Evolution of song and color in island birds

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ABSTRACT—Island birds are often less colorful and sing different songs than their mainland counterparts. Given that trade-offs can occur in the expression of costly sexually selected traits, it is not clear whether island species with less colorful plumage than their mainland counterparts have compensated with increased complexity of song structure. To examine potential trade-offs in sexually selected traits in island birds, we examined concurrent patterns of coloration and song structure in island and mainland (sub)species across 3 widespread and speciose songbird families: Fringillidae, Meliphagidae, and Monarchidae. Phylogenetically controlled analyses revealed a shift away from white plumage and towards melanin-based plumage in island (sub)species but only in the Meliphagidae. Contrary to our predictions, we found no evidence that song structure in island birds differed from their mainland counterparts. Although a number of inverse correlations were identified between song structure and plumage coloration when all birds were considered, this pattern became weaker when only island populations were examined. Instead, we found island size affected song structure leading to a lower number of syllables and lower minimum frequency on smaller islands. Birds on smaller islands also had reduced carotenoid plumage but this pattern was only significant in the Fringillidae. These results indicate that island environments can influence the evolution of both song and color in some taxa, but that selection is tempered by island size, rather than through correlated evolution across signaling modalities.

Key words: evolution, island, ornament, sexual selection, trade-off

Islands have long fascinated evolutionary biologists because they act as natural, replicated experiments that can reveal parallel evolutionary mechanisms across taxonomic groups. Within vertebrates, an ‘insularity syndrome’ has been widely documented, with island populations exhibiting marked parallel changes compared to mainland counterparts. For example, the ‘island rule’ (Lomolino 1985, 2005) describes a trend towards dwarfism in large vertebrates and gigantism in small vertebrates on islands (but see Meiri et al. 2008, Durst and Roth 2012, Lomolino et al. 2013). Island populations also appear to experience parallel shifts in life histories towards *K*-selected reproductive traits, such as low fecundity, slow development, and high survival (Alder and Levins 1994, Novosolov et al. 2013). Less well-studied and well-understood, however, are apparent shifts in signaling systems such as coloration and vocal complexity.

Early studies on signaling in birds documented a preponderance of dull-colored species on islands (e.g., Grant 1965) although most surveys were restricted to small geographic areas, such as small island chains, or a small number of species (Figuerola and Green 2000, Fabre et al. 2012; but see Fitzpatrick 1998). Recently, Doutrelant et al. (2016) undertook an ambitious global analysis of bird coloration on closely related island and continental species-pairs and clearly demonstrated a reduction in brightness and intensity of coloration and reduction in the number of color patches in island species. The authors also found evidence of a positive relationship between the number of confamilial species and number of color patches, suggesting that a reduction in the number of closely related sympatric species on islands may reduce selection on species-recognition through plumage signals (Doutrelant et al. 2016).

If sexually selected traits, such as plumage coloration, are influenced by island effects, signals in other sensory modalities are likely to be similarly influenced. Song is an important inter- and intra-sexual signal in birds (Catchpole 1987) and may be similarly influenced by island effects (Baker 1996, 2006). Bird song is an evolutionary labile trait and intra-specific variation in bird song can be influenced by both inter- and intra-specific competition, habitat structure, and changes to the acoustic environment (Searcy and Yasukawa 1996, Badyaev and Leaf 1997). In one of the few broad-scale studies of song on islands, Morinay et al. (2013) demonstrated island-specific changes in song structure, including reduced occurrence of broadband song and putative aggressive song elements (rattles and buzzes) but increased bandwidth. Similar to the findings of Doutrelant et al. (2016) on plumage coloration in birds, Morinay et al. (2013) found that song structure also appears to be influenced by a decrease in the number of same-family sympatric species. This supports the hypothesis that a reduction in the number of closely related species on islands makes species recognition easier and lessens any constraints imposed on vocal signals in continental birds that are sympatric with a larger number of related species (the 'character release hypothesis;' Kroodsma 1985).

Although the colonization of islands appears to influence the evolution of both song and plumage in birds, whether these changes happen concurrently remains unknown. If the expression of sexually selected traits, such as increased song complexity (e.g., longer songs, larger repertoires, greater diversity of notes) and more elaborate plumage (e.g., increased number and size of carotenoid-based plumage patches, increased size of feather ornaments) are both condition-dependent (Hill 1991), island environments might favor a trade-off such that changes in one signal may be associated with changes in another signal. This trade-off has been observed in continental species of fringillid finches, in which song complexity was negatively related to elaboration of plumage ornaments (Badyaev and Weckworth 2002), although other researchers have found either the reverse pattern or none at all in other groups of birds (e.g., Matysiokova et al. 2017). Island birds might be especially subject to trade-offs between sexually selected condition-dependent signals if a reduction in resources on islands places greater energetic constraints on individuals than their counterparts in continental areas. For example, the impoverished food webs found on small islands could place greater nutritional challenges on colonizing birds, leading to trade-offs (Blanco et al. 2014). On the other hand, changes in both coloration and songs could occur without any trade-off if the costs of sexually selected traits are relaxed on islands; such alleviation of expression costs could be due to decreased predator numbers or changes in habitat structure that favor traits that increase detectability to conspecifics (Price et al. 1993, Shutler and Weatherhead 1990).

Here, we examine changes in both plumage coloration and song structure across 3 widespread, diverse, and ecologically distinct avian families: Fringillidae, Meliphagidae, and Monarchidae. Using phylogenetically controlled analyses, we predicted a reduction in plumage ornamentation (e.g., loss of color types) and changes in song structure (e.g., increased bandwidth) on islands as found by previous authors (Doutrelant et al. 2016, Morinay et al. 2013), but we also tested whether these changes occur concurrently or whether there is a trade-off between plumage coloration and song structure in island birds. Finally, because islands vary drastically in size, we asked whether island size was associated with song and color, with the prediction that island effects would be more intense on smaller islands.

Methods

Data collection

We collected color data for 731 species and subspecies. Of those, we were also able to collect song data from 145 species and subspecies. We collected data from species and subspecies within Fringillidae (n_{color} = 70 island, 265 mainland, n_{song} = 15 island, 41 mainland), Meliphagidae (n_{color} = 138 island, 87 mainland, n_{song} = 13 island, 23 mainland), and Monarchidae (n_{color} = 136 island, 35 mainland, n_{song} = 41 island, 12 mainland). For species list, see Table S6; for reference, there are 227 recognized species in Fringillidae, 187 in Meliphagidae, and 100 in Monarchidae (Rodewald 2020). These families were chosen because they are widely distributed globally, speciose, and have colonized many island systems on multiple occasions, providing replicates to examine patterns of change in the plumage and song of island birds.

Because we were unable to attain spectrophotomeric color measurements for island subspecies (see below), we examined plates from the Handbook of the Birds of the World, supplemented by photographs and field guides, to record the presence or absence (1/0) of 4 color classes (carotenoid, melanin, structural, white) on 5 body regions: head, back, breast, wings, and tail. Thus, each bird received a score from 0-5 for each color class; note that these scores were non-exclusive and body regions could be scored in multiple color classes (e.g., the black and yellow head of a male American goldfinch [*Carduelis tristis*] would receive a score of 1 for melanin, 0 for white, 1 for carotenoid, and 0 for structural). We scored females and males of each species separately.

We recognize that there are several limitations to our approach. First, scoring relies on human observation and there is a risk of misclassification, especially in terms of reddish hues. For example, though yellow, orange, and red plumage is typically produced by carotenoid pigments, reddish hues can also be produced by the deposition of phaeomelanins (though these are typically more ruddy; McGraw 2006a) or psittacofulvins, which produce a range of colors in parrots (McGraw 2006b), but not passerines. As such, it is possible that some body regions classified as containing carotenoid coloration were produced by other sources. Second, structural colors depend on the arrangement of pigments, such as melanosomes, in the feather microstructure; for our purposes, however, we classified iridescent, blue, purple, and green feathers as ‘structural’, as opposed to structural and melanin-based. Greenish coloration, however, which is produced by a combination of carotenoid pigments and structural properties (Prum 2006), was scored as both carotenoid and structural. It is important to also note that carotenoid coloration relies upon structural properties in order to produce colorful feathers (Shawkey and Hill 2005), but, for our purposes, red/orange/yellow putatively carotenoid-based coloration was only classified as ‘carotenoid.’ White coloration can also be considered a structural color (Igic et al. 2018), but, because the mechanism of production differs from typical structural colors, we classified it separately. Finally, we classified black/grey/brown/ruddy-reddish colors as a single group (‘melanin’) rather than separated by eumelanin (black) and phaeomelanin (rufous).

An ideal approach would be to measure plumage colors using spectrometry combined with models of avian vision (e.g., Doutrelant et al. 2016). However, we were primarily interested in subspecies on remote oceanic islands for which museum specimens are either limited, unavailable, or difficult to access. Thus, while we recognize the value of a spectrophotometric approach, it was not feasible for this study. An alternative approach for quantifying plumage color employed by Dale et al. (2015) was to score digitally scanned images from Handbook of the Birds of the World, which resulted in scores for nearly 6,000 passerines. Unfortunately, that analysis did not take into account subspecific variation, which was of primary interest in our study, and would have reduced our available sample by over 60% and not allowed us to address our questions. The advantage to our approach over that of Dale et al. (2015) is that the loss or gain of a small, but colorful, patch is more detectable than in an approach where color values are averaged over an entire bird. However, our analysis is not as sensitive as a spectrophotometric approach (*sensu* Doutrelant et al. 2016) that would reveal changes in hue (e.g., red to orange or yellow carotenoid-based coloration) or other aspects of avian color. As such, we consider our approach conservative; any patterns revealed should represent major changes in avian coloration (gains/losses in color types).

We were able to obtain song recordings for 145 (sub)species from Xeno-canto (www.xeno-canto.org). When possible, we obtained 5 recordings from each (sub)species and averaged values across recordings. Only male song was analyzed as recordings of female song were limited. We then used Avisoft-SASLab-Pro (Vs 5.2.13, Avisoft Bioacoustics, Germany) on a Hamming window with 1024 FFT length to extract the following information from the spectrogram of 1 song per recording: song length, minimum frequency, maximum frequency, bandwidth, number of syllables per song, and syllable rate (Fig. 1). Syllables were defined as temporally distinct elements, determined from visual inspection of a waveform/spectrogram combination of each song. Syllable rate was calculated by dividing the total number of syllables within a single song by the length of the song. Thus, a species with a low syllable rate produced fewer syllables per song. To obtain a metric of song complexity, we plotted the species-average Frequency Bandwidth across all syllables against average Syllable Rate (*cf*. Podos 2001) and calculated the residual score for each species. These residual scores provide a relative measure of modulation frequency of the song, which we use as an index of relative song complexity. We considered species with positive residual scores to have a higher frequency modulation than expected by their syllable rate as well as having a higher complexity score than species with negative residual scores (cf. Crouch and Mason-Gamer 2019 “modulation index”).

Information on island size and latitude was obtained from a variety of web sources, including the Island Directory (http://islands.unep.ch/isldir.htm) and Wikipedia pages for each island (http://wikipedia.org). For species that occur on more than 1 island in an archipelago, we used the total area of all islands to estimate the size of its range. Island size was transformed with the natural log prior to analysis. At this stage there is not enough known about the patterns of speciation in our sample to separate those (sub)species that are the result of a colonization event from those that are the result of adaptive radiation within an archipelago. However, our statistical analysis accounts for the non-independence of related species and does not assume that each island species represents a separate colonization event.

We did not consider the degree of island isolation from other nearby islands or to the nearest continent. Measuring degree of isolation is tricky as a simple distance is likely to be biased since some species are more mobile than others, the direction of prevailing winds can modify the 'ease' of colonizing islands, and as pointed out above, movement within archipelagos could also be a factor. Thus, for the present analysis we assumed that the degree of isolation was similar across taxa. As we restricted our analysis to taxonomically delineated subspecies and species on islands, islands with high levels of gene flow would by definition not be included if ongoing immigration was so high it would prevent the formation of distinct island morphologies.

Phylogenetic methods

We downloaded 10,000 possible phylogenies from birdtree.org (based on Jetz et al. 2012, 2014) for 731 species belonging to Fringillidae, Meliphagidae, and Monarchidae. We then used TreeAnnotator in BEAST v1.10 (Suchard et al. 2018) to construct a maximum clade credibility tree (the most probable tree) using a 1% burn-in and median node heights. Because the subspecific relationships for most taxa in our phylogeny remain unresolved, we subsequently added subspecies to each species, resulting in polytomies at the tips for species with multiple subspecies. To deal with issues arising from polytomies with branch lengths of zero, we used the multi2di function in the *phytools* v6.99 R package (Revell 2012) to randomly assign the arrangement of polytomies, with branch lengths set to 1e-6 of the total branch tree length. Phylogenies were created separately for the 731 species for which we had color data and the 145 for which we had song data. We also created 3 separate phylogenies for the different families for the color data. We used Pagel's λ (Harvey and Pagel 1991) as a measure of phylogenetic signal, which we obtained from the phylosig function in the *phytools* v6.99 R package (Revell 2012).

Statistical analysis

All analyses were conducted in R 3.6.3 (R Core Development Team 2017). To ask whether plumage coloration and song varied between islands and the mainland, we used phylogenetic ANOVA with 10,000 simulations using the *phytools* v6.99 (Revell 2012), *ape* v5.3 (Paradis and Schliep 2018), and *geiger* v2.0.6.2 (Harmon et al. 2008) R packages. For the color data, we analysed all the families together and then separately for each color type.

Next, we used a phylogenetic least-squares (PGLS) approach using the *nlme* v.3.1.145 package in R (Pinheiro et al. 2018) to test (a) whether there was a relationship between plumage coloration and song with an interaction of the family and (b) whether song or plumage coloration on islands were associated with island size (km^2). The latter analysis (b) was restricted to only (sub)species present on islands. The analyses to test the relationship between plumage coloration and song (a) included both mainland and island (sub)species and were repeated to only included island (sub)species. Figures were created using the *phytools* v6.99 (Revell 2012) and *ggplot2* v.3.2.1 (Wickham 2016) packages.

Results

Differences in color between island and mainland (sub)species

When we examined differences in plumage coloration between island and mainland (sub)species, we found no difference when considering all 3 families together (Table S1), but the phylogenetic signal λ was significant for every color (all $p < 0.001$) except for carotenoid in Monarchidae ($\lambda = 0.55$, $p = 0.064$). When analysing the families separately, only Meliphagidae showed differences in coloration between island and mainland (Table S1). For the Meliphagidae family, male birds on islands have significantly less white coloration than mainland species ($F = 26.7$, $p = 0.001$). For the females, island species have more melanin ($F = 16.82$, $p = 0.001$) and marginally more structural coloration ($F = 7.18$, $p = 0.051$) coloration, but less white coloration ($F = 18.55$, $p = 0.005$) than mainland species.

Differences in song between island and mainland (sub)species

We found no differences in song characteristics between island and mainland (sub)species for any song variable (Table S2): syllable rate: $F = 5.12$, $p = 0.58$), minimum frequency ($F = 1.07$, $p = 0.80$), maximum frequency ($F = 1.08$, $p = 0.83$), bandwidth ($F = 0.31$, $p = 0.89$), number of syllables ($F = 0.02$, $p = 0.98$), song length ($F = 0.96$, $p = 0.80$), or our measure of complexity ($F = 0.22$, $p = 0.98$). The phylogenetic signal λ was significant for every song characteristic (all $p < 0.001$).

Correlated evolution between color and song

For the analysis including both mainland and island (sub)species, we found an evolutionary association between color and song variables for the carotenoid and melanin colors only (SOM

Table S3 A, B). Carotenoid coloration was positively associated with song length ($t = 3.41$, $p = 0.0008$) and number of syllables ($t = 2.26$, $p = 0.03$). Carotenoid coloration was also negatively associated with maximum frequency for Meliphagidae ($t = -2.58$, $p = 0.01$), bandwidth for Meliphagidae ($t = -2.57$, $p = 0.01$), and song complexity for Meliphagidae ($t = -2.66$, $p = 0.009$). Melanin was positively associated with minimum frequency for Fringillidae ($t = 2.47$, $p = 0.01$). Melanin was also negatively associated song length for Monarchidae ($t = -2.47$, $p = 0.02$). For structural and white plumage coloration, we found no association with any song variable (SOM Table 3 C, D; all $p > 0.07$).

For the analysis including only the island (sub)species, we found an evolutionary association between color and song variables for the carotenoid and melanin colors only (SOM Table 4A, B). Song length and number of syllables were both positively associated with carotenoid coloration ($t = 3.43$, $p = 0.001$ and $t = 2.58$, $p = 0.01$, respectively). Carotenoid coloration was positively associated with number of syllables for Fringillidae ($t = 2.15$, $p = 0.035$) and Meliphagidae ($t = 2.20$, $p = 0.031$), with bandwidth for Monarchidae ($t = 2.34$, $p = 0.023$), and negatively associated with syllable rate for Meliphagidae ($t = -2.21$, $p = 0.03$). Melanin was positively associated with minimum frequency for Fringillidae ($t = 2.54$, $p = 0.013$) and negatively associated with song complexity for Fringillidae ($t = -2.01$, $p = 0.049$). For structural and white plumage coloration, we found no association with any song variable (Table 4C, D; all $p > 0.19$).

Color and song versus island size

No plumage colors were associated with the natural log of island size for the 3 families together (all $p > 0.13$), Meliphagidae (all $p > 0.094$), or Monarchidae (all $p > 0.094$) families (Table S5).

However, for Fringillidae, males on smaller islands were evolutionary associated with less carotenoid ($T = 2.37$, $p = 0.02$) and less white ($T = 2.47$, $p = 0.02$).

We detected significant relationships between island size and number of syllables ($t_{67} = 2.45$, $p = 0.02$) and minimum frequency ($t_{67} = 2.13$, $p = 0.04$), where birds on smaller islands sang songs with fewer syllables and lower minimum frequencies (Fig. S1). We detected no relationships between island size and syllable rate ($t_{67} = 0.99$, $p = 0.33$), song length ($t_{67} = 1.53$, $p = 0.13$), maximum frequency ($t_{67} = -0.02$, $p = 0.98$), bandwidth ($t_{67} = -0.09$, $p = 0.37$), or complexity ($t_{67} = -1.20$, $p = 0.24$).

Discussion

Our comparative analyses confirmed that the plumage of island Meliphagidae species differs from that of their continental counterparts. Island Meliphagidae species were characterized by a decrease in the extent of white colored plumage and, for females uniquely, there was an increase in melanin-based plumage. For the other families, our comparative analyses were unsuccessful in showing variation between island and mainland birds. Our results also did not indicate any changes in song characteristics between island and mainland birds. However, smaller islands were associated with a decrease in the number of syllables and minimum frequency of songs. Plumage characteristics were not associated with island size for Meliphagidae and Monarchidae, but carotenoid-based and white plumages were associated with increased island size for Fringillidae. We found multiple evolutionary associations between carotenoid and melanin plumages and song characteristics when all species (continental and island) were considered together, supporting the hypothesis that birds might trade-off signaling modalities, but the pattern was much weaker when restricted to just island species. These associations also varied among families and song characteristics.

One explanation for a change in plumage on islands is an expected reduction in the intensity of social and/or sexual selection in island populations of birds. The evolution of carotenoid coloration and other plumage ornaments through sexual selection is well supported by a variety of studies (reviewed in Hill 2006), and social selection may also be responsible for the evolution of some conspicuous signals (reviewed in: Senar 2006). Given that species diversity tends to be lower on islands, a reduction in number of sympatric species could select for less conspicuous signals for species recognition through both plumage and vocal modalities (Doutrelant et al. 2016). However, we found little evidence for a change in plumage colors, with only the Meliphagidae displaying less white (both sexes) and more melanin (females only) on islands. The loss of white and increase of melanin is likely to reduce contrast in plumage, which is consistent with a reduction in the need for conspicuous plumage signals on islands, but the lack of a similar pattern in the Fringillidae and Monarchidae indicates that the loss of plumage signals is not present in all families.

Contrary to our expectation, we did not find any differences in song structure between island and continental birds, even in the structures of song that have previously been found to differ in previous studies (e.g., bandwidth; Morinay et al. 2013). The reason for this difference is not clear. Due to a lack of recordings for many species in our sample (and particularly island populations), our metrics of song structure were necessarily simplistic. Other measures of song complexity, such as repertoire size, might provide a more realistic measure of song complexity (and intensity of sexual selection) but have been lacking from comparative studies of song in island birds. Recordings of female song were even less available and would also warrant further study (Riebel 2019), especially since female song is well developed in some island birds (e.g. New Zealand Bellbird [*Anthornis melanura*]; Brunton and Li 2006).

The downward shift in minimum frequency (but no change in maximum frequency) on smaller islands may be due to increased body mass in island birds; unfortunately, body mass measurements were unavailable for most island (sub)species and we were unable to test this hypothesis. Alternatively, this downward shift may also reflect a reduction in interspecific competition for acoustic space, as the risk of spectral overlap and interference from other species is reduced on islands with lower species diversity (Kroodsma 1985; Morinay et al. 2013). In contrast, population densities of island birds tend to be higher, suggesting insular species experience greater intraspecific competition and leading to an increase in *K*-selected life history traits (e.g., increased longevity, reduced rates of reproduction; Covas 2012).

The evolution of larger body size has also been proposed to be a direct adaptation to the increased intraspecific competition on islands (Clegg and Owens 2002), but as larger birds have lower pitched songs and syllable rates, traits posited as indices of quality (Ryan and Brenowitz 1985; Gil and Gahr 2002), changes in body size and song structure of island birds may be shaped by either sexual selection or competition. Clearly, reconciling how the effects of increased intraspecific competition, and reduced interspecific competition, affect the intensity of social and sexual selection is needed before we can understand why birds on smaller islands show changes in their song.

As both conspicuous plumage colors and elaborate song repertoires may be condition dependent traits in birds, and thus costly to produce, it might be expected that trade-offs would occur between these 2 modalities of communication under stressful conditions (Cooney et al. 2013). For example, if increased intraspecific competition on islands restricted resource availability to males, it may not be possible for individuals to elaborate both their plumage and song simultaneously, and selection may instead favor females to select mates based on only the most reliable traits. Such a situation could arise if a species with extensive carotenoid-based plumage colonized an island in which dietary sources of carotenoids were so rare or absent that such plumage could not be expressed and this favored a switch to mate choice based on songs as an indicator of male quality. In such a scenario, one would expect island birds to show an inverse relationship between plumage color and song elaboration, with species losing plumage colors showing increased complexity of their songs (and vice versa). Instead, we found associations between plumage and song characteristics varied among the families and these did not indicate a clear trade-off between song complexity and plumage coloration. For example, we found increased song complexity with a decrease of carotenoid coloration in Meliphagidae when comparing island and mainland birds, but we also observed an increase of number of syllables with an increase of carotenoid in Monarchidae.

The multiple associations we found do not go in the same direction and, as a result, do not support a consistent pattern of inverse trade-offs. This is similar to the lack of a trade-off found by Mason et al. (2014) in a comparative analysis of sexual signals in the tanagers (Family Thraupidae). It is possible both modalities are constrained, or that other selective pressures have favored the independent changes in plumage and song we observed, a conclusion also reached by Mason et al. (2014).

Our finding that songs became lower pitched (i.e., decrease in minimum frequency) with fewer syllables on smaller islands could also be explained by differences in the signaling environment of insular habitats compared to that inhabited by their continental relatives or (sub)species living on larger islands (Morton 1975, Derryberry et al. 2018). A decrease in minimum frequency is thought to be advantageous in dense forest habitats due to greater levels of attenuation of high frequencies (Wiley and Richard 1978). Unfortunately, information on forest structure is not available for most of the islands in our analysis, but as many of the continental species in both the Meliphagidae and Monarchidae are found in the eucalypt forests of Australia, a habitat that is generally more open than closed-canopy forests found on the nearby islands of Indonesia and the South Pacific, the difference in song structure may be due to this habitat difference rather than an island effect per se. Similarly, habitat may exert an influence on the evolution of plumage coloration; however, the shift away from white coloration in Meliphagidae on islands runs contrary to predictions based on the Light Environment Hypothesis, which posits that long-wavelength colors should be favored in more closed environments (Endler 1993). Measures of habitat structure need to be quantified before these hypotheses can be tested.

Island size only seemed to influence coloration in Fringillidae for carotenoid and white colors where species on bigger islands had more carotenoid and white colors. A decrease in carotenoid-based plumage traits on smaller islands may reflect a greater difficulty faced by birds in acquiring the necessary carotenoid precursors in the diet (Hill 1993). This could be due either to the lack of the appropriate sources (e.g., due to a lower diversity of plants and animals on small islands), or to the greater competition for the dietary precursors as a result of higher levels of intraspecific competition. The decrease in the extent of red plumage in House Finches (*Haemorhous mexicanus*) introduced to the Hawaiian Islands may be an example of this phenomenon; shortly after their introduction from the west coast of North America, the characteristic red wash over the head and breast of male house finches on the mainland was soon replaced by a pale yellow or orange in Hawaii (Hill 1993). Supplemental feeding experiments in the lab confirmed that a diet limited in carotenoids can reduce the extent of red in the plumage of male house finches (Hill 1993). If a similar reversion to brighter carotenoid-based plumage could be induced in birds on small island through food supplementation experiments, this would support the hypothesis that at least some of the changes in ornamentation are due to environmental constraints and not necessarily an adaptation to the insular environment.

Overall, we found a complex pattern of changes in plumage coloration and song structure between island and continental birds. In contrast to previous studies, changes in plumage or song signals were either not found, or if present restricted to just 1 or 2 families, suggesting that broad generalisations found in previous comparative studies may mask interesting patterns at lower taxon levels. As with previous studies, comparative analyses of island birds continue to suffer from a lack of data at all levels, restricting comparisons to crude indices of plumage and song, and again potentially masking more subtle patterns. Finally, our identification of island size as an important covariate in comparative studies highlights the need to not treat all islands equally as the selective pressures that drive changes in insular populations of birds may be the features of the islands themselves and these need to be considered in understanding how island birds may sometimes differ from their continental counterparts.

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Literature cited

Adler GH, Levins R. 1994. The island syndrome in rodent populations. Quarterly Review of Biology 69:473–490.

Avisoft Bioacoustics. 2017. Glienicke, Germany.

Badyaev AV, Hill GE, Weckworth BV. 2002. Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. Evolution 56:412–419.

Badyaev AV, Leaf ES. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. Auk 114:40–46.

Baker MC. 1996. Depauperate meme pool of vocal signals in an island population of singing honeyeaters. Animal Behavior 51:853–858.

Baker MC. 2006. Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection on songs. Ethology 112:757–771.

Blanco G, Laiolo P, Fargallo JA. 2014. Linking environmental stress, feeding-shifts and the ‘island syndrome’: a nutritional challenge hypothesis. Population Ecology 56:203–216.

Brunton DH, Li X. 2006. The song structure and seasonal patterns of vocal behavior of male and female bellbirds (*Anthornis melanura*). Journal of Ethology 24: 17–25.

Catchpole CK 1987. Bird song, sexual selection and female choice. Trends in Ecology and Evolution 2:94–97.

Clegg SM, Owens IPF. 2002. The ‘island rule’ in birds: medium body size and its ecological explanation. Proceedings of the Royal Society of London B 269: 1359–1365.

Cooney CR, MacGregor HEA, Seddon N, Tobias JA. 2018. Multi-modal signal evolution in birds: re-examining a standard proxy for sexual selection. Proceedings of the Royal Society of London B 285: 20181557.

Covas R. 2012. Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society of London: B 279: 1531–1537.

Crouch NMA, Mason-Gamer RJ. 2019. Identifying ecological drivers of interspecific variation in song complexity in songbirds (Passeriformes, Passeri). Journal of Avian Biology: e02020.

Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527: 367–370.

Derryberry EP, Seddon N, Derryberry GE, Claramunt S, Seeholzer GF, Brumfield RT, Tobias, JA. 2018. Ecological drivers of song evolution in birds: disentangling the effects of habitat and morphology. Ecology and Evolution. Doi: 10.1002/ece3.3760.

Endler JA. 1993. The color of light in forests and its implications. Ecological Monographs 63:1–27.

Doutrelant C, Paquet M, Renoult JP, Gregoire A, Crochet PA, Covas R. 2016. Worldwide patterns of bird colouration on islands. Ecology Letters. Doi: 10.1111/ele/12588.

Durst PAP, Roth VL. 2012. Mainland size variation influences informs predictive models of exceptional insular body size change in rodents. Proceedings of the Royal Society of London B 282: 20150239.

Fabre P-H, Irestedt M, Fjeldså J, Bristol R, Groombridge JJ, Irham M. Jønsson KA. 2012. Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (*Terpsiphone*, Monarchidae). Journal of Biogeography 39:1900–1918.

Figuerola J, Green AJ. 2000. The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. Functional Ecology 14:701–710.

Fitzpatrick S. 1998. Intraspecific variation in wing length and male plumage coloration with migratory behaviour in continental and island populations. Journal of Avian Biology 29:248–256.

Gil D, Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits. Trends Ecology and Evolution 17:133–141.

Grant PR. 1965. Plumage and the evolution of birds on islands. Systematic Zoology 14:47–52.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Hill GE. 1991. Plumage colouration is a sexually selected indicator of male quality. Nature 350:337–339.

Hill GE. 1993. Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). Biological Journal of the Linnean Society 49:63–86.

Hill GE. 2006. Female mate choice for ornamental coloration. In: Bird Coloration. Vol. 2. Function and Evolution (Ed. by GE Hill & KJ McGraw), pp. 137–200. Cambridge, Massachusetts: Harvard University Press.

Igic B, D'Alba L, Shawkey M. 2018. Fifty shades of white: how white feather brightness differs among species. Naturwissenschaften 105:3–4.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers O. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Jetz W, Thomas GH, Joy JB, Redding DW, Hartmann K, Mooers AO. 2014. Global distribution and conservation of evolutionary distinctness in birds. Current Biology 24:919–930.

Kroodsma DE. 1985. Geographic variation in songs of the Bewick's wren: a search for correlations with avifaunal complexity. Behavioral Ecology and Sociobiology 16:143–150.

Lomolino MV. 1985. Body size of mammals on islands: the island rule reexamined. The American Naturalist 125:310–316.

Lomolino MV. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

Lomolino MV, van der Geer AA, Lyras GA, Palombo MR, Sax DF, Rozzi R. 2013. Of mice and mammoths: generality and antiquity of the island rule. Journal of Biogeography 40:1427–1437.

Matysiokova B, Friedman N, Turcokova L, Remes V. 2017. The evolution of feather coloration and song in Old World orioles (genus *Oriolus*). Journal of Avian Biology 48:1015–1024.

Mason NA, Shultz AJ, Burns KJ. 2014. Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. Proceedings of the Royal Society of London B 281:20140967.

McGraw KJ. 2006a. Mechanics of Melanin-based Coloration. In: Bird Coloration. Vol. 1. Mechanisms and Measurements (Ed. by GE Hill & KJ McGraw), pp. 243–294. Cambridge, Massachusetts: Harvard University Press.

McGraw KJ 2006a. The mechanics of uncommon colors: pterins, porphyrins, and psittacofulvins. In: Bird coloration. Vol. 1. Mechanisms and measurements (Ed. by GE Hill & KJ McGraw), pp. 295–253. Cambridge, Massachusetts: Harvard University Press.

Meiri S, Cooper N, Purvis A. 2008. The island rule: made to be broken? Proceeding of the Royal Society of London B 275:141–148.

Morinay J, Cardoso GC, Doutrelant C, Covas R. 2013. The evolution of birdsong on islands. Ecology and Evolution 3:5127–5140.

Morton ES. 1975. Ecological sources of selection on avian sounds. The American Naturalist 109:17–34.

Novosolov M, Raia P, Meiri S. 2013. The island syndrome in lizards. Global Ecology and Biogeography 22:184–191.

Paradis E, Schliep K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–137.

Podos J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. Nature 409:185–188.

Price T, Schluter D, Heckman NE. 1993. Sexual selection when the female directly benefits. Biological Journal of the Linnean Society 48:187–211.

Prum RO. 2006. Anatomy, physics, and evolution of structural colors. In: Bird coloration. Vol. 1. Mechanisms and measurements (Ed. by GE Hill & KJ McGraw), pp. 354–397. Cambridge, Massachusetts: Harvard University Press.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Riebel K, Odom KJ, Langmore NE, Hall ML. 2019. New insights from female bird song: towards an integrated approach to studying male and female communication roles. Biology Letters 15: 20190059.

Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. The American Naturalist 126:87–100.

Shutler D, Weatherhead PJ. 1990. Targets of sexual selection: song and plumage of wood warblers. Evolution 44:1967–1977.

Searcy WA, Yasukawa K. 1996. The reproductive success of secondary females relative to that of monogamous and primary females in red-winged blackbirds. Journal of Avian Biology 27:225–230.

Senar JC. 2006. Colour displays as intrasexual signals in birds. In: Bird coloration. Vol. 2: Function and fvolution (Ed. by GE Hill & KJ McGraw), pp. 87–136. Cambridge, Massachusetts: Harvard University Press.

Shawkey MD, Hill GE. 2005. Carotenoids need structural colours to shine. Biology Letters 1:121–124.

Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut, A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evolution 4: vey016.

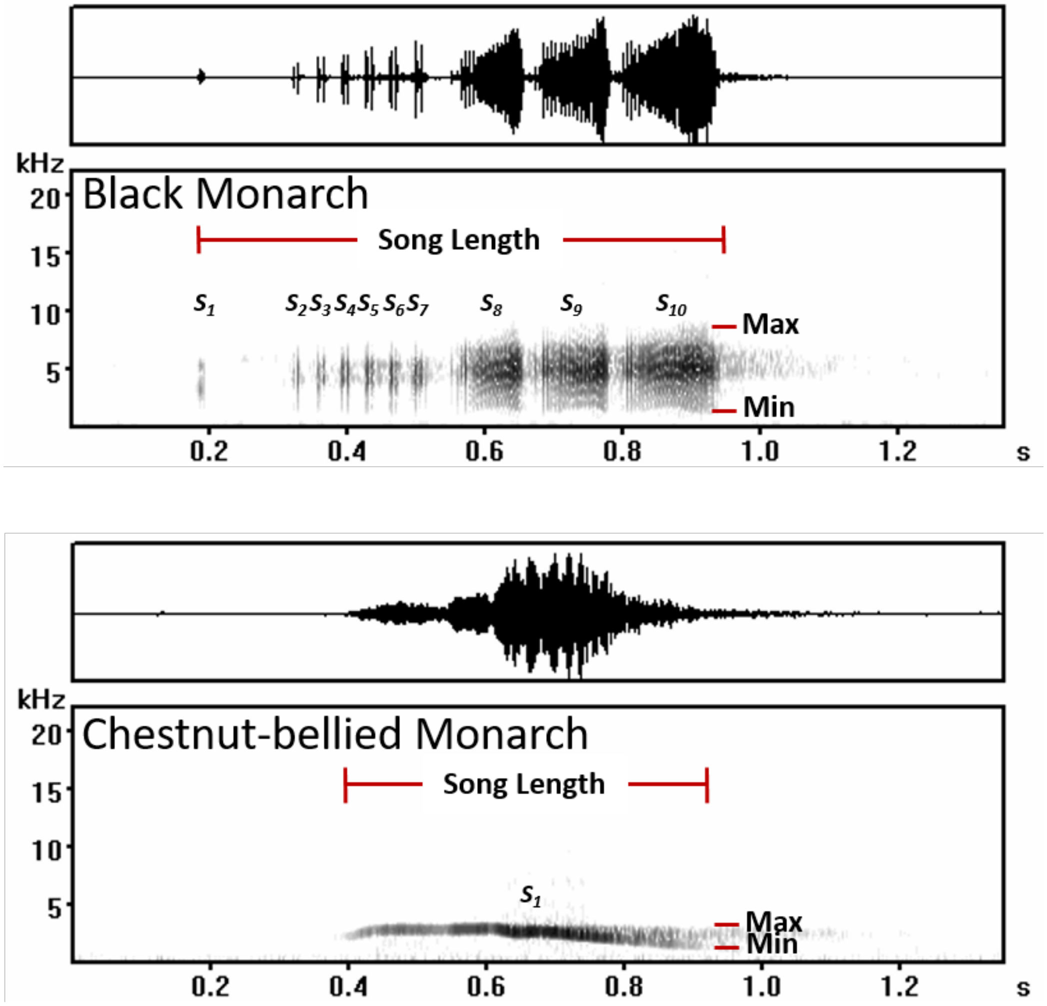
Wickham H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3: 69–94.

Figure legends

Fig. 1. Examples of 2 species in the Family Monarchidae, Black Monarchs (*Monarcha axillaris axillaris*) that occupy larger islands and Chestnut-bellied Monarchs (*M. castaneiventris obscurior*) occupying smaller islands. Song length(s) is measured from start of first distinct syllable in the song to the end of the last syllable—for single syllable songs song length equals syllable length. Number of distinct syllables were identified as continuous sound pulses in waveforms (S_1, S_2 etc). Maximum and minimum frequencies (Hz) were determined by examining the Power Envelope at all points along the syllables in SAS-LAB Pro, and the difference between maximum and minimum frequencies was calculated as the bandwidth (Hz).

Fig. 1


kHz
20
15
10
5
Black Monarch
Song Length
S_1
S_2 S_3 S_4 S_5 S_6 S_7
S_8
S_9
S_{10}
Max
Min
0.2
0.4
0.6
0.8
1.0
1.2
s
kHz
20
15
10
5
Chestnut-bellied Monarch
Song Length
S_1
Max
Min
0.2
0.4
0.6
0.8
1.0
1.2
s