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ISLAND LIVING REDUCES ORNAMENTAL PLUMAGE COLOURATION IN PASSERINES

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ISLAND LIVING REDUCES ORNAMENTAL PLUMAGE COLOURATION IN PASSERINES

by

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ABSTRACT

Island systems provide unique opportunities to explore patterns of plumage evolution. The few studies that have examined colour on islands have indicated a general pattern of reduced brightness, but this research is limited to restricted geographic areas and relatively few species. Here, I tested the hypothesis that island living results in a reduction in bird colouration across the order Passeriformes. To do so, I performed a phylogenetic comparative analysis with 5810 passerine species. Compared to mainland passerines, island females had higher overall plumage colouration scores, while island males showed had no difference in overall plumage colouration. There was no apparent change in the extent of sexual dichromatism. When I focussed on red and blue colour scores independent of the other colours, I found that both red and blue plumage colours were reduced in island passerines when compared to mainland species. These results may demonstrate a reduction in carotenoid and structural-based plumage in island birds, suggesting a relaxation in sexual selection pressures in island species.

Thesis Supervisor: Matthew Reudink

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occupation and passerine plumage colouration, using geographic ranges located in the Americas.

INTRODUCTION

Animal colouration provides important and complex signals used in both inter- and intraspecific interactions (Bradbury et al. 2000). Colour is thought to change in response to a variety of evolutionary mechanisms including natural selection, sexual selection, genetic drift, arbitrary mate preferences (Prum 2010), or some combination of these factors. It has also been shown to change as a direct response to environmental conditions (Hill 2006). In birds, plumage coloration varies widely among species (Peterson 1996), as does the degree of sexual dichromatism (Price et al. 1996), and colour signals play important roles in mate choice, species recognition, and predator avoidance (West-Eberhard 1983). As such, there is considerable interest in understanding the factors driving patterns of plumage colouration (Fitzpatrick 1998, Grant 1965, Figuerola et al. 2000, Roulin et al. 2010, Fabre et al. 2012, Doutrelant et al. 2016).

Island systems provide unique opportunities to explore patterns of plumage colouration. Islands are isolated, relatively small, and are repeated widely throughout the world, making them ideal systems to study the evolutionary processes that shape variation in traits (Bailey et al. 2015). A variety of "Island syndrome" studies have documented the parallel evolution of island vertebrates when compared to mainland populations (Lomolino 1985, 2005). According to the "island rule" (Foster 1964), body sizes in large vertebrates trend towards dwarfism while small vertebrates trend towards gigantism when compared to mainland populations (Meiri et al. 1998, Durst et al. 2012, Lomolino et al. 2013). Relative to their mainland counterparts, island vertebrates exhibit more K-selected life history strategies, including by lower fecundity, relatively longer developmental periods, and annual higher survival rates (Alder et al. 1994, Novosolov et al. 2013). In fact, most island studies have focussed on body size and life history traits, while the impact of island living on ornamental traits is less understood. The few studies examined avian colour on islands have indicated a general pattern of reduced brightness. However, most of this research is limited to restricted geographic areas and to only a relatively few species. (Grant 1965, Figuerola 2000, Fabre et al. 2012, but see Fitzpatrick 1998). A recent worldwide analysis by Doutrelant et al. (2016) compared the plumage colouration of 116 island species to that of closely related mainland birds and found a reduction in plumage brightness and colour intensity as well as a reduction in the number of colour patches in island species. Another large-scale study from Reudink et al. (in review) found that members of Meliphagidae shifted towards melanin-based plumage coloration and Fringillidae shifted away from carotenoid plumage on islands.

Several hypotheses have been developed to explain colour loss in island birds. First, island systems may contain fewer sympatric species (Grant 1965, Figuerola et al. 2000). If exaggerated color expression is under condition dependent sexual selection (Hill 1991), then island species may become less colourful because of reduced sexual selection pressure on islands (Figuerola et al. 2000, Botero et al. 2012). Sexual selection is predicted to be relaxed on islands because of reduced genetic diversity from founder effects (Frankham 1997) and/or reduced parasite pressure (Ishtiaq et al. 2012), either of which may diminish the indirect fitness benefits that may result from extra-pair copulations (Hamilton et al. 1982). The idea of reduced sexual selection pressure is supported by lower rates of extra-pair paternity rates in island species (Griffith 2000). Alternatively, predation pressure on islands is often lower (Beauchamp 2004) and this could promote elaboration of plumage colouration since camouflage is not as critical (Runemark et al. 2014, Bliard et al. 2020). Second, island species may show decreased territoriality in part due to fewer congeners, relaxed sexual selection pressure, and/or increased resource availability, possibly reducing the need to signal territory ownership during species interactions (Stamps et al. 1985).

Third, food resources on islands may differ from those on the mainland; if the diets of island birds are carotenoid-deficient this would reduce carotenoid-based (red, orange, yellow) plumage expression (Hill 1993).

Although several studies have documented colour differences between mainland and island bird populations using specific families or subsets of species (e.g., Doutrelant et al. 2016, Reudink et al. in review), no study has assessed this using an entire order of birds, calling into question the generalizability of the island syndrome for plumage coloration. Using a phylogenetic statistical framework, I tested the general hypothesis that bird colouration differs between mainland and island populations. I tested this hypothesis using Passeriformes, because in general, plumage colouration of this speciose order is ornate relative to other orders, and there is high variation in colouration among species. Specifically, I predicted that male and female passerines occupying islands would be less colourful and the increased reduction in male plumage colour would exhibit diminished sexual dichromatism than those occupying the mainland (*sensu* Doutrelant et al. 2016). In addition, because island size may influence species richness, resource availability and predation pressure (*sensu* Doutrelant et al. 2016, Bliard et al. 2020), I also tested the effect of island size on coloration using a subset of species in the American islands (North, Central, and South America).

MATERIALS AND METHODS

Data Collection

I collected island occupation data for 5810 passerine species and subspecies (Appendix). To do so, I used global range maps from the International Union of Conservation of Nature's Red List of Threatened Species (IUCN 2021) to determine ranges of extant native species. I then classified each passerine range as either mainland or island. I considered mainland to be a land mass larger or equal to 7.7 million km² or the size of Australia, the smallest defined continent (Weigelt et al. 2013). I also defined islands as smaller or equal to 2.2 million km² or the size of Greenland, the largest defined island (Weigelt et al. 2013; UNEP Island Directory1998). Passerines for which approximately 80% of the range covered a continent (such as North America or Australia) were classified as "mainland" species while passerines where 80% of the range covered smaller non-continental landmasses (such as the Hawaii islands or New Zealand) were classified as "island" species. If the predominant land type was less than approximately 80% of the total range, the passerine was considered "intermediate" and was categorized as "mainland." Although our method to categorize island versus mainland species may introduce statistical noise, this approach, if anything, should diminish any effects making the approach conservative.

I listed the islands occupied by each island species and compiled the average surface area of islands for each species. I used UN Environmental Programme island directory (UNEP Island Directory 1998) and the Google Earth-Measure Area tool to obtain the surface area of each island. I chose to focus on North and South American datasets since the Americas are understudied despite possessing a rich diversity of passerines.

Plumage colour was quantified using the methods of Dale et al (2015) using digitally scanned images from the Handbook of the Birds of the World to score plumage colour from six patches (crown, forehead, nape, throat, upper breast, and lower breast). Colour patch values were measured to obtain red-green-blue (RGB) values, in which each of the three scores range from a score of 0-255 and create a single colour dependent on relative differences between values. RGB values were corrected using similar coloured species within a RGB colour space and then averaged to provide a single plumage colour score for each passerine sex and species. I used the overall plumage colour scores to provide a measure of the general degree of colour elaboration regardless

of specific colour. Because carotenoid- and structural-based colouration produce colouration through different physiological mechanisms, I next used red and blue colour scores extracted from the RGB values generated by Dale (2015). I used red plumage colour scores since variation in carotenoid diet may produce diverse carotenoid-based colouration in passerines. I used blue colour scores due to the importance of short wave-length structural colours (e.g., blue, purple) for sexual signaling. I calculated the absolute difference between male and female plumage colour scores for each species assess sexual dichromatism.

Phylogenetic Methods

I downloaded 1000 potential phylogenies from birdtree.org (Jetz et al. 2012; 2014) for the 5810 passerine species and subspecies included in the dataset. I used TreeAnnotator in BEAST v1.10.1 (Suchard et al. 2018) to construct a maximum clade credibility tree using 1% burn in and mean node heights. I added subspecies to the tree as polytomies using R packages *ape* (Paradis et al. 2018) and *phytools* (Revell 2012). I repeated these steps with the 151 island passerines from North and South American that I used to examine the effect of island size.

Statistical Analysis

All analyses were performed using R 3.5.3 (R Core Team 2017). I used phylogenetic generalized least squares (PGLS), as my comparison method to control for control for evolutionary history. The PGLS from R package *ape* (Paradis et al. 2018), *nlme* (Pinheiro et al. 2018) and *geiger* (Harmon et al. 2008) were used to determine whether (a) there was a relationship between plumage colouration and island occupation, and (b) plumage colouration in island passerines is associated with island surface area (km²). Figures were created using the R package *phytools* and *ggplot* (Revell 2012).

RESULTS

Colour Differences Between Island and Mainland Passerines

I found no association between island occupancy and overall male plumage colour for passerines worldwide (Fig. 3, $F_{1,5534} = 1.85$, p = 0.16); however, when I examined red and blue colouration separately, I found that island males had both reduced red (Fig. 1, $F_{1,5534} = 37.11$, p < 0.0001) and blue (Fig. 1, $F_{1,5534} = 26.10$, p < 0.0001) colouration relative to mainland males. When examining female passerines, I found that island species on islands had higher overall colour scores than those on the mainland (Fig. 3, $F_{1,5534} = 43.54$, p < 0.0001). In addition, females similarly had reduced red plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 43.54$, p < 0.0001) and blue plumage colouration (Fig. 2, $F_{1,5534} = 19.32$, p < 0.0001) relative to mainland females. There was no relationship between the degree of sexual dichromatism and island occupation (Fig. 3, $F_{1,5534} = 1.17$, p = 0.31).

| Plumage | Plumage score | Average | Standard Deviation |
|---------------------|---------------|---------|-----------------------|
| Male | Red | 144.33 | 42.48 |
| | Blue | 106.95 | 42.48 |
| | All colour | 51.01 | 8.19 |
| Female | Red | 154.46 | 36.07 |
| | Blue | 111.93 | 39.83 |
| | All colour | 47.53 | 7.00 |
| Sexual dichromatism | All colour | 4.98 | 6.47 |

Table 1. Measures of dispersion and central tendency for world passerine species (n=5810).

| Territory | Plumage | Plumage score | DF | F | р |
|---------------|---------------------|---------------|--------|-------|----------|
| World | Male | Red | 15,534 | 37.11 | <0.0001* |
| | | Blue | 15,534 | 26.10 | <0.0001* |
| | | All colour | 15,534 | 1.85 | 0.16 |
| | Female | Red | 15,534 | 43.54 | <0.0001* |
| | | Blue | 15,534 | 19.32 | <0.0001* |
| | | All colour | 15,534 | 9.94 | <0.0001* |
| | Sexual dichromatism | All colour | 15,534 | 1.17 | 0.31 |
| Americas | Male | Red | 2403 | 8.21 | 0.0003* |
| | | Blue | 2403 | 5.53 | 0.004* |
| | | All colour | 2403 | 2.14 | 0.12 |
| | Female | Red | 2403 | 20.55 | <0.0001* |
| | | Blue | 2403 | 10.59 | <0.001* |
| | | All colour | 2403 | 5.25 | 0.0053* |
| | Sexual dichromatism | All colour | 2403 | 0.73 | 0.48 |
| *Indicates si | gnificance | | | | |

Table 2. Phylogenetic Generalized Least-Square (PGLS) analysis of the relationship between island and mainland passerine plumage colouration.



Figure 1. Plumage variation between island and mainland populations for (a) red colouration and (b) blue colouration in passerine species males. After controlling for phylogeny, there were relationships between males occupying islands and red colour score, as well as males occupying islands and blue colour score. Boxplots show range (whiskers), interquartile range (box), median (horizontal line, and outlier values (points).



Figure 2. Plumage variation between island and mainland populations for (a) red colouration and (b) blue colouration in passerine species females. After controlling for phylogeny, there were relationships between females occupying islands and red colour score, as well as females occupying islands and blue colour score. Boxplots show range (whiskers), interquartile range (box), median (horizontal line, and outlier values (points).



Figure 3. Plumage variation between island and mainland populations for (a) males, (b) females, and (c) dichromatism in passerine species. After controlling for phylogeny, there were no relationships between island and mainland plumage colour. Boxplots show range (whiskers), interquartile range (box), median (horizontal line), and outlier values (points).

Because I was interested in testing for the relationship between island size and plumage colouration in the Americas, I first tested whether the patterns observed in the worldwide passerine dataset also occurred in the Americas. Here again, there was no relationship between island occupancy and overall male plumage score ($F_{1,5534} = 2.14$, p = 0.12). As in the worldwide dataset, island males exhibited reduced red ($F_{2403} = 8.21$, p = 0.0003) and blue colouration ($F_{2403} = 5.53$, p = 0.004). Island females also exhibited reduced red ($F_{2403} = 20.55$, p < 0.0001) and blue colouration ($F_{2403} = 10.59$, p < 0.001), as well as overall plumage scores ($F_{2403} = 5.25$, p < 0.005). I found no relationship between sexual dichromatism score and island occupancy ($F_{2403} = 0.73$, p = 0.48).

Relationship Between Plumage Colour and Island Size

I found no relationships between overall plumage colouration scores and island size for males ($F_{150} = 0.09$, p = 0.77), or females ($F_{150} = 0.04$, p = 0.84), nor did I detect a difference in the degree of dichromatism ($F_{150} = 0.005$, p = 0.94). Similarly, there were no relationships between red and blue colour scores and island size (Table 3).

| Table | 3. | Phylogenetic | c Generalized | Least-Square | (PGLS) | analysis | of the | relationship | between |
|--------|-----|--------------|---------------|--------------|------------|------------|---------|--------------|-----------|
| island | siz | e occupation | and passerine | plumage colo | uration, u | using geog | graphic | ranges locat | ed in the |
| Ameri | cas | | | | | | | | |

| Plumage | Plumage score | DF | F | р |
|-------------|---------------|-----|-------|------|
| Male | Red | 150 | 0.58 | 0.45 |
| | Blue | 150 | 0.54 | 0.46 |
| | All colour | 150 | 0.09 | 0.77 |
| Female | Red | 150 | 0.28 | 0.60 |
| | Blue | 150 | 0.004 | 0.95 |
| | All colour | 150 | 0.04 | 0.84 |
| Dichromatic | All colour | 150 | 0.005 | 0.94 |

DISCUSSION

My phylogenetic comparative analysis demonstrated that the plumage colouration of island species differs from that of their mainland counterparts. Passerines exhibit reduced red and blue colouration for both male and female plumage, suggesting a reduction in carotenoid and structuralbased plumage in island birds. In contrast to other studies, however, female island passerines had an increase in overall colour score compared to mainland species. Surprisingly, there were no differences in the degree of sexual dichromatism between island and mainland birds. Contrary to our predictions, we did not detect any relationships between island size and plumage colouration.

The reduced red colour in island species suggests a reduction in carotenoid-based colouration. Since carotenoid-based colouration is obtained through the consumption, metabolic conversion, and deposition of carotenoid pigments, this reduction in colouration may reflect variation in diet rather than an adaptation to the island environment. The reduction in red colouration could be attributed to reduced availability of carotenoid precursors in the environment or reflect increased intraspecific competition for sources rich in carotenoid precursors (Hill 1993). For example, when introduced to the Hawaiian Islands, house finches (*Carpodacus mexicanus*), which typically exhibit a red head and breast patches, became orange or yellow soon after being established (Hill 1993). During supplemental feeding experiments, Hill (1993) replicated the loss of red plumage in male house finches using carotenoid restricted diets. As suggested by Reudink et al. (2021), dull island passerines should be able to re-establish carotenoid-based plumage if supplemented with carotenoid rich food.

In addition to the reduction in red colouration, I observed a reduction in blue colour in island species, suggesting a reduction in structural-based coloration. Doutrelant et al. (2016)

previously reported that the reduction in plumage brightness in island birds was not associated with increased black coloured plumage, such as through status signals like melanin-based badges (Tibbetts and Safran 2009, Uy and Vargas-Castro 2015), but rather was the result of a continuous shift toward duller colours. This due by increased melanin or carotenoid content in the feathers, both of which could create thicker keratin cortexes in feathers and reduce the incoherent scattering of light (Doucet et al. 2004) necessary for blue-shifted reflectance (Prum 2006). If our measures of blue coloration capture structural-based colours caused by feather nanostructure, our results may support the hypothesis that reduced brightness would also indicate loss of structural blue coloration. Further research will be needed to investigate the mechanisms of reduced blue colouration. Spectrometry analysis along with microscopy of feather nanostructure would elucidate this finding.

Another key finding from our study was the lack of difference in sexual dichromatism between island and mainland birds. This result is consistent with previous studies that examined between island and mainland birds using estimates of dichromatism (Grant 1965, Figuerola and Green 2000) and spectrophotometry (Doutrelant et al. 2016). This result is somewhat surprising, however, because sexual dimorphism in body is lower on islands (Raia et al. 2010); this result thus suggests that body size and colour are under different selection pressures. Relative to species-rich mainland communities, in the species-poor communities, found on many on islands, there may be less pressure to recognize conspecifics, resulting in selection for reduced plumage complexity (Seddon et al. 2008, Doutrelant et al. 2016).

The similarities in mating systems exhibited by mainland and island birds may help explain the lack of difference in sexual dichromatism. In passerines, socially monogamous mating systems with biparental care are commonplace (Lack 1968, Moller 1986). Monogamous breeders tend to

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be less dichromatic (Price and Eaton 2014) and island species are more likely to be monogamous (Sorci et al. 1998, Covas 2012). Island birds also invest more in parental care (Covas 2012), which may create a trade-off via diminished sexual signals (Figuerola 2000). Monogamous breeding coupled with biparental care may contribute to the observed dichromatism similarities between island and mainland birds. Future analyses should examine ecological, behavioural, and life history traits that may help explain plumage evolution in island systems.

Phylogenetic comparative studies, such as this, are important for understanding large scale evolutionary patterns. In this case, my results clearly demonstrate that across the Order Passeriformes, plumage colouration differs between island and mainland species. However, my results were not consistent with a simple shift towards reduced colouration (i.e., in overall colour score), but rather specific shifts in red and blue colouration. In addition, some patterns are perplexing, such as finding of higher female overall plumage colour on islands, which seems to contradict the island rule, and the lack of difference in sexual dichromatism between island and mainland species. This study provides a strong foundation for future studies regarding the role of island living on the evolution of colour in birds.

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APPENDIX

Island Signals Data Input

Data for this project is freely available as xlsx file: https://drive.google.com/file/d/1qtpfJD7J6hPf8qBBRDeKybxzIyoSHBj8/view?usp=sharing

Island Signals R Script

Code for this project is freely available as document and R-script file: https://drive.google.com/file/d/1-DILpdb9lMxtYneEUcVuJJHj6BCtY13R/view?usp=sharing

https://drive.google.com/file/d/1Em6B3VIIo__cM35--o9m49zAEVP9argu/view?usp=sharing