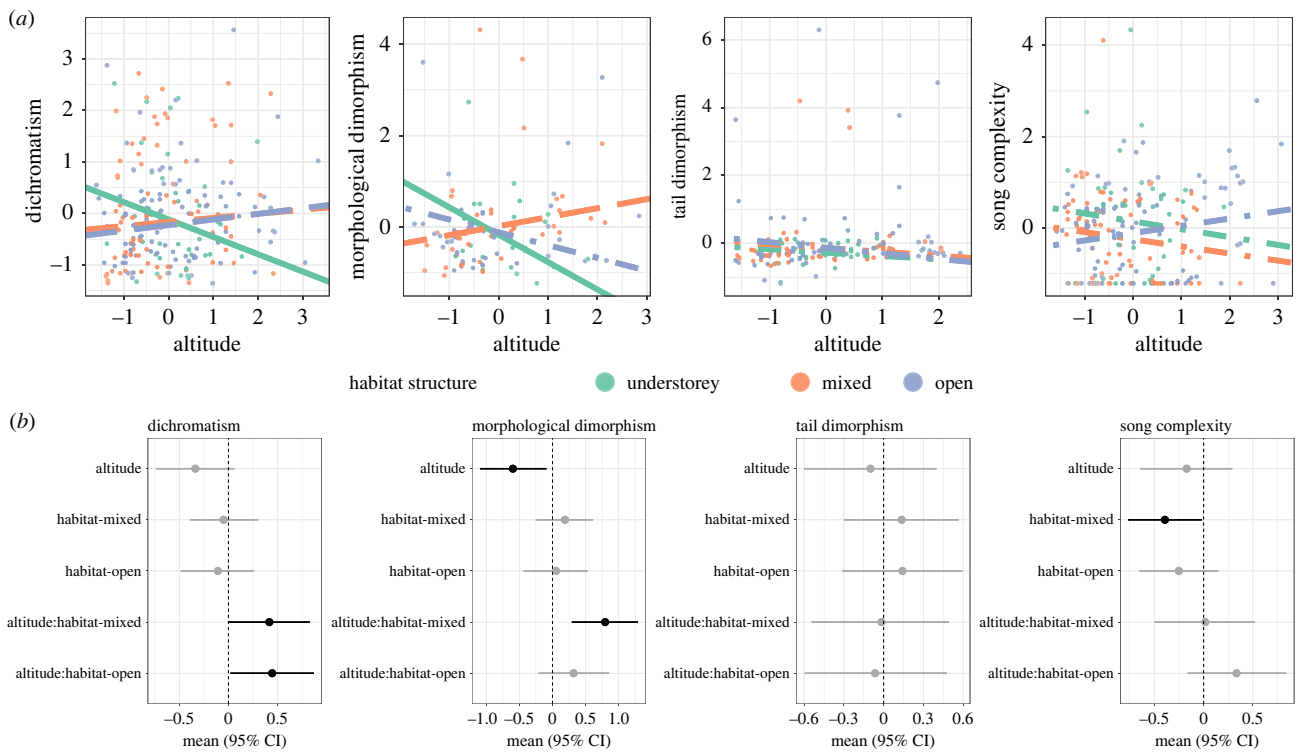


Figure 2. Relationships between altitude and habitat structure with hummingbird dimorphic traits. (a) Scatterplots showing the relationship between altitude and each dimorphic trait. Each dot represents a species. Solid lines represent significant effects of elevation and habitat structure (marginally significant in dichromatism), dashed lines indicate relationships significantly different from the understory, dot-dash lines indicate non-significant associations. Colours represent each type of habitat structure. Vertical and horizontal axes are standardized. (b) Model coefficients estimated by BPMMs. Dots indicate posterior median and bars show 95% HDI. Grey segments indicate non-significant effects, and black segments indicate significant effects. Segments on the left of dotted lines indicate negative effects and segments on the right indicate positive effects. (Online version in colour.)

and colourful plumage, rather than females (electronic supplementary material, figure S3), and that dichromatism is highly correlated with male colour complexity ($\rho = 0.70$), while weakly correlated with female colour complexity ($\rho = 0.21$). We also found that most dichromatic species show colourful males and that colourful monochromatism is rare and unrelated to elevation or a particular habitat type (electronic supplementary material, figure S3). Song complexity was significantly lower in mixed habitats compared to the understory when altitude is average (approx. 1500 m.a.s.l.). Conversely, TLD did not show significant relationships with altitude or habitat structure, nor were the relationships different among habitats (figure 2b; electronic supplementary material, table S3).

(b) Associations among dimorphic traits

We found a significant positive relationship between dichromatism and song complexity (figure 3a, electronic supplementary material, figure S4; posterior median = 0.24, 95% HDI: 0.02–0.45; electronic supplementary material, table S6). This association remained positive even after removing the two most extreme points in the song complexity distribution (electronic supplementary material, table S6), though with a marginal loss of significance (posterior median = 0.27, 95% HDI: –0.01–0.56). When considering the effects of altitude and habitat structure, the significance of the relationship between dichromatism and song complexity was lost, but remained positive for all habitats, hence, the association between these traits was not limited to a specific covariate. To evaluate if the most dichromatic patches were

responsible for this association, we ran five more BPMMs with the dichromatism of each patch as response and song complexity as predictor. These models showed strong significant associations in the crown and gorget (figure 3b,c), with a weaker association in the mantle (electronic supplementary material, table S7), implying that the most dichromatic patches are indeed the ones responsible for the association with song complexity. Additionally, a weak negative association was found between TLD and song complexity in the understory, and this relationship became more negative at higher elevations (posterior median = –0.15, 95% CI: –0.29 to –0.02; electronic supplementary material, figure S4 and table S6), suggesting a potential trade-off between signalling modalities. We also found positive correlations between TLD and MD, especially in mixed and open habitats (electronic supplementary material, table S6). All other comparisons were non-significant with and without the interactions (electronic supplementary material, table S6 and figure S4).

4. Discussion

We show that variation in sexually dimorphic traits of multiple signalling modalities is partly associated with elevation gradients and habitat structure, supporting the idea that these dimorphisms are the result of a complex balance between natural and sexual selection. We also found that, in some cases but not others, altitude and habitat structure influence covariance patterns between dimorphic traits from different signalling modalities. For example, dichromatism and song complexity were positively associated, unaffected by elevation/habitat,

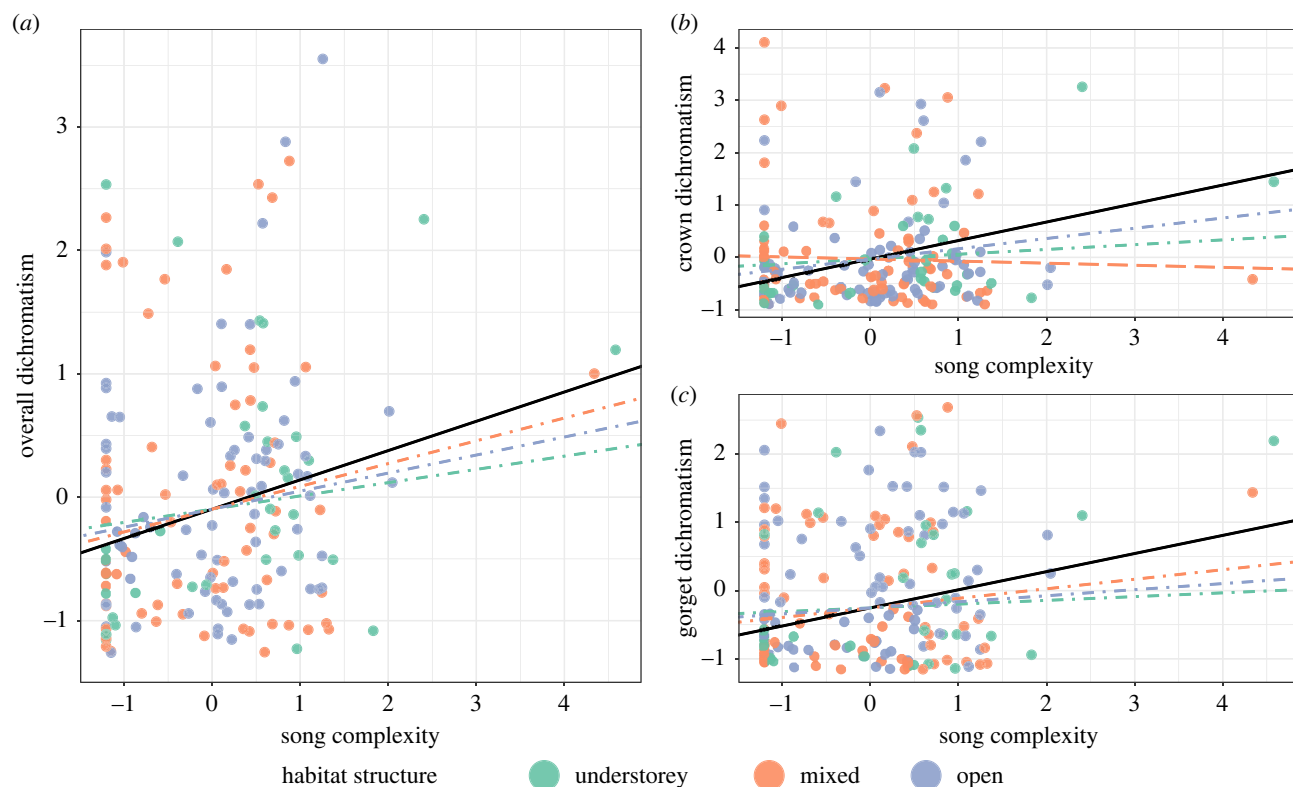


Figure 3. Scatterplots showing the relationship between dichromatism and song complexity. (a) Average dichromatism of the whole plumage and song complexity are positively associated regardless of altitude and habitat structure. Relationship between (b) crown and (c) gorget dichromatism and song complexity. Each dot represents a species and are coloured according to their corresponding habitat structure. Lines represent relationships estimated from BPMMs: regardless of other covariates (black), interaction with altitude and habitat structure (colours). Solid lines represent significant effects, dashed lines indicate relationships significantly different from the understorey, dot-dash lines indicate non-significant associations. Vertical and horizontal axes are standardized. (Online version in colour.)

suggesting that communication signals in hummingbirds could deliver complementary information if these are sexually selected. Conversely, tail length and song complexity are inversely correlated, with a steeper negative association at higher elevations in the understorey. Our results suggest that sexual dimorphisms are associated with natural selection, and that some visual traits correlate with acoustic traits, consistent with a redundant signal hypothesis; while others show a trade-off, in line with the transference hypothesis.

Altitude and habitat structure have been found to affect sexually dimorphic traits in other bird clades with contrasting results. For example, dichromatism in finches decreases with elevation [71,72], which was attributed to three factors: (i) colder nesting temperatures and fewer resources select for increased male parental care and therefore decreased polygyny, (ii) harsh conditions at high elevations select for less elaborated plumage due to metabolic costs and (iii) predators may be attracted to the nest by colourful males [71]. We found that hummingbird dichromatism increases with elevation in mixed and open habitats, while it decreases at high altitude for understorey species. Hummingbirds are all polygynous [73], thus, neither increased male parental care nor different mating systems [74] can explain the reduced dichromatism that we detected at high elevations for understorey species. However, differences in displaying strategies (e.g. lekking) could explain dichromatism variation in hummingbirds [75,76]. The increased cost of colourful plumage maintenance at high elevations due to UV and near-infrared exposure could decrease dichromatism by selecting for less elaborated plumage on both sexes [77–80], but further research is required to evaluate how colourfulness changes

with elevation and the benefits/costs of maintaining structural colours at high altitudes. Predation pressure in hummingbirds is thought to be stronger in juveniles and females, due to the vulnerable offspring rearing period [81]; hence reduced predation pressure at high elevations [53] would relax the pressure against evolving colourful plumage in females and juveniles. Adult males employ their flashy feathers during courtship and aggressive encounters [82], and females and juveniles would also benefit from male-like colour-rich plumage in social interactions [49]. However, we found that most females and most monochromatic species are not more colourful at high altitudes, suggesting that relaxed predation pressure is not promoting colour-enriching in females with elevation. Furthermore, we found that instances of dichromatic species where the female is the colourful sex are rare (electronic supplementary material, figure S3). It has been suggested that females of many hummingbird species exhibit plumage polymorphism—including a ‘male-like’ morph [49,83], but the phenomenon has only been confirmed for three species [84,85]. Hence, one possible hypothesis is that increased dichromatism in high-elevation mixed and open habitats is the result of enhanced visibility [29] and relaxed predation pressure against colourful plumage.

Our results show that hummingbird MD decreased with altitude in the understorey. In the species analysed here, MD is mostly male-biased, although the pattern found here does not include many of the smallest species of the ‘bee’ clade, where females have been found to be larger than males [86]. Including more species of this subclade may affect the magnitude of the effect. However, we consider unlikely that this will

change the overall pattern given how widespread male-biased dimorphism is across all other subclades. We consider that a more diverse morphological dataset like the one used here is more appropriate for inferring the effect of ecological factors on overall MD. Moreover, in hummingbirds as a whole, males tend to be the larger sex [54], despite recent claims of the opposite [86]; therefore, the predominant female-biased size dimorphism in the 'bee' clade is an exceptional case for the family.

Several studies have demonstrated that elevation strongly affects flight in hummingbirds, imposing a selective pressure on displaying males [12,16,52]. Our results partially agree with biomechanical studies on hummingbirds showing an increase in male wing size to compensate for lower air density at high elevations [10], though this only applies to open habitats where aerial displays could be more exaggerated (e.g. [87]), and may also influence foraging flight affecting both sexes. In the understorey, these biomechanical factors may be weakened because vegetation density would constrain maximum flight speed. Hence, it is important for future studies to account for habitat structure on altitudinal effects on morphology. We showed that differences in overall body size extend to other traits such as bill shape, which may be associated with resource specialization [8,88], and intra-sexual competition and aggressive interactions [7,9]. By contrast, dimorphism in tail length was not affected by either altitude or habitat structure, which supports that the main selective regime affecting this trait in hummingbirds is sexual selection [43]. However, our models showing a positive association between MD and TLD when considering altitude and habitat, suggest a tight association between tail and wing length with changes in elevation, agreeing with previous studies [10,14]. A non-significant association between altitude and TLD is noteworthy in terms of flight mechanics because it suggests that variation in tail length may entail only modest flight costs [89].

Habitat structure and its interaction with elevation have been documented to affect specific song properties, with a study showing that low-frequency songs are common at higher elevations and in open areas [19]. A recent study on hummingbirds showed that transmission of high-frequency vocalizations is affected by habitat structure [90]. We show that songs are simpler in mixed habitats compared to the understorey at middle elevations. This pattern is consistent with the idea that habitat structure and acoustic competition shapes the evolution of acoustic properties. Future studies should evaluate if and how the environment affects hummingbird song and if it follows the predictions of the acoustic adaptation hypothesis [18], as well as the effects of species richness and acoustic competition in hummingbirds [24,26].

We found a positive correlation between dichromatism and song complexity, regardless of habitat or altitude, and that the most dichromatic patches were responsible for this pattern. The use of multiple cues to signal condition or to attract the opposite sex is important in many animal groups [31,91], and several hypotheses have been proposed to explain the evolution of signal integration. The pattern shown here is particularly alluring given that it integrates distinct perception axes (visual and auditory), and it could represent a case of evolution of redundant signals [39,92]. If signalling traits are associated with good condition, a single sexual character could partially represent the quality of the individual and complementary traits

could provide a better overall assessment. In hummingbirds, male song could function as a long-range female attractor, and conspicuous coloration of the crown and gorget can act as a secondary quality indicator when in visual contact [93]. This relationship in hummingbirds contrasts with a negative relationship between plumage ornamentation and song elaboration found in cardueline finches [94]. These contrasting results could potentially be explained by higher colour compartmentalization, which is common in many hummingbirds. Specific patches are brightly coloured (crown and gorget) and used during displays, while others are drab and associated with crypsis, yielding dissociation and colour divergence due to simultaneous pressures from sexual and natural selection [45,46].

Interestingly, we found altitude-dependent correlations between TLD and song complexity. At higher altitudes, the two traits are negatively correlated, while in lower altitudes the relationship is positive (due to a negative coefficient for the interaction). This negative association at high altitudes can be interpreted as an example of the transference hypothesis [35,36], which could explain why in these environments species with complex songs lack long tails. It is fascinating that a visual trait such as coloration can relate to an acoustic trait in one direction, while another visual trait, such as long tails, shows an opposite association.

Given the evidence presented here and in other studies, sexual dimorphism can be seen as a product of pressures ranging from ecological differences between sexes [8,95] to differences as a result of intra- [7,9] and inter-sexual selection [74,96]. Although a universal trait that represents the strength of sexual selection can be convenient for comparative studies, it is likely that a single trait is insufficient, and that some traits useful as proxies in some clades are not in others [97]. Nonetheless, TLD in hummingbirds seems a promising character to indicate effects produced mainly by sexual selection. Future research should explore how the traits studied here relate to physiological indicators of sexual selection, such as testis size, hormonal condition and reproductive success [74,98,99]. Our results are consistent with the hypothesis that sexually dimorphic traits are shaped by forces other than sexual selection and should encourage future research to expand traditional views about the evolution of communication signals, providing a broader framework to understand their role in diversification, ecology and social behaviour.

Data accessibility. Data and code to replicate analyses are available from GitHub (<https://github.com/diegobeltran>) and the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b5mkkwhgf> [100].

Supplementary material is available online [101].

Authors' contributions. D.F.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; M.A.-S.: conceptualization, data curation, formal analysis, methodology, supervision, validation, writing—review and editing; J.L.P.: conceptualization, data curation, funding acquisition, investigation, methodology, supervision, validation, writing—review and editing; F.G.S.: data curation, writing—review and editing; A.R.-G.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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