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

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**Abstract**

Animal traits that exhibit differences between sexes have been of special interest in the study of phenotypic evolution. Classic hypotheses attribute the evolution of sexually dimorphic traits to intrasexual competition and mate selection, although 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 limiting the strength of sexually selected trends. This hypothesis predicts an association between the degree of dimorphism and variation in the ecological environment. Here, we evaluate the variation in dimorphism across ecological gradients using rich databases of morphology, colouration, and song for up to 224 hummingbird species. We show that morphological dimorphism decreases with elevation while dichromatism increases at high altitudes in open and mixed habitats, consistent with increased flight constraints and decreased predation pressure at high elevations, and that habitat structure limits song complexity. Dichromatism and male song complexity were positively associated, consistent with the signal redundancy hypothesis. Our results demonstrate that trait divergence between sexes is the result of an interplay between sexual and natural selection, and that considering various communication modalities may be necessary to understand how different selective pressures shape ornaments and behaviour.

**Keywords:** Dimorphism, elevation, habitat structure, Trochilidae, communication signals, signal redundancy.

**Introduction**

Evolutionary divergence of phenotypic traits and social signals is a proposed mechanism by which populations differentiate and new species are formed (1,2). 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 (3–5). Nonetheless, the evolution of sexual differences can also be the product of natural selection, or via an interaction between the two (3,6). One captivating example of sexually dimorphic traits evolving under both sexual and natural selection are avian bills used in physical combat, thus evolving as intrasexually selected weapons, (6,7), and simultaneously shaped by competition for resources (8).

In birds, elevation and habitat structure are some ecological factors proposed to be drivers of trait divergence between sexes through natural selection. Both oxygen availability and atmospheric pressure decrease with elevation, posing physiological and biomechanical constraints on flight performance (9,10), which affect display manoeuvres (11), and the use of ornaments such as elongated tails (12). Habitat structure may produce sexual dimorphism in feeding apparatus morphology when there is food niche partitioning between sexes (8,13), and it may also affect how songs are transmitted and perceived (14–17). Additionally, changes in elevation can alter species richness and composition of assemblages (18–20), affecting inter- and intra-sexual acoustic competition (21–23) and visual communication (24,25). Habitat structure (e.g., forested vs. open areas) also affects visual signals, through changes in available light and viewing geometry (26,27), which may alter how ornaments like colourful plumages and elongated tails are perceived. Given what we know about the effect of the environment on sexually dimorphic traits, we can make predictions about when and how these traits are expected to change along environmental gradients.

Furthermore, covariation of dimorphic traits can help us understand the extent to which the same selective regimes may shape dimorphism across different modalities. Animals usually rely on multiple sensory modalities (e.g., acoustic, and visual) to communicate (28,29). Sexually dimorphic traits might be under different selective pressures that may also change depending on the environmental context (16,30,31). For example, a mating preference for a conspicuous signal might differ between environments with different light conditions (32). 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 sexually dimorphic traits.

Classic ideas by Darwin and Wallace (33,34) 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 (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 (29,38). Finally, the unreliable signal hypothesis states that many secondary sexual characters are dissociated from individual condition, and thus are not expected to be correlated with one another (39). These contrasting hypotheses, all applicable to the evolution of avian communication signals, suggest that there may be variation in the strategies employed by different taxa, and that it may be necessary to incorporate additional information to better understand the coevolution of sexually dimorphic traits.

Within birds, a morphologically, colourfully, and acoustically diverse family are the hummingbirds (Trochilidae). Hummingbirds are monophyletic (40), species-rich, and occur in many different environments and elevations across the Americas. In this family, a variety of morphological and locomotion-related traits have been extensively studied (12,31,41,42), showing that wing, bill, and tail traits are involved in intra- and inter-sexual interactions, but are also under natural selection for access to resources through interference and exploitative competition (7,8,12). Hummingbird colouration is highly diverse and has been associated with both sexual selection for mate attraction and natural selection for camouflage (24,43–46). Along the acoustic axis of phenotypic variation, hummingbirds also display a wide array of song complexity and diversity (47,48).

Here, we use hummingbirds to evaluate if morphological, visual, and acoustic sexual dimorphisms, often attributed to sexual selection, are correlated, uncorrelated or evolving independently. We expect these traits to correlate negatively under the transference hypothesis, because of high metabolic costs involved in the production of secondary sexual traits (35,36). Nonetheless, because the costs of these traits may vary along elevational or habitat structure gradients, these associations could vary as well. We also evaluate if these sexually dimorphic traits vary across altitudinal and habitat structure gradients. Specifically, we predict dimorphism in morphology to be reduced at high elevations, as morphological modifications would compromise the already tight energy budget at extreme conditions (9,49); and in open habitats because of restricted resource partitioning between sexes (8). A particular morphological dimorphism presumed to be mostly under sexual selection, tail length, should decrease at higher altitudes, given that high elevation hummingbirds have been shown to have less elaborated tails and larger wings, possibly due to flight constraints (9,12); habitat structure should have no effect on tail dimorphism, as it is mostly used on close-range displays (35). Sexual dichromatism should increase at higher elevations and open habitats, due to lower predation pressure (50) and higher chance for visibility (26,30), respectively. Finally, we expect that song would be affected by elevation through the changes in species richness and acoustic competition (14,20), hence, species at mid elevations, where species richness increases, should have higher song complexity than those in the other two extremes (18). As for habitat structure, closed environments should negatively affect male song complexity, by increasing signal degradation as a result of higher vegetation density (15,17). In a broader perspective, we expect that sexually dimorphic traits in this family reflect an interplay between sexual and natural selection and an example of how environmental variables and signal redundancy shape the evolution of complex communication signals.

**Methods**

***Hummingbird traits***

*Morphological and tail dimorphism*

We quantified morphological dimorphism based on 14 measurements taken from field captures: body mass, total and exposed culmen, commissure width, bill height, folded and spread wing length, wing width, wing shape and aspect ratio, wing taper, wing loading, wing area, and length of the longest rectrix. We measured only adult individuals, of both sexes where available, for a total of 109 species with complete data for both sexes 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 (Table S1). We included body mass in in the PCA to characterize sexual size differences that have been shown to be important for inter and intra-specific interactions (51). We then calculated Morphological Dimorphism (MD) as the Euclidean distance between males and females in the multidimensional space defined by the 14 PCs for each species (Fig. 1). We confirmed that this approach was able to detect multivariate dimorphism using simulations (see Supplemental Material for details).. To identify cases of male- or female-biased MD (i.e., 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 morphological dimorphism was mostly male-biased (i.e., males larger; 107 species, 91.5%) while only 10 species (8.5%) were female-biased (Fig. S1).

Next, we calculated Tail Length Dimorphism (TLD) using the database from Clark (12), which includes length for all rectrices for 332 species. Additionally, we used the Colwell (51) body mass database with additional values for missing species from various sources (56–58; Dennys Plazas, unp. data; Rico-Guevara, unp. data) for 244 species with weight data for both sexes. We then corrected for size by dividing tail length of each sex by the square root of the corresponding body mass of each sex, given that tail length allometry has been shown to be 0.5 in hummingbirds (12), 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 (Fig. 1). This agrees with Clark (12), which states that typically just one tail-feather elongates in hummingbirds.

*Sexual dichromatism*

To quantify sexual dichromatism, we used a reflectance dataset for hummingbirds (45). This dataset contains 237 species with colour data for both sexes. For each of these species, we calculated the colour distance between sexes using the receptor-noise visual model (55,56). 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 noise-to-signal ratio in the signal processing. We calculated these distances in the chromatic portion of the spectrum only (56,57). Finally, we averaged the colour distances among patches to obtain a general measure of sexual dichromatism for each species (Fig. 1). All calculations were made in the R package *pavo* (58,59).

*Song complexity*

Data availability on hummingbird song is male-biased given that female vocalizations are rare, despite evidence of female vocalizations in a few species (47,60). Nonetheless, male song output has become a common indicator for the intensity of sexual selection (61), so we focused on male song. We collected recordings for 262 species from bioacoustics libraries and personal collections (see Supplemental 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 an undirected vocalization (not aimed towards nearby individuals) 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. Four parameters describing song complexity were calculated for each recording: element types, acoustic space, element transition diversity, and between-song variation (see supplementary methods for details on calculation). 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 (Fig. 1; Table S2).

*Altitude and habitat structure*

We used the Rangel et al. (62) 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 kept medium altitude only for further analyses. For habitat structure, we used the Parker III et al. (63) 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.

***Comparative analyses***

*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 (BPMMs) implemented in the R package *MCMCglmm* (64,65). 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. 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 of all runs and computed the median and High-Density Interval (HDI) of the pooled distributions. We used flat, uninformative distributions for the residuals and random effects covariance matrices as priors. Each model was run for 500000 generations, sampling every 300 generations with a burn-in of 10000 . We evaluated this configuration for convergence with a Gelman-Rubin diagnostic under 1.1 (66). Each set of models included as many species as possible with altitude and habitat structure data: 224 species for dichromatism, 107 for MD, 161 for TLD, and 213 for song complexity (Fig. 1).

*Correlation between traits*

To evaluate the relationship between dimorphic traits, we ran BPMMs with all the possible 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 as above 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. Models were run over the same sample of phylogenetic trees and summarised as the models above. 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. We exchanged the response and predictor for each model to ensure results remained consistent.

**Results**

*Altitude and habitat structure affect dimorphic traits*

. Morphological dimorphism decreased with increasing elevation (Fig. 2; posterior median = -0.59, 95% HDI: -1.09 – -0.09; Table S3), however, in mixed habitats the relationship between MD and altitude was positive. To determine if the MD association was attributable to either body size or wing length, we ran PGLS models with a lambda correlation with initial value of 1 between the log10 sex differences in body size, wing length, and folded wing length, and the same predictors as BPMMs. Wing measurements were corrected for size by dividing each trait by the cubic root of body mass. Results showed only one significant effect in the wing length model, which did not fully account for the results obtained in the MD BPMM (Table S4). To determine if increased sampling of species of the “Bee” clade (Fig. 1) would influence our results, we ran two additional sets of models using the AVONET (67) dataset only, and a combination of AVONET and our own (See supplementary methods for details). These models failed to find any significant associations with altitude or habitat structure, despite including more species of the “Bee” clade (Table S3).

Dichromatism also showed a significant relationship with elevation but only when considering habitat structure (Table S3). Dichromatism increased at higher elevations in open and mixed habitats, while it decreased with elevation for understorey species (Fig. 2). To rule out that the associations with dichromatism were produced mainly by the conspicuous colouration of the crown or gorget (i.e., the most dichromatic patches), we ran five additional BPMMs using only the dichromatism of each patch as response variable (Table S5). These models showed no significant associations for the crown or gorget, revealing that the association with altitude and habitat structure is not attributable to the most dichromatic patches. Song complexity showed a significant effect of habitat structure, regardless of altitude (Fig. 2B; posterior median = -0.4, 95% HDI: -0.77 – -0.02). Specifically, song complexity was lower in mixed habitats compared to the understorey. Conversely, TLD was not affected by altitude nor habitat structure (Fig. 2B; Table S3).

*Dimorphic traits are associated*

BPMMs between pairs of traits showed a significant positive relationship between dichromatism and song complexity (Fig. 3A, S2; posterior median = 0.24,95% HDI: 0.02 – 0.45; Table S6). This association remained positive even after removing the two most extreme points in the song complexity distribution (*Lampornis calolaemus* and *Elvira cupreiceps*, 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 and strength 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 (Fig. 3B-C), with a weaker association in the mantle (Table S7), implying that the most dichromatic patches are responsible for the association with song complexity. Additionally, a weak negative association was found between TLD and song complexity, when considering the interaction with altitude (Posterior median = -0.15, 95% CI: -0.29 – -0.02; Fig. S2; Table S6). We also found positive correlations between TLD and MD only when considering the interactions with altitude and habitat structure (Table S6). All other comparisons were non-significant with and without the interactions, including the AVONET models (Table S6; Fig. S2).

**Discussion**

We show that dimorphic traits of multiple signalling modalities are the result of a complex interaction between natural and sexual selection. We found that altitude and habitat structure influence evolutionary patterns of dimorphic traits. We also found that dichromatism and song complexity were positively associated, suggesting that sexually selected communication signals from different modalities could deliver complementary information. Conversely, tail length and song complexity were traded off, with a steeper negative association at high elevations. Our results provide evidence that sexual dimorphisms are associated to natural selection, and that some visual traits can evolve in concert with acoustic traits, consistent with a redundant signal hypothesis; while others evolve in a trade-off, in line with the transference hypothesis.

Altitude and habitat structure have been found to affect sexually dimorphic traits in other clades, for example, dichromatism in finches decreases with elevation (68,69). This was attributed to three factors: 1) colder nesting temperatures and fewer resources select for increased male parental care and therefore decreased polygyny, 2) harsh conditions at high elevations select for less elaborated plumages, and 3) lower predation pressure at high elevations allows for more conspicuous plumages (68). Hummingbirds are all polygynous (70), thus, neither increased male parental care or different mating systems (71) 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, warranting further study (72,73). The cost of plumage maintenance at high elevations due to UV and near-infrared exposure could also explain altitudinal variation in dichromatism (74–77), but further research is required to evaluate how colourfulness changes with elevation and the costs of maintaining structural colours at high altitudes. Also, predation pressure in hummingbirds is thought to be stronger in juveniles and females, due to the vulnerable nesting period (78); hence reduced predation pressure at high elevations (50) could explain our result of increased dichromatism in mixed and open habitats, through relaxed pressure against colourful male plumages.

Previous studies that have examined changes in morphological traits along ecological gradients have found important effects of altitude on morphological dimorphism (51,79). Our results show that hummingbird MD decreased with altitude regardless of habitat structure. In the species analysed here, morphological dimorphism 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 (51). We believe that including more species of this subclade would not change the patterns observed here, given the monophyly of the other subclades (40), and that a more detailed morphological dataset seems more important to detect the effect of ecological variables on overall morphological dimorphism.

Several studies on hummingbird flight have demonstrated that elevation strongly affects flight, imposing a selective pressure on displaying males (13,31,49). Our results agree with biomechanical studies on hummingbirds showing an increase in male wing size to compensate for lower air density at high elevations (9), with the additional insight that altitudinal effects on morphology also depend on habitat structure and resource availability (8). We showed that differences in size extend to other traits such as bill shape, which may be associated with resource specialization (8,80), and intra-sexual competition and aggressive interactions (6,7). In 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 (42). Although this contrasts with our models showing a positive association between MD and TLD when considering altitude and habitat, which agrees with a study showing a tight association between tail and wing length with changes in elevation (9,12). A non-negative association between altitude and TLD is exciting in terms of flight mechanics because it suggests that variation in tail length may not entail flight costs as much as assumed (81).

Habitat structure and its interaction with elevation have been documented to affect certain song properties, different from those studied here, with a study showing that low-frequency songs are common at higher elevations and in open areas (16). A recent study on hummingbirds showed that transmission of high-frequency vocalizations is affected by habitat structure (82). We show that habitat structure negatively affects song complexity, with songs being simpler in mixed habitats compared to the understorey. This pattern is consistent with the idea that habitat structure shapes the evolution of acoustic properties (i.e., the acoustic adaptation hypothesis). However, given the weak evidence in support for this hypothesis in other groups (15), further research is required into the critical distance in which habitat structure may become a limitation to song transmission and frequency (15,17).

We found a positive correlation between dichromatism and song complexity, regardless of habitat or altitude, and that the most dichromatic patches (crown and gorget) 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 (28,83), and several hypotheses have been proposed to explain the evolution of signal integration. The pattern shown here is particularly interesting given that it integrates distinct perception axes (visual, and auditory), and it could represent a case of evolution of redundant signals (39,84). 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 quality 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 (85). This relationship in hummingbirds contrasts with the one found in cardueline finches (86), where there is a trade-off between plumage ornamentation and song elaboration. Although we did not include a measurement of plumage colour complexity, these contrasting results could potentially be explained by higher colour compartmentalization in hummingbirds. Colour compartmentalization is common in many hummingbirds species, were specific patches are brightly coloured (crown and gorget) and associated with sexual selection, while others are drab and associated with crypsis which could be the result of strong sexual selection, in conjunction with other interacting forces such as natural selection (43,45).

Interestingly, we found an altitude-dependent trade-off between tail length dimorphism and song complexity. At higher altitudes the two traits are negatively correlated, while in lower altitudes the relationship is positive. Although this negative association at high altitudes can be interpreted as an example of the transference hypothesis (35,36), tail elaboration is milder at higher elevations (12), 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. This variation highlights the complexities of animal communication and reveals that different multi-modal strategies can be found even within groups.

Given the evidence presented here and in other studies, we believe sexual dimorphism should be considered as a product of pressures ranging from ecological differences between sexes (87) to differences as a result of sexual selection (7,88). Although a universal trait to indicate the strength of sexual selection has been a great desire in 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 (89). Nonetheless, tail length dimorphism 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 (71,90,91). Our results provide further evidence that 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 behaviour.

**Data accessibility**

Data and code to replicate analyses are available on GitHub (https://github.com/diegobelttran) and Dryad.

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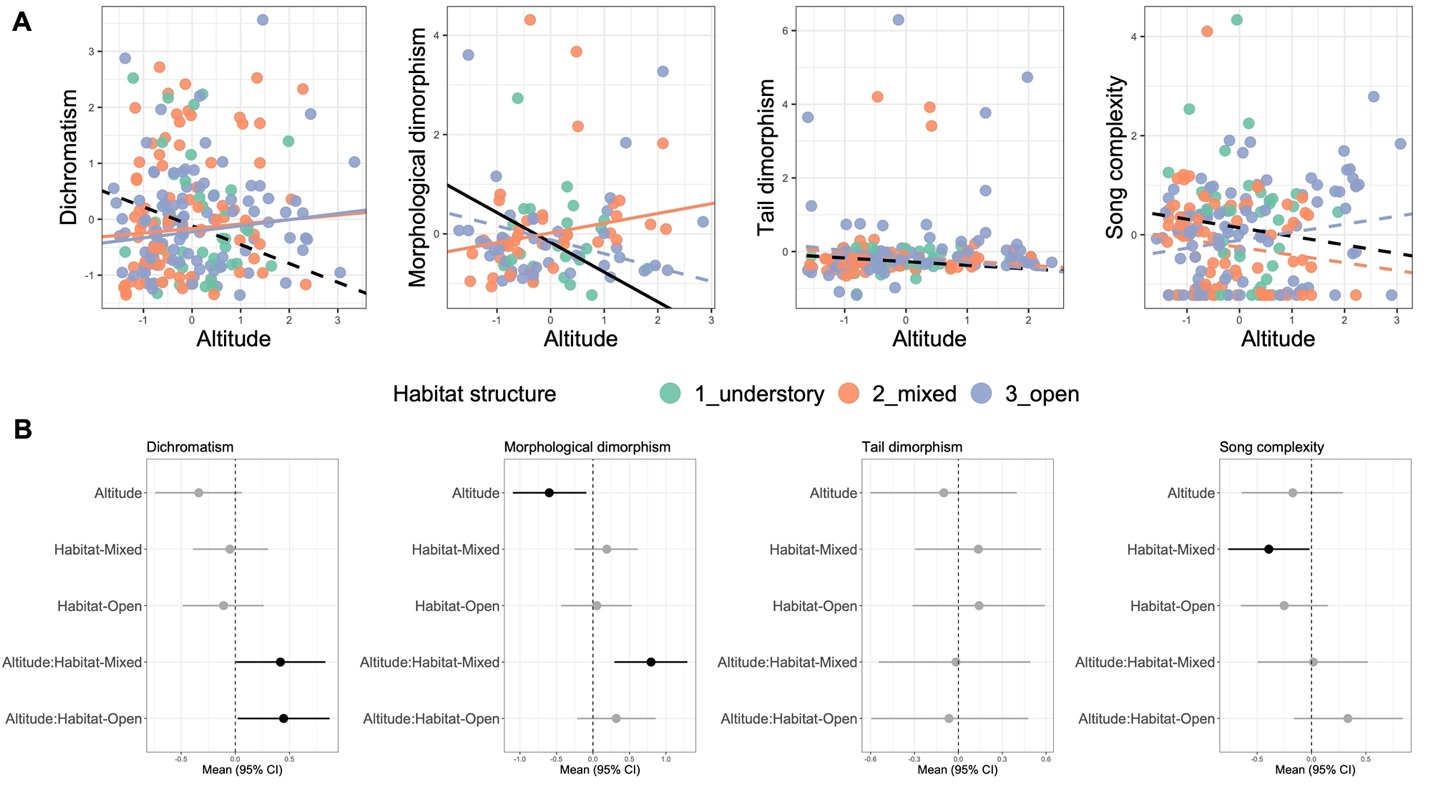
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**Figures**

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**Figure 1.** Distribution of hummingbird dimorphic traits. TLD was separated into male and female-biased (i.e., the predominantly larger sex), so that a species may only be one or the other. Song complexity was converted to a distance by summing the minimum value and adding 1 to all values to differentiate between minimum song complexity and missing data. All traits were then converted to percentages relative to each distribution. On the left, the full hummingbird phylogeny with branch lengths coloured according to the sum of all trait percentages to show species with the lowest (lightest) and highest (darkest) pooled values. On the right, barplots showing the sum of all percentages and the magnitude of each dimorphic trait for each species.Illustrations show the male and female of the species with the highest summed dimorphisms of each subclade. From bottom to top: *Topaza pella, Eutoxeres aquila* (only one illustration shown)*, Heliothryx barroti, Ocreatus underwoodi, Aglaiocercus coelestis, Lampornis calolaemus, Thaumastura cora, Chrysuronia oenone.* Permission to use illustrations will be requested upon manuscript acceptance.



**Figure 2.** Relationships between altitude and habitat structure with hummingbird dimorphic traits. (A) Scatterplots showing the relationship between altitude and each dimorphic trait. Altitude and habitat structure significantly affect dichromatism, morphological dimorphism, and acoustic complexity. Each dot represents a species and colours represent each type of habitat structure. Solid lines represent significant effects estimated by BPMMs, coloured according to type of habitat structure. Black lines represent altitude effects regardless of habitat structure. Dashed lines represent non-significant effects. Vertical and horizontal axes are standardized. (B) Model coefficients estimated by BPMMs show significant effects on dichromatism, MD, and acoustic complexity. 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.

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**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. (B) Relationship between crown dichromatism and song complexity. (C) Relationship between 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 (grey), and interaction with habitat structure relative to the understorey. Vertical and horizontal axes are standardized.