VOL. 197, NO. 5 THE AMERICAN NATURALIST MAY 2021

Rethinking Gloger's Rule: Climate, Light Environments, and Color in a Large Family of Tropical Birds (Furnariidae)

Rafael S. Marcondes,[1,*,†] **Jonathan A. Nations,**[1,*] **Glenn F. Seeholzer,**[1,2] **and Robb T. Brumfield**[1]

1. Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803;
2. Department of Ornithology, American Museum of Natural History, New York, New York 10024

Submitted April 18, 2020; Accepted November 6, 2020; Electronically published March 23, 2021

Online enhancements: supplemental PDF. *Dryad data:* https://doi.org/10.5061/dryad.cnp5hqc3d, https://doi.org/10.5061/dryad.s86434s.

ABSTRACT: Ecogeographic rules provide a framework within which to test evolutionary hypotheses of adaptation. Gloger's rule predicts that endothermic animals should have darker colors in warm/rainy climates. This rule also predicts that animals should be more rufous in warm/dry climates, the so-called complex Gloger's rule. Empirical studies frequently demonstrate that animals are darker in cool/wet climates rather than in warm/wet climates. Furthermore, sensory ecology predicts that, to enhance crypsis, animals should be darker in darker light environments. We aimed to disentangle the effects of climate and light environments on plumage color in the large Neotropical passerine family Furnariidae. We found that birds in cooler and rainier climates had darker plumage even after controlling for habitat type. Birds in darker habitats had darker plumage even after controlling for climate. The effects of temperature and precipitation interact so that the negative effect of precipitation on brightness is strongest in cool temperatures. Finally, birds tended to be more rufous in warm/dry habitats but also, surprisingly, in cool/wet locales. We suggest that Gloger's rule results from complementary selective pressures arising from myriad ecological factors, including crypsis, thermoregulation, parasite deterrence, and resistance to feather abrasion.

Keywords: Gloger's rule, light environments, Furnariidae, coloration, melanin, thermal melanism.

Ecogeographic rules describe correlations between organismal phenotypes and features of their environment. Their repeated observation across taxa and space is prima facie evidence that they are driven by common selective pressures (Mayr 1963; James 1991; VanderWerf 2012). Gloger's rule (Rensch 1929) is a long-standing ecogeographic rule describing correlations between the colors of mammals and birds and the climatic conditions they occupy. In its simplest version (Delhey 2017, 2019; Marcondes et al. 2020*b*), the rule states that animals tend to be darker in warm/rainy climates and brighter in cool/dry climates.

The prediction that animals should be darker in rainier climates has received widespread support in intraspecific (e.g., Burtt and Ichida 2004; Patten et al. 2004; Amar et al. 2014; Romano et al. 2019; Marcondes et al. 2020*b*) and interspecific (e.g., Kamilar and Bradley 2011; Delhey 2018; Stanchak and Santana 2018; Delhey et al. 2019; Miller et al. 2019; Cerezer et al. 2020) empirical studies (reviewed in Delhey 2019). In contrast, the prediction that animals should be darker in warmer climates has rarely been supported (reviewed in Delhey 2019). More often, it has been found that populations inhabiting warmer climates tend to be brighter than their counterparts from cooler locales (e.g., Rising et al. 2009; Amar et al. 2014; Delhey et al. 2019; Miller et al. 2019; Dufour et al. 2020; Marcondes et al. 2020*b*). This pattern has been dubbed Bogert's rule or the thermal melanism hypothesis and is often attributed to thermoregulatory advantages (Clusella Trullas et al. 2007; Rising et al. 2009; Delhey 2019).

Apart from climate, another major ecological axis to consider when investigating correlates of variation in animal color, particularly brightness, is habitat type, or light environment. Endler (1993) predicted that, to enhance crypsis, animals inhabiting dark light environments (e.g., the interior of dense forests) should be darker than those inhabiting open areas with bright ambient light (e.g., nonforest habitats), a prediction that has received wide support from comparative studies on birds (McNaught and Owens 2002; Gomez and Théry 2004; Dunn et al. 2015; Hernández-Palma 2016; Maia et al. 2016; Shultz and Burns 2017; Marcondes and Brumfield 2019). However, the joint effects of light environment and climate on color variation have yet to be tested. The relative roles of climate, light

---

[*] Served as co–lead authors for the project.

[†] Corresponding author; email: raf.marcondes@gmail.com.

ORCIDs: Marcondes, https://orcid.org/0000-0002-1242-3217; Nations, https://orcid.org/0000-0002-1170-7656; Seeholzer, https://orcid.org/0000-0003-1337-2084; Brumfield, https://orcid.org/0000-0003-2307-0688.

Am. Nat. 2021. Vol. 197, pp. 000–000.
DOI: 10.1086/713386

environment, and their interaction on color variation remain enigmatic.

A further poorly studied aspect of Gloger's rule (hereafter, simply "Gloger's") is its so-called complex version (Delhey 2017, 2019; Marcondes et al. 2020*b*). Whereas the simple version of Gloger's makes predictions relating to overall melanin content, its complex version makes predictions about the ratio of pheomelanins to eumelanins. Eumelanins confer black and gray colors, and pheomelanins confer brown and rufous colors (Galván and Wakamatsu 2016). Complex Gloger's predicts that eumelanins prevail in warm/humid climates and pheomelanins prevail in warm/dry climates, so that animals tend to be gray or black in the former and brown or rufous in the latter (Delhey 2017, 2019; Marcondes et al. 2020*b*). This version of Gloger's has historically received little attention (but see Roulin and Randin 2015) until it was revived by Delhey (2017, 2019). It was recently tested by Marcondes et al. (2020*b*), who found clear support for it at the intraspecific level in *Thamnophilus caerulescens* (Passeriformes: Thamnophilidae). Noting that drier areas tend to have redder soils (Brady et al. 2008; Donald et al. 2017) and browner, sparser vegetation, Marcondes et al. (2020*b*) suggested background matching as a tentative adaptive explanation for complex Gloger's.

The present study represents, to the best of our knowledge, the first study to jointly analyze plumage color variation in relation to both climate and light environments within the same modeling framework. It is also the first interspecific phylogenetic test of complex Gloger's. We investigate the effects of climate and light environment on plumage brightness (a proxy for overall melanin content) and redness (a proxy for relative pheomelanin content) of the Neotropical endemic passerine family Furnariidae (the woodcreepers, ovenbirds, foliage gleaners, and allies). This family is well suited for this work because (1) furnariids are found at extremes of both precipitation and temperature, from the warm and rainy Amazonian rain forests to warm and arid Chaco savannas and from cool and dry high-elevation puna grasslands to cool and rainy Andean cloud forests (Remsen 2003; Brumfield 2012); (2) furnariids occupy every Neotropical terrestrial biome and habitat type, including a large variety of light environments (Remsen 2003; Brumfield 2012); and (3) furnariids are festooned almost exclusively in countless shades of brown and rufous (Remsen 2003) that, while quite variable, are presumably all melanin based and generated by variation in eumelanin and pheomelanin content (for the few exceptions, see Thomas et al. 2014). For example, furnariid colors range from light and creamy brown in the puna- and desert-inhabiting *Ochetorhynchus* earthcreepers to dark and rich brown in some species of tropical rain forest–dwelling *Xiphorhynchus* woodcreepers.

If Gloger's is driven primarily by climate, then we predict that species inhabiting warm/rainy climatic regimes are darker than those from cool/dry regimes, regardless of their habitat preference. In contrast, if Gloger's is mainly a result of birds adapting to be darker in darker (forest) habitats, then we predict that bird species occupying forest habitats are darker than their non-forest-based relatives, even if they inhabit similar climatic regimes. Marcondes and Brumfield (2019) previously demonstrated that furnariids have evolved to be darker in darker habitats, consistent with Endler's (1993) predictions for crypsis, but the analyses did not include the effects of climatic variables on brightness. Testing for complex Gloger's, we further predict that species occupying warm/dry climates should be colored in richer, more reddish-brown tones than those from cool/rainy climates (Delhey 2017, 2019; Marcondes et al. 2020*b*).

Methods

Color Data

We used the color data set previously described in Marcondes and Brumfield (2019), which has been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.s86434s; Marcondes and Brumfield 2021). Briefly, this data set includes reflectance data for 250 (84%) furnariid species, with an average of 6.4 specimens per species (range: 1–8). For each specimen, this data set includes reflectance spectra from seven plumage patches divided into a dorsal (crown, back, rump, and tail) and a ventral (belly, breast, and belly) set. We calculated plumage brightness in the R package pavo (Maia et al. 2013, 2019) as the mean percent reflectance over the 300–700-nm spectral range. We calculated redness as the slope of the regression of percent reflectance on wavelength, a parameter that is positively correlated with pheomelanin content (Galván and Wakamatsu 2016). We follow Marcondes et al. (2020*b*) in referring to this variable as "redness," although we note that no furnariids display highly chromatic red colors typically produced by carotenoid pigments. Even the "reddest" furnariid would be referred to in lay language at most as "rich brown" or "reddish brown" (e.g., *Synallaxis kollari* and *Megaxenops parnaguae*). We calculated brightness and redness for each specimen in our data set and then averaged them across specimens to obtain mean species-level values. Because the Furnariidae are sexually monochromatic with no evidence of cryptic sexual dichromatism (Remsen 2003; Tobias et al. 2012; Diniz et al. 2016; Marcondes and Brumfield 2019), we considered the sexes together in our analyses. Our color data set for downstream analyses thus consisted of 14 variables: mean species-level brightness and redness for each of seven plumage patches.

Habitat and Climatic Data

We used Marcondes and Brumfield's (2019) categorization scheme of habitat types, which is based on Endler's (1993) discussion of natural light environments. In brief, each of the 250 furnariid species we analyzed was assigned to one habitat type, in decreasing order of ambient light intensity: nonforest, intermediate, and forest. The forest category includes only species that occupy the dimly lit middle and lower strata of rain forests; we assigned canopy and edge species to the intermediate category because these areas are more intensely illuminated than the forest interior (Endler 1993; Marcondes and Brumfield 2019).

To obtain climatic data for each furnariid species, we used the georeferenced locality records data set of Seeholzer et al. (2017). This extensively vetted data set contains 23,588 occurrence records (average = 70.4 records/species) gathered from museum specimens, audio recordings, and observational records. For each locality, we obtained mean annual temperature and mean annual precipitation from the BioClim database (Hijmans et al. 2005), and for each species, we took the median of temperature and precipitation across all its occurrence localities. Because of their different magnitudes and units (°C for temperature and mm/yr for precipitation), we scaled each climatic variable to have a mean of 0 and a standard deviation of 1 before fitting any statistical models (see below). The Furnariidae occurrence and climatic data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.cnp5hqc3d; Marcondes et al. 2020*a*)

Statistical Analyses

To test our hypotheses regarding the effects of climate and habitat on plumage brightness in the Furnariidae, we fitted a series of phylogenetic Bayesian multilevel linear models using the modeling software Stan (Carpenter et al. 2017) as implemented in the R library brms (Bürkner 2017). This Bayesian multilevel model framework allowed us to fit linear models with multiple predictor variables (Gelman 2006; McElreath 2016), use regularizing priors that minimize false discovery (Gelman and Tuerlinckx 2000; Gelman et al. 2012), and include group-level effects that incorporate the error from the statistical nonindependence of species data due to shared phylogenetic history (de Villemereuil and Nakagawa 2014; Bürkner 2017). Our models include redness and brightness of each plumage patch as response variables, climate and habitat data as population-level predictor variables, and the phylogenetic correlation matrix—a species-level matrix of scaled phylogenetic branch lengths from the phylogeny of Harvey et al. (2020)—as a single group-level predictor (de Villemereuil et al. 2012; Bürkner 2017).

We first tested the hypothesis that brightness and redness are primarily driven by climate. Under this hypothesis, we expect that species occupying warm/wet locales will be darker than those from cool/dry locales and that species from warm/dry locales will have a richer, redder color than those from cool/rainy climates, regardless of light environment (Rensch 1929; Delhey 2017, 2019). We fitted seven phylogenetic multivariate linear regression models for brightness—one per plumage patch—and seven for redness (table 1). Model 1 estimates the effect of precipitation, temperature, and the interaction parameter of precipitation and temperature on brightness or redness. Because redness and brightness are calculated from the same spectral curve, these variables may not be independent. We accounted for this correlation by including redness as a predictor in the brightness models, and vice versa (see table 1). Each of the models included four chains run for 10,000 generations with 5,000 generations of warm-up and 5,000 chains of sampling. We assessed chain convergence using the Gelman-Rubin diagnostic $\hat{R}$, and we assessed chain efficiency using effective sample size (ESS). Values of $\hat{R} < 1.01$ and ESS > 400 (100 per chain) represent acceptable convergence and mixing in Stan (Stan Development Team 2018).

We also tested the hypothesis that plumage brightness and redness are dependent on light environments regardless of climatic variables. Under this hypothesis, we expect species occupying forest habitats to be darker than those inhabiting nonforest habitats, even if the nonforest species are in warmer/rainier climates. Specifically, we separated the effects of habitat from the effects of climate by fitting a phylogenetic multiple regression model with brightness or redness as our response and temperature, precipitation, and the categorical habitat as predictor variables (model 2; table 1). As in model 1, we included our phylogenetic correlation matrix as a group-level effect. Model 2 generates three population-level outcomes: (1) the effect of precipitation on plumage brightness or redness, conditioned on the influence of temperature, habitat, and phylogeny; (2) the effect of temperature on plumage brightness or redness, conditioned on precipitation, habitat, and phylogeny; and (3) a posterior distribution of the mean plumage brightness or redness value of each light environment, conditioned on the phylogenetic relationships and the effects of precipitation and temperature. To determine whether plumage color values differ between light environments, we calculated the difference between each habitat's brightness and redness estimates (i.e., contrasts [nonforest-intermediate, nonforest-forest, intermediate-forest]; Kruschke 2013; McElreath 2016; Roycroft et al. 2019) using the compare_levels function in the R library tidybayes (Kay 2020). If ≥95% of the difference distribution does not overlap zero, then we can confidently say

Table 1: Descriptive summary of our models 1, 2, and 3 demonstrating the role of redness and brightness as response variables, climate and habitat as predictors, and the phylogenetic covariance matrix as the group-level predictor

Model	Response	Population-level predictors	Group-level predictor
Brightness models 1	Patch brightness	Temperature, precipitation, temperature × precipitation, redness	Phylogenetic covariance matrix
Redness models 1	Patch redness	Temperature, precipitation, temperature × precipitation, brightness	Phylogenetic covariance matrix
Brightness models 2	Patch brightness	Temperature, precipitation, light environment	Phylogenetic covariance matrix
Redness models 2	Patch redness	Temperature, precipitation, light environment	Phylogenetic covariance matrix
Brightness null models	Patch brightness	. . .	Phylogenetic covariance matrix
Redness null models	Patch redness	. . .	Phylogenetic covariance matrix

Note: The null models tested the hypothesis that redness and brightness are influenced simply by phylogeny and not climate or habitat.

that plumage differs between those habitats. As in model 1, we used regularizing priors, fitted all models in a single multivariate model framework, ran four chains of 10,000 generations, and checked for convergence with $\hat{R}$ and ESS.

As a null model, we also fitted intercept-only phylogenetic multilevel models for each patch's brightness and richness (model 3; table 1). These models have no predictor variables and only estimate the intercept of the group-level effect, in our case the phylogenetic correlation matrix. Comparing with the null model allowed us to verify that precipitation, temperature, and habitat improved the predictive ability of our models rather than phylogeny alone explaining differences in brightness and richness. Model comparison also allowed us to assess whether the climate interaction model or the climate and habitat model was a better predictor of our brightness data. We performed model comparison of our three models using the difference in expected log predictive density (ELPD) from the Watanabe-Akaike information criteria (WAIC; Watanabe 2010) using the waic() function in the R package loo (Vehtari et al 2018). WAIC is recommended as an appropriate choice for Bayesian linear modeling (Gelman et al. 2013).

Results

All Bayesian multilevel models converged properly, and all parameters had $\hat{R} < 1.01$ and ESS > 2,000. Results of model 1 showed a strong negative effect of precipitation on brightness in all dorsal patches (table 2; fig. 1), indicating that as precipitation increases, dorsal plumage gets darker, as predicted by Gloger's. Model 1 also showed a strong positive effect of temperature on crown, back, rump, and breast brightness (table 2; fig. 1), demonstrating that as temperature increases, plumage gets brighter, contra Gloger's but consistent with Bogert's rule. Precipitation had no effect on the redness of any plumage patch, and temperature had a positive effect only on tail redness (table 2; figs. 1, S1; figs. S1, S2 are available online).

We found a positive interaction between temperature and precipitation on crown, back, and rump brightness. This interaction means that precipitation has a stronger negative effect on brightness in colder temperatures than in warmer temperatures (table 2; figs. 1, 2, S1, S2). In other words, the precipitation component of Gloger's is more notable in species living in cool habitats than species living in warm habitats. Our findings for redness are similar but opposite: we found a negative interaction between temperature and precipitation on back, rump, and tail redness. These interactions demonstrate that precipitation has a more positive effect on redness in colder temperatures than in warmer temperatures. This interaction is especially strong on back and rump redness, enough to change the direction of the effect of precipitation on redness from negative to positive depending on the temperature (fig. 1*C*).

Model 2 estimated the posterior distributions of mean plumage brightness for each habitat, conditioned on phylogenetic effects and climatic variables (table 3; fig. 3). We found that birds living in nonforest habitats have brighter backs, rumps, throats, breasts, and bellies than birds in forest or intermediate habitats (fig. 3). Birds in forest and intermediate habitats have similar brightness in all patches except the back, where intermediate species' brightness lies between nonforest and forest species (fig. 3).

Redness differed far less between habitats than brightness. Only in the back were forest and intermediate birds redder than nonforest birds (fig. 3). In addition, birds in intermediate habitats had redder rumps and tails than either forest or nonforest birds. Ventral redness did not reliably differ between habitats.

We used the ELPD scores of the WAIC analysis to compare models 1 and 2 with the null model. We found that models 1 and 2 predicted plumage brightness and redness better than the null model for all patches (table S1, available online). Model 1, which did not include habitat, better predicted rump, throat, and breast brightness, while model 2 better predicted crown and tail brightness. Model 1 better

Table 2: Mean parameter estimates from brightness and redness models 1, with standard errors in parentheses

	Intercept α	Precipitation β	Temperature β	Temperature × precipitation β	Redness	Error σ	Phylogenetic error (SD)
Brightness models 1:							
Crown	.06 (−.28 to .41)	**−.24** **(−.33 to −.15)**	.06 (−.04 to .16)	**.14** **(.06 to .22)**	.75 (.68 to .83)	.47 (.41 to .53)	.50 (.35 to .65)
Back	.09 (−.39 to .57)	**−.31** **(−.40 to −.21)**	**.14** **(.04 to .24)**	**.18** **(.09 to .26)**	.54 (.47 to .61)	.39 (.33 to .44)	.75 (.63 to .88)
Rump	.04 (−.52 to .6)	**−.23** **(−.33 to −.14)**	**.23** **(.12 to .34)**	**.14** **(.05 to .23)**	.55 (.48 to .63)	.34 (.28 to .40)	.91 (.78 to 1.03)
Tail	.22 (−.25 to .71)	**−.08** **(−.16 to .00)**	−.03 (−.13 to .06)	.06 (−.02 to .14)	.86 (.79 to .93)	.31 (.25 to .37)	.77 (.66 to .89)
Throat	.21 (−.36 to .78)	**−.1** **(−.19 to −.01)**	−.07 (−.18 to .03)	−.03 (−.12 to .05)	.70 (.62 to .77)	.32 (.26 to .38)	.92 (.79 to 1.05)
Breast	−.12 (−.62 to .37)	**−.15** **(−.24 to −.06)**	.04 (−.06 to .15)	**.09** **(.00 to .17)**	.66 (.59 to .74)	.39 (.33 to .45)	.78 (.63 to .92)
Belly	−.12 (−.53 to .3)	**−.07** **(−.15 to .00)**	**.10** **(.01 to .18)**	.03 (−.04 to .10)	.72 (.66 to .78)	.32 (.27 to .38)	.63 (.51 to .76)

	Intercept α	Precipitation β	Temperature β	Temperature × precipitation β	Brightness	Error σ	Phylogenetic error (SD)
Redness models 1:							
Crown	−.13 (−.61 to .35)	.05 (−.04 to .14)	−.03 (−.13 to .07)	−.07 (−.15 to .01)	.75 (.68 to .82)	.37 (.32 to .43)	.75 (.62 to .88)
Back	.03 (−.52 to .58)	.01 (−.10 to .12)	.06 (−.06 to .19)	**−.16** **(−.26 to −.07)**	.74 (.64 to .83)	.44 (.36 to .53)	.87 (.69 to 1.05)
Rump	.13 (−.41 to .68)	−.08 (−.19 to .03)	.09 (−.03 to .22)	**−.13** **(−.23 to −.04)**	.65 (.56 to .75)	.44 (−.37 to .52)	.84 (.68 to 1.01)
Tail	−.11 (−.58 to .36)	.01 (−.06 to .08)	**.11** **(.03 to .20)**	**−.12** **(−.19 to −.05)**	.72 (.65 to .78)	.26 (.20 to .32)	.75 (.65 to .85)
Throat	−.08 (−.58 to .41)	.02 (−.07 to .12)	.09 (−.02 to .20)	.00 (−.09 to .08)	.68 (.61 to .76)	.41 (.34 to .49)	.76 (.60 to .92)
Breast	−.05 (−.37 to .28)	−.02 (−.12 to .08)	.09 (−.02 to .20)	−.04 (−.12 to .05)	.74 (.67 to .82)	.54 (.49 to .60)	.45 (.37 to .53)
Belly	.05 (−.36 to .45)	−.04 (−.12 to .04)	.00 (−.09 to .09)	−.02 (−.09 to .06)	.85 (.78 to .92)	.38 (.33 to .43)	.62 (.48 to .76)

Note: For each model, α is the intercept, βs are population-level effects and their interactions, σ is the residual error in the model, and phylogenetic error is the error in the model attributed to the phylogenetic correlation matrix. Population-level predictors in bold have a 95% credible interval that does not overlap zero, which we consider a robust result.

predicted back redness, while model 2 better predicted crown, tail, throat, and breast redness. In the remaining patches, the standard error of the ELPD scores of models 1 and 2 overlapped, leaving the model comparison ambiguous (table S1).

Discussion

Gloger's is a long-standing ecogeographic principle predicting that birds and mammals that inhabit warmer/rainier climates tend to be darker than their counterparts (intra- and interspecific) in cooler/drier places (Gloger 1833; Rensch 1929; Mayr 1956, 1963; Delhey 2017, 2019). Here, we found strong support in the Furnariidae for the predicted relationship between brightness and precipitation. In contrast, we found that furnariid species tended to be darker in cooler climates, contrary to the second prediction of Gloger's but consistent with a pattern dubbed Bogert's rule or thermal melanism, which is often observed in ectothermic animals (Clusella Trullas et al. 2007). We also found a large interaction between precipitation and brightness in many plumage patches, meaning that the negative relationship between precipitation and plumage brightness becomes stronger in cooler climates (figs. 1, 2,

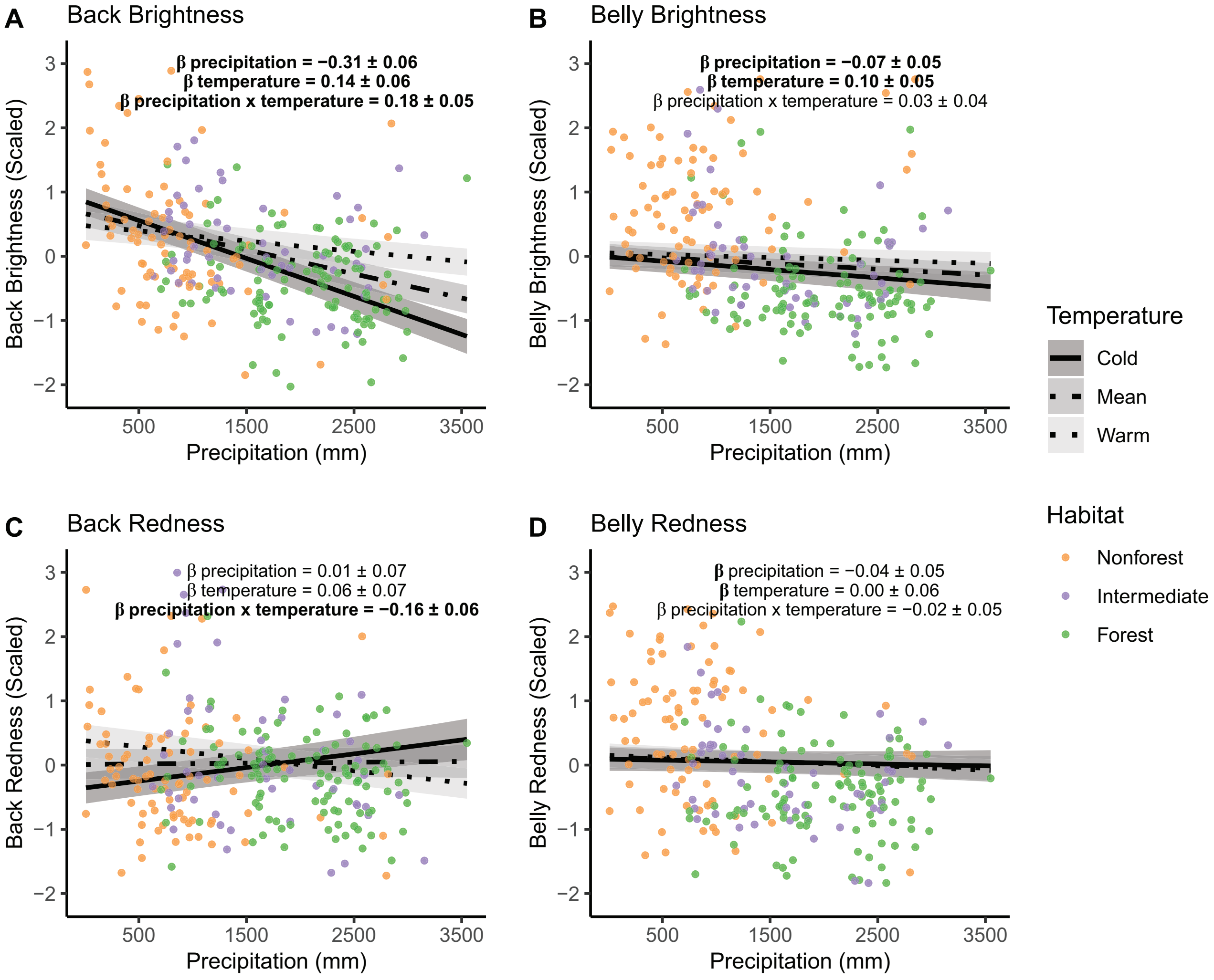


Figure 1: The strength of the effect of precipitation on plumage brightness and redness changes with varying temperatures owing to the interaction between precipitation and temperature. Back and belly patches demonstrate contrasting patterns of climate effects. In each plot, dots represent species, colored by habitat, and regression lines represent the effect of precipitation on plumage in cold (mean − 1 SD; solid line), average (dashed line), and warm (mean + 1 SD; dotted line) temperatures. All parameter estimates that are reliably nonzero are in bold. *A*, Both precipitation and temperature have a strong, nonzero effect on back brightness, and the robust interaction of precipitation can be seen by the varying slopes at different temperatures. *B*, In contrast, precipitation and temperature have strong effects on belly brightness, but as can be seen with the similar slopes of the regression plots, the interaction between climate variables is weak. *C*, Precipitation and temperature alone do not have an effect on back redness; however, their interaction is robust, causing precipitation to have a negative effect on redness in warm temperatures and a positive effect in cold temperatures. *D*, Climate variables have no effect on belly redness. Equivalent plots for all plumage patches are shown in figure S1.

S1, S2). Furthermore, we found that forest-based lineages tended to have darker plumage than non-forest-based lineages, consistent with a previous study on furnariids and other closely related families (Marcondes and Brumfield 2019). But here, we expanded on that previous finding by showing that the tendency for birds to have darker plumage in darker habitats persists even after controlling for the effects of climate (fig. 3). This indicates that climate and light environments have separate but complementary effects in driving macroevolutionary patterns of plumage color variation in this bird family. We also conducted the first phylogenetic comparative analysis of the complex version of Gloger's, finding equivocal support for the separate influence of temperature or precipitation on redness. However, we found strong interaction effects between temperature and precipitation in three of four dorsal patches that suggest redness is highest in cool/wet and warm/dry climates (table 2; figs. 1, 2, S1, S2).

Gloger's Rule, Precipitation, and Temperature

Rensch (1929, p. 160), defining Gloger's, wrote that "melanins . . . increase with higher temperature and humidity" (translation from the German by Delhey [2019]). The test of time—and of modern quantitative techniques—has validated Rensch's (1929) prediction for humidity, but intraspecific (e.g., Rising et al. 2009; Amar et al. 2014; Marcondes et al. 2020*b*) and interspecific (e.g., Delhey 2018; Galván et al. 2018; Delhey et al. 2019; Dufour et al. 2020) comparisons, including this study, have failed to support Rensch's (1929) prediction for temperature. Our models 1 and 2 instead showed a positive effect of temperature on brightness for most plumage patches (figs. 1, 3). This is the opposite of Rensch's (1929) formulation, but it is in accordance with intraspecific findings in the black sparrowhawk (*Accipiter melanogaster*; Amar et al. 2014), savannah sparrow (*Passerculus sandwichensis*; Rising et al. 2009), and variable antshrike (*Thamnophilus caerulescens*; Marcondes et al. 2020*b*), as well as comparative results from analyses of the Australian avifauna (Delhey 2018), the world's passerines (Delhey et al. 2019), and the world's gulls (Dufour et al. 2020).

These findings are consistent with Bogert's rule, a lesser-known ecogeographical rule usually considered to apply only to ectothermic animals (Clusella Trullas et al. 2007; Delhey 2018, 2019). This rule predicts that animals should be darker in cooler climates to enhance thermoregulation. For example, among 96 bird species in the Iberian Peninsula, those with darker plumage had constrained thermal niches characterized by cool temperatures and little solar radiation (Galván et al. 2018). The consistency of results showing this pattern in birds suggests that Bogert's rule may be more applicable to endotherms than previously thought. There are also indications of a possible correlation between melanism and temperature in mammals (Wacker et al. 2016). Evidence for the functional relationship between plumage pigmentation and thermoregulation comes indirectly from the frequent occurrence of bare skin patches, which act as heat dissipaters, in birds with heavily melanized plumages (Negro et al. 2006; Galván et al. 2017, 2018). Furthermore, dark pigeons displayed a greater increase in cloacal temperatures under direct solar exposure than light pigeons (Angelier 2020). These results suggest that the negative correlation between melanin deposition and temperature may arise to avoid overheating in warm climates (Galván et al. 2017) rather than to help maintain warm body temperatures in cool climates. Experimental work would be better suited to advance our knowledge in that area (Delhey 2018; Angelier 2020)

Our models showed that the interaction between precipitation and temperature is a significant predictor of brightness for many plumage patches (figs. 1, 2), meaning that in cooler temperatures, the correlation between greater precipitation and lower brightness was stronger than in warmer temperatures. For illustration, consider four species of furnariids, each occupying a different climatic regime (fig. 2): the Peruvian recurvebill (*Syndactyla ucayalae*; warm/rainy), the necklaced spinetail (*Synallaxis stictothorax*; warm/dry), the Itatiaia spinetail (*Asthenes moreirae*; cool/rainy), and the cream-rumped miner (*Geositta isabellina*; cool/dry). Consistent with the simple negative correlation between precipitation and brightness, the two species inhabiting dry climates are brighter than the two species inhabiting rainy climates. But owing to the interaction between precipitation and temperature, the difference in brightness between *G. isabellina* (cool/dry) and *A. moreirae* (cool/rainy) is greater than the difference in brightness between *S. stictothorax* (warm/dry) and *S. ucayalae* (warm/rainy).

These results can be contrasted with previous studies. Delhey et al. (2019), like us, found support for Gloger's for precipitation and partial support for Bogert's rule for temperature across the world's passerines; however, they did not test for their interaction. Delhey et al. (2019) proposed a general framework whereby the effect of temperature on plumage brightness is quadratic or U shaped, with birds being brighter at low and high temperatures and darker in intermediate temperatures, given the same levels of precipitation. But our results suggest a more nuanced scenario where temperature and precipitation cannot be considered separately: birds are lighter in cool/dry climates, but in cooler/rainier climates, the effect of precipitation becomes more prevalent, leading to darker plumage (figs. 1–3, S1, S2).

The difference between our conclusions and those of Delhey et al. (2019) highlights a fundamental challenge of comparative biology: that the conclusions we obtain depend on the clade and on the scale on which we choose to conduct our studies (Beaulieu and O'Meara 2019; Stoddard et al. 2019). Results at a broadly inclusive level (all passerines) may not be directly translatable to a more restricted clade (Furnariidae). This is likely because the furnariids include proportionally fewer species occupying very cold climates relative to passerines as a whole. The minimum temperature in our data set was 1.7°C, whereas in Delhey et al.'s (2019), it was lower than −10°C. Those species from very cold climates, which are also usually dry climates, may have a disproportionate effect on the results. Furthermore, furnariids are much more limited in their mechanisms of color production than passerines as a whole, which include large numbers of species colored by carotenoid pigments, structural coloration, or their combination. Furnariids may be a better model to test Gloger's, since their colors depend mainly on melanin deposition.

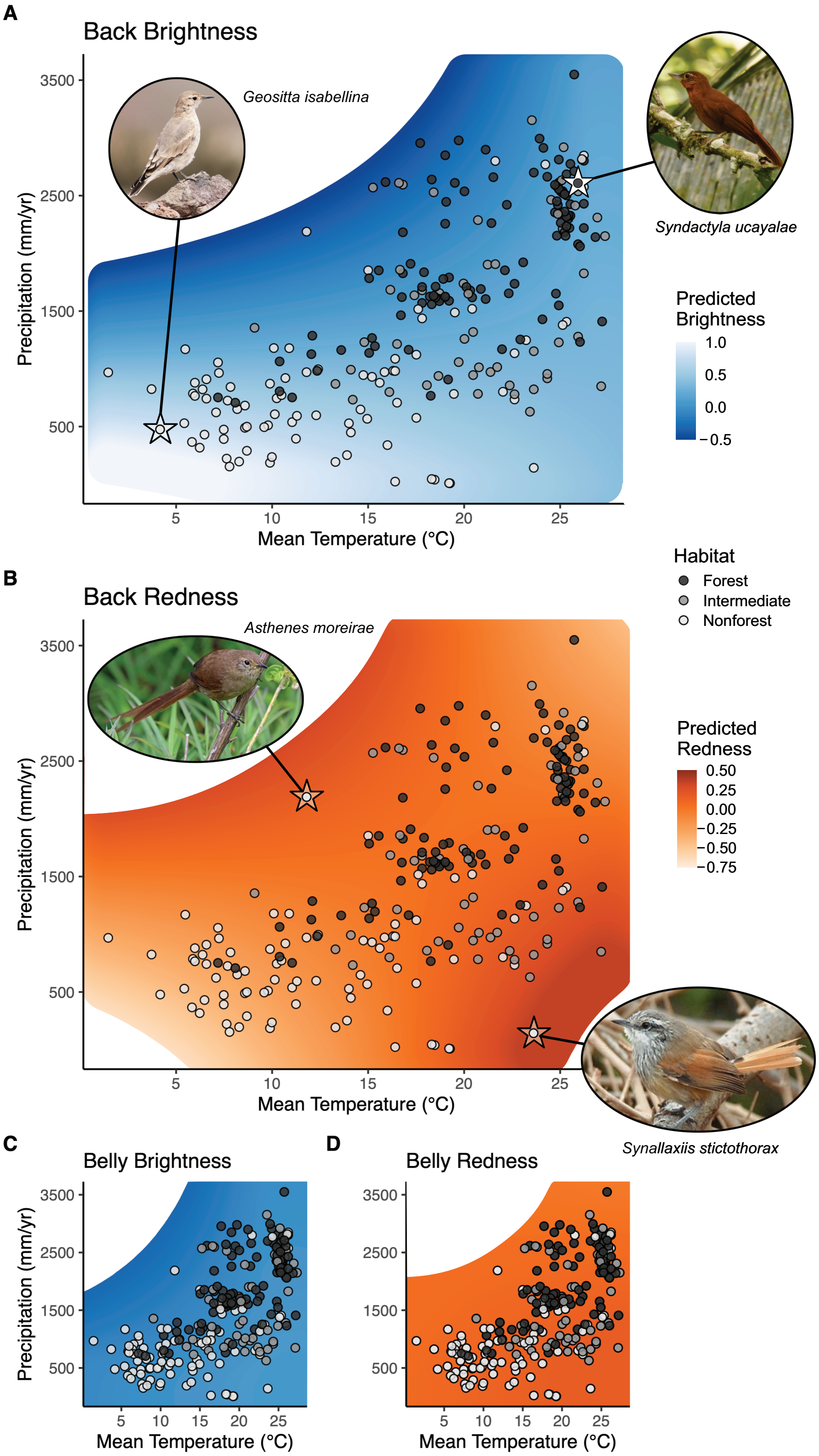
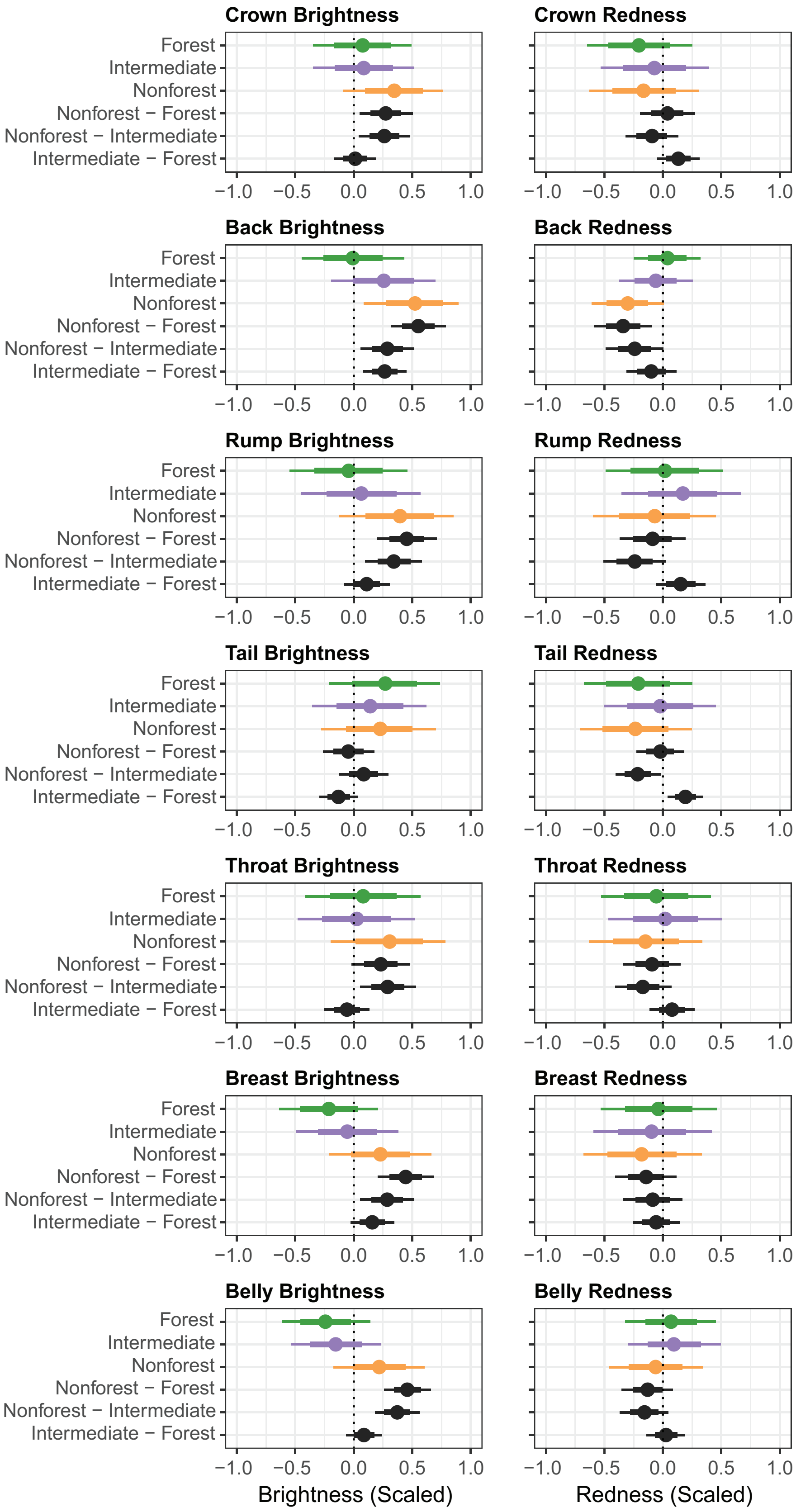


Figure 2: A complex interaction between precipitation and temperature predicts brightness (*A*) and redness (*B*) in the back patches of Furnariidae, but climate has no effect on belly brightness (*C*) or belly redness (*D*). The colors in the heat maps represent brightness or redness as predicted by model 1, which includes precipitation, temperature, and their interaction as predictors. Photographs: *Geositta isabellina*, © Cindy Franklin; *Syndactyla ucayalae*, © Rubens Matsushita; *Asthenes moreirae*, Nigel Voaden, CC BY-SA 2.0; *Synallaxis stictothorax*, © Roger Ahlman.

Table 3: Mean parameter estimates from brightness and redness models 2, with standard error of the posterior distribution in parentheses

	Forest β	Intermediate β	Nonforest β	Temperature β	Precipitation β	Redness	Error σ	Phylogenetic error (SD)
Brightness models 2:								
Crown	.07	.09	.35	.01	**−.15**	.78	.38	.67
	(−.35 to .49)	(−.35 to .52)	(−.09 to .78)	(−.08 to .11)	**(−.23 to −.07)**	(.71 to .85)	(.34 to .43)	(.56 to .79)
Back	−.01	.26	.54	.07	**−.19**	.52	.39	.72
	(−.45 to .43)	(−.19 to .71)	(.09 to 1.00)	(−.03 to .17)	**(−.28 to −.11)**	(.45 to .59)	(.34 to .45)	(.60 to .85)
Rump	−.04	.07	.41	**.19**	**−.15**	.54	.34	.89
	(−.55 to .46)	(−.46 to .57)	(−.12 to .93)	**(.08 to .30)**	**(−.24 to −.06)**	(.46 to .62)	(.29 to .40)	(.79 to .99)
Tail	.27	.14	.22	−.04	−.06	.86	.27	.81
	(−.21 to .75)	(−.35 to .62)	(−.28 to .72)	(−.13 to .05)	(−.13 to .02)	(.79 to .93)	.21 to .33)	(.77 to .88)
Throat	.08	.02	.31	−.04	**−.11**	.70	.36	.84
	(−.41 to .57)	(−.48 to .52)	(−.19 to .83)	(−.14 to .06)	**(−.20 to −.02)**	(.62 to .77)	(.30 to .43)	(.77 to .92)
Breast	−.08	.01	−.21	.01	**−.08**	.65	.42	.69
	(−.17 to .00)	(−.09 to .11)	(−.64 to .21)	(−.09 to .11)	**(−.17 to .00)**	(.58 to .73)	(.36 to .48)	(.62 to .77)
Belly	−.24	−.15	.22	**.10**	**−.03**	.70	.32	.60
	(−.61 to .14)	(−.54 to .24)	(−.17 to .61)	**(.02 to .19)**	**(−.10 to .04)**	(.63 to .76)	(−.27 to .37)	(.50 to .71)
	Forest β	Intermediate β	Nonforest β	Temperature β	Precipitation β	Brightness	Error σ	Phylogenetic error (SD)
Redness models 2:								
Crown	−.20	−.07	−.16	−.02	.02	.74	.36	.76
	(−.65 to .25)	(−.53 to .40)	(−.63 to .31)	(−.11 to .08)	(−.06 to .10)	(−.67 to .80)	(.30 to .41)	(.66 to .86)
Back	.04	−.06	−.30	**.18**	**−.11**	.72	.62	.38
	(−.25 to .32)	(−.37 to .26)	(−.61 to .01)	**(.07 to .29)**	**(−.22 to .00)**	(.63 to .81)	(.56 to .68)	(.30 to .46)
Rump	.02	.17	−.07	**.12**	**−.14**	.64	.44	.87
	(−.49 to .52)	(−.35 to .68)	(−.60 to .45)	**(.00 to .24)**	**(−.24 to −.04)**	(.55 to .74)	(.36 to .52)	(.71 to 1.03)
Tail	−.21	−.02	−.24	**.13**	−.03	.72	.20	.82
	(−.69 to .25)	(−.50 to .46)	(−.72 to .25)	**(.05 to .22)**	(−.10 to .03)	(.66 to .78)	(.16 to .23)	(.74 to .90)
Throat	−.06	.02	−.15	.07	.02	.69	.39	.79
	(−.53 to .41)	(−.47 to .50)	(−.64 to .34)	(−.03 to .18)	(−.07 to .11)	(.61 to .77)	(.33 to .46)	(.72 to .87)
Breast	−.04	−.09	−.18	.05	−.03	.74	.39	.86
	(−.53 to .46)	(−.60 to .42)	(−.69 to .33)	(−.05 to .16)	(−.12 to .06)	(.66 to .82)	(.30 to .47)	(.73 to .99)
Belly	.07	.10	−.06	−.01	−.05	.86	.37	.61
	(−.32 to .45)	(−.30 to .50)	(−.46 to .34)	(−.10 to .08)	(−.13 to .03)	(.79 to .94)	(.31 to .42)	(.48 to .75)

Note: For each model, βs are population-level effects, σ is the residual error in the model, and phylogenetic error is the error in the model attributed to the phylogenetic correlation matrix. β forest, β intermediate, and β nonforest values represent the mean brightness or the mean redness of each habitat type, conditioned on the effects of climate and phylogeny. β temperature and β precipitation values are in bold, and the 95% credible interval of the posterior distribution does not overlap zero.


Crown Brightness
Crown Redness
Back Brightness
Back Redness
Rump Brightness
Rump Redness
Tail Brightness
Tail Redness
Throat Brightness
Throat Redness
Breast Brightness
Breast Redness
Belly Brightness
Belly Redness
Forest
Intermediate
Nonforest
Nonforest − Forest
Nonforest − Intermediate
Intermediate − Forest
−1.0
−0.5
0.0
0.5
1.0
Brightness (Scaled)
Redness (Scaled)

Gloger's Rule and Light Environments

Numerous studies have shown that bird species of dark light environments (e.g., forests) tend to be darker than their relatives from open habitats, a pattern attributed to natural selection for crypsis (Endler 1993; McNaught and Owens 2002; Gomez and Théry 2004; Dunn et al. 2015; Hernández-Palma 2016; Maia et al. 2016; Shultz and Burns 2017; Marcondes and Brumfield 2019), but these studies have been conducted largely separately from investigations of Gloger's (e.g., Delhey 2018; Delhey et al. 2019). We calculated the differences between mean brightness in each habitat while controlling for differences in the climatic variables and the effect of shared evolutionary history. These contrasts showed that species from bright light environments (nonforest) are brighter than those from intermediate light environments (forest edge and canopy) and forest interior habitats in that order (fig. 3). Tail plumage is the only exception.

Zink and Remsen (1986) suggested background matching as the main adaptive mechanism responsible for Gloger's. The aforementioned comparative work and our results corroborate this. Birds tend to be darker in darker (forested) habitats. Because forest habitats also tend to receive more precipitation (in our data set: forests = 2,009 ± 611 mm precipitation/yr; intermediate habitats = 1,597 ± 700 mm/yr; nonforest habitats = 852 ± 631 mm/yr), the correlation between brightness and habitat could be spuriously driven by climate. Our results show that is not the case. The difference in brightness across habitats persists even after controlling for climatic variables, demonstrating that they have separate effects on the evolution of plumage brightness.

Zink and Remsen (1986, p. 22) also suggested that "humidity per se presumably has little direct influence" on plumage color. Because our model 2 showed negative correlations between brightness and precipitation, even while including habitat as a predictor (table 3), we disagree. Higher precipitation by itself does correlate with darker plumage. A potential explanation for this is protection against feather-degrading bacteria. It is well documented that increased melanization makes feathers more resistant to feather-degrading bacteria (Goldstein et al. 2004; Gunderson et al. 2008) and that these bacteria are common on plumages of wild birds (Burtt and Ichida 1999, 2004; Kent and Burtt 2016). However, before it can be conclusively said that feather-degrading bacteria drive increased pigmentation in birds living in rainier habitats, evidence is needed that these bacteria are in fact more abundant in rainier habitats.

The tail was the only plumage patch that did not clearly tend to be darker in forest-based species. The nonforest-forest and nonforest-intermediate tail brightness contrasts were equivocal, and the tail of forest species was credibly brighter than that of intermediate species (fig. 3). This difference between the tail and other plumage patches might be driven by several species of foliage gleaners in the genera *Automolus*, *Philydor*, and allies, typical denizens of the middle and lower strata of Neotropical rain forests, that have light tails clearly contrasting with darker back and wings. These species are adept participants in mixed-species foraging flocks and often fan their tails, making them strikingly visible (Sick 1993), perhaps suggesting a communication role.

Gloger's Rule and Vegetation Density

Previous studies have found that birds tend to be darker in more heavily vegetated habitats (Delhey et al. 2019). This is similar to, and consistent with, our findings. But our analyses based on habitat preference offer further insight because bird species occupy habitat types differentially even within the same locality, a pattern that cannot be captured by other methods, such as remote sensing-based metrics of vegetation cover. For example, at a typical resolution, remote sensing data may show that a 30 × 30-m cell is covered in very dense, tall vegetation (rain forest). But different species of furnariids occupying that cell may experience diverse light environments. For example, in western Amazonia that cell may be occupied by the orange-fronted plushcrown (*Metopothrix aurantiaca*) in the intensely sunlit forest canopy and the tawny-throated leaftosser (*Sclerurus mexicanus*) in undergrowth vegetation near the forest floor in the dim forest interior.

Remote sensing analyses may also be complicated by the fact that they are often based on museum specimens collected up to a few decades ago, before recent intense anthropogenic landscape change is reflected in the data. The landscape where a bird was collected many years ago may have little resemblance to the landscape at that same locality today.

Nevertheless, vegetation density by itself might also favor increased pigmentation because greater melanin

Figure 3: There are robust differences in mean plumage brightness of nonforest and forest or intermediate birds in most patches across light environments, but differences in redness across light environments were not as pronounced. Colored symbols represent posterior distributions of mean brightness/redness for each light environment after controlling for climatic variation and phylogenetic history; black symbols represent differences between distributions. Circles denote the mean of the posterior distribution; thick lines contain 66% of the distribution, and thin lines contain 95% of the distribution.

content makes feathers harder and more resistant to abrasion (Barrowclough and Sibley 1980; Burtt 1986; Bonser 1995). This is often considered in the context of abrasion from airborne particles, but it is conceivable that abrasion from vegetation might also be a selective factor favoring heavier plumage pigmentation (Kale 1966; Burtt 1986; Surmacki et al. 2011; Kroodsma and Verner 2013), although this demands further empirical study.

The Complex Version of Gloger's Rule in Furnariidae

The little-studied complex version of Gloger's, recently revived by Delhey (2017, 2019) and Marcondes et al. (2020*b*), predicts that bird plumages have a higher relative pheomelanin content in warm/dry areas. In our results, neither precipitation nor temperature by itself had a robust effect on plumage redness. However, there was a strong interaction effect of temperature and precipitation on plumage redness in three dorsal plumage patches (back, rump, and tail; figs. 1, 2, S1; table 1). In warm/dry climates, furnariids are redder than in cool/dry or warm/wet climates, a pattern consistent with the complex version of Gloger's. Interestingly, we also found that the strong interaction of temperature and precipitation predicts redder birds in cool/wet climates.

In contrast with other ecogeographical rules, Gloger's had no mechanism associated with it when it was formulated (Delhey 2019). Whereas several tentative but compelling mechanisms have since been proposed for simple Gloger's (see above), the only mechanistic hypothesis of complex Gloger's was the cursory speculation by Marcondes et al. (2020*b*) that more reddish colors in drier climates might be favored because of background matching. Whereas our results do support this hypothesis in part, background matching does not explain increased redness in cool/wet environments.

Conclusion

Gloger's is a classic ecogeographic principle predicting, in its simple version, that animals should be darker in wetter and warmer regions. We have shown—on the basis of comparative analyses of the Furnariidae, a family of >200 Neotropical passerine species—that the prediction related to precipitation is borne out in our data, but the prediction related to temperature is not. In fact, we found that furnariids tend to be darker in cooler regions. We also found a previously undescribed interaction between precipitation and temperature, whereby the negative effect of precipitation on plumage brightness becomes stronger under cool temperatures. Furthermore, we also showed that species in this family tend to be darker in darker light environments and that this effect persists even after controlling for the effects of climate.

On the basis of previous results and ours, we suggest that the pattern encapsulated by Gloger's is produced by a combination of the partially correlated effects of habitat type, precipitation, and vegetation density. The effect of habitat type is driven by natural selection for enhanced crypsis in darker light environments (Zink and Remsen 1986; Endler 1993; McNaught and Owens 2002; Gomez and Théry 2004; Dunn et al. 2015; Maia et al. 2016; Shultz and Burns 2017; Marcondes and Brumfield 2019). The effect of precipitation may be due to feather-degrading bacteria (Burtt and Ichida 1999, 2004; Goldstein et al. 2004; Gunderson et al. 2008; Kent and Burtt 2016), and the effect of vegetation density may be related to feather abrasion (Kale 1966; Burtt 1986; Surmacki et al. 2011; Kroodsma and Verner 2013), although the latter two effects still demand further empirical work to be conclusively demonstrated. There appears to also be a general effect of temperature on plumage brightness, but it is in the opposite direction than that stated by Gloger's: birds tend to be darker in cooler places. This is possibly for thermoregulatory reasons (Negro et al. 2006; Galván et al. 2017, 2018; Angelier 2020).

Finally, our tests for complex Gloger's demonstrate that redness is associated with an interaction between precipitation and temperature. However, these results are difficult to interpret in the absence of a mechanistic framework within which to discuss a potential correlation between climate and relative pheomelanin content. We suggest future tests of complex Gloger's at a macroevolutionary level will be easier to devise and interpret once we have a better handle on its potential ecological and physiological bases.

Acknowledgments

This work was partially supported by a National Science Foundation (NSF) grant to R.T.B. (DEB-1146265), a Science Without Borders doctoral fellowship from Brazil's National Council for Scientific and Technological Development to R.S.M. (CNPq; 201234/2014–9), and an NSF Graduate Research Fellowship to J.A.N. We thank Perrin Teal-Sullivan for assistance with figures and Jake Esselstyn (Louisiana State University) and Chris Witt's lab group (University of New Mexico) for helpful suggestions.

Statement of Authorship

R.S.M. and J.A.N. conceptualized the project, R.S.M. and G.F.S. collected the data, R.S.M. and J.A.N. analyzed the data and wrote the first draft, all authors participated in reviewing and editing, R.S.M. and R.T.B. acquired funding and resources, and R.T.B. supervised the project.

Data and Code Availability

Color data and climatic data have been deposited in the Dryad Digital Repository (color: https://doi.org/10.5061/dryad.s86434s; Marcondes and Brumfield 2021; climatic: https://doi.org/10.5061/dryad.cnp5hqc3d; Marcondes 2020*a*). R scripts are available on GitHub (https://github.com/jonnations/Gloger_rule_Furnariidae) and on Zenodo (https://doi.org/10.5281/zenodo.4328757; Nations 2020).

Literature Cited

Amar, A., A. Koeslag, G. Malan, M. Brown, and E. Wreford. 2014. Clinal variation in the morph ratio of black sparrowhawks *Accipiter melanoleucus* in South Africa and its correlation with environmental variables. Ibis 156:627–638.

Angelier, F. 2020. Pigeons in the sun: thermal constraints of eumelanic plumage in the rock pigeon (*Columba livia*). Journal of Thermal Biology 90:102601.

Barrowclough, G. F., and F. C. Sibley. 1980. Feather pigmentation and abrasion: test of a hypothesis. Auk 97:881–883.

Beaulieu, J. M., and B. C. O'Meara. 2019. Diversity and skepticism are vital for comparative biology: a response to Donoghue and Edwards (2019). American Journal of Botany 106:613–617.

Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. Condor 97:590–591.

Brady, N. C., and R. R. Weil. 2008. Pages 662–710 *in* The nature and properties of soils. 13th ed. Prentice Hall, Upper Saddle River, NJ.

Brumfield, R. T. 2012. Inferring the origins of lowland Neotropical birds. Auk 129:367–376.

Bürkner, P.-C. 2017. brms: an R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80:1–28.

Burtt, E. H. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. Ornithological Monographs 38:1–126.

Burtt, E. H., and J. M. Ichida. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. Auk 116:364–372.

———. 2004. Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. Condor 106:681–686.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1–32.

Cerezer, F. O., J. R. Ribeiro, M. Graipel, and N. C. Cáceres. 2020. The dark side of coloration: ecogeographical evidence supports Gloger's rule in American marsupials. Evolution 74:2046–2058.

Clusella Trullas, S., J. H. van Wyk, and J. R. Spotila. 2007. Thermal melanism in ectotherms. Journal of Thermal Biology 32:235–245.

Delhey, K. 2017. Gloger's rule. Current Biology 27:689–691.

———. 2018. Darker where cold and wet: Australian birds follow their own version of Gloger's rule. Ecography 41:673–683.

———. 2019. A review of Gloger's rule, an ecogeographical rule of colour: definitions, interpretations and evidence. Biological Reviews 94:1294–1316.

Delhey, K., J. Dale, M. Valcu, and B. Kempenaers. 2019. Reconciling ecogeographical rules: rainfall and temperature predict global colour variation in the largest bird radiation. Ecology Letters 22:726–736.

de Villemereuil, P., and S. Nakagawa. 2014. General quantitative genetic methods for comparative biology. Pages 287–303 *in* L. Z. Garamszegi, ed. Modern phylogenetic comparative methods and their application in evolutionary biology. Springer, Berlin.

de Villemereuil, P., J. A. Wells, R. D. Edwards, and S. P. Blomberg. 2012. Bayesian models for comparative analysis integrating phylogenetic uncertainty. BMC Evolutionary Biology 12:1–16.

Diniz, P., P. H. L. Ribeiro, G. S. Rech, and R. H. Macedo. 2016. Monochromatism, cryptic sexual dimorphism and lack of assortative mating in the rufous hornero, *Furnarius rufus albogularis*. Emu 116:294–300.

Donald, P. F., P. Alström, and D. Engelbrecht. 2017. Possible mechanisms of substrate colour-matching in larks (Alaudidae) and their taxonomic implications. Ibis 159:699–702.

Dufour, P., J. Guerra Carande, J. Renaud, J. P. Renoult, S. Lavergne, and P. A. Crochet. 2020. Plumage colouration in gulls responds to their non-breeding climatic niche. Global Ecology and Biogeography 29:1704–1715.

Dunn, P. O., J. K. Armenta, and L. A. Whittingham. 2015. Natural and sexual selection act on different axes of variation in avian plumage color. Science Advances 1:e1400155.

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

Galván, I., D. Palacios, and J. J. Negro. 2017. The bare head of the northern bald ibis (*Geronticus eremita*) fulfills a thermoregulatory function. Frontiers in Zoology 14:1–9.

Galván, I., S. Rodríguez-Martínez, and L. M. Carrascal. 2018. Dark pigmentation limits thermal niche position in birds. Functional Ecology 32:1531–1540.

Galván, I., and K. Wakamatsu. 2016. Color measurement of the animal integument predicts the content of specific melanin forms. RSC Advances 6:79135–79142.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 1:515–533.

Gelman, A., J. Hill, and M. Yajima. 2012. Why we (usually) don't have to worry about multiple comparisons. Journal of Research on Educational Effectiveness 5:189–211.

Gelman, A., J. Hwang, and A. Vehtari. 2014. Understanding predictive information criteria for Bayesian models. Statistics and Computing 24:997–1016.

Gelman, A., and F. Tuerlinckx. 2000. Type S error rates for classical and Bayesian single and multiple comparison procedures. Computational Statistics 15:373–390.

Gloger, C. W. L. 1833. Das Abändern der Vögel durch Einfluss des Klimas. August Schulz, Breslau, Germany.

Goldstein, G., K. R. Flory, B. A. Browne, S. Majid, and J. M. Ichida. 2004. Bacterial degradation of black and white feathers. Auk 121:656–659.

Gomez, D., and M. Théry. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. Ecology Letters 7:279–284.

Gunderson, A. R., A. M. Frame, J. P. Swaddle, and M. H. Forsyth. 2008. Resistance of melanized feathers to bacterial degradation: is it really so black and white? Journal of Avian Biology 39:539–545.

Harvey, M. G., G. A. Bravo, S. Claramunt, A. M. Cuervo, G. E. Derryberry, J. Battilana, G. F. Seeholzer, et al. 2020. The evolution of a tropical biodiversity hotspot. Science 370:1343–1348.

Hernández-Palma, A. 2016. Light matters: testing the "light environment hypothesis" under intra- and interspecific contexts. Ecology and Evolution 6:4018–4031.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

James, F. C. 1991. Complementary descriptive and experimental studies of clinal variation in birds. American Zoologist 31:694–706.

Kale, H. W. 1966. Plumages and molts in the long-billed marsh wren. Auk 83:140–141.

Kamilar, J. M., and B. J. Bradley. 2011. Interspecific variation in primate coat colour supports Gloger's rule. Journal of Biogeography 38:2270–2277.

Kay, M. 2020. tidybayes: tidy data and geoms for Bayesian models. R package version 2.1.1. https://zenodo.org/record/3900954.

Kent, C. M., and E. H. Burtt. 2016. Feather-degrading bacilli in the plumage of wild birds: prevalence and relation to feather wear. Auk 133:583–592.

Kroodsma, D. E., and J. Verner. 2013. Marsh wren (*Cistothorus palustris*), version 2.0. In A. F. Poole, ed. The birds of North America. Cornell Lab of Ornithology, Ithaca, NY.

Kruschke, J. K. 2013. Bayesian estimation supersedes the *t*-test. Journal of Experimental Psychology 142:573.

Maia, R., C. M. Eliason, P. P. Bitton, S. M. Doucet, and M. D. Shawkey. 2013. pavo: an R package for the analysis, visualization and organization of spectral data. Methods in Ecology and Evolution 4:906–913.

Maia, R., H. Gruson, J. A. Endler, and T. E. White. 2019. pavo 2: new tools for the spectral and spatial analysis of colour in R. Methods in Ecology and Evolution 10:1097–1107.

Maia, R., D. R. Rubenstein, and M. D. Shawkey. 2016. Selection, constraint, and the evolution of coloration in African starlings. Evolution 70:1064–1079.

Marcondes, R. S., and R. T. Brumfield. 2019. Fifty shades of brown: macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. Evolution 73:704–719.

———. 2021. Data from: Fifty shades of brown: macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. Evolution 73:704–719, Dryad Digital Repository, https://doi.org/10.5061/dryad.s86434s.

Marcondes, R. S., J. A. Nations, G. F. Seeholzer, and R. T. Brumfield. 2020*a*. Data from: Rethinking Gloger's rule: climate, light environments and color in a large family of tropical birds (Furnariidae). American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.cnp5hqc3d.

Marcondes, R. S., K. F. Stryjewski, and R. T. Brumfield. 2020*b*. Testing the simple and complex versions of Gloger's rule in the variable antshrike (*Thamnophilus caerulescens*, Thamnophilidae). Auk 137:1–13. https://doi.org/10.1093/auk/ukaa026.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10:105–108.

———. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA.

McElreath, R. 2016. Statistical rethinking. Taylor & Francis, Boca Raton, FL.

McNaught, M. K., and I. P. F. Owens. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? Journal of Evolutionary Biology 15:505–514.

Miller, E. T., G. M. Leighton, B. G. Freeman, A. C. Lees, and R. A. Ligon. 2019. Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. Nature Communications 10:1–10.

Nations, J. A. 2020. jonnations/Gloger_rule_Furnariidae: first release (version V1.0). Zenodo, https://doi.org/10.5281/zenodo.4328757.

Negro, J. J., J. H. Sarasola, F. Fariñas, and I. Zorrilla. 2006. Function and occurrence of facial flushing in birds. Comparative Biochemistry and Physiology A 143:78–84.

Patten, M. A., J. T. Rotenberry, and M. Zuk. 2004. Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. Evolution 58:2144–2155.

Remsen, J. V. 2003. Family Furnariidae (ovenbirds). Pages 162–357 *in* J. del Hoyo, A. Elliott, and D. A. Christie, eds. Handbook of the birds of the world. Vol. 8. Lynx, Barcelona.

Rensch, B. 1929. Prinzip geographischer rassenkreise und das problem der artbildung. Borntraeger, Berlin.

Rising, J. D., D. A. Jackson, and H. B. Fokidis. 2009. Geographic variation in plumage pattern and coloration of savannah sparrows. Wilson Journal of Ornithology 121:253–264.

Romano, A., R. Séchaud, A. H. Hirzel, and A. Roulin. 2019. Climate-driven convergent evolution of plumage colour in a cosmopolitan bird. Global Ecology and Biogeography 28:496–507.

Roulin, A., and C. Randin. 2015. Gloger's rule in North American barn owls. Auk 132:321–332.

Roycroft, E. J., J. A. Nations, and K. C. Rowe. 2019. Environment predicts repeated body size shifts in a recent radiation of Australian mammals. Evolution 74:671–680.

Seeholzer, G. F., S. Claramunt, and R. T. Brumfield. 2017. Niche evolution and diversification in a Neotropical radiation of birds (Aves: Furnariidae). Evolution 71:702–715.

Shultz, A. J., and K. J. Burns. 2017. The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). Evolution 71:1061–1074.

Sick, H. 1993. Birds in Brazil. Princeton University Press, Princeton, NJ.

Stanchak, K. E., and S. E. Santana. 2019. Do ecogeographical rules explain morphological variation in a diverse, Holarctic genus of small mammals? Journal of Biogeography 46:110–122.

Stan Development Team. 2018. Stan modeling language users guide and reference manual. Version 2.18.0. http://mc-stan.org.

Stoddard, M. C., C. Sheard, D. Akkaynak, E. H. Yong, L. Mahadevan, and J. A. Tobias. 2019. Evolution of avian egg shape: underlying mechanisms and the importance of taxonomic scale. Ibis 161:922–925.

Surmacki, A., M. Liu, A. Mercadante, and G. E. Hill. 2011. Effect of feather abrasion on structural coloration in male eastern bluebirds *Sialia sialis*. Journal of Avian Biology 42:514–521.

Thomas, D. B., K. J. McGraw, M. W. Butler, M. T. Carrano, O. Madden, and H. F. James. 2014. Ancient origins and multiple appearances of carotenoid-pigmented feathers in birds. Proceedings of the Royal Society B 281:20140806.

Tobias, J. A., J. D. Brawn, R. Brumfield, E. P. Derryberry, A. N. G. Kirschel, and N. Seddon. 2012. The importance of suboscine birds as study systems in ecology and evolution. Ornitologica Neotropical 23:261–274.

VanderWerf, E. A. 2012. Ecogeographic patterns of morphological variation in elepaios (*Chasiempis* spp.): Bergmann's, Allen's, and Gloger's rules in a microcosm. Ornithological Monographs 73:1–34.

Vehtari, A., A. Gelman, and J. Gabry. 2018. loo: efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.3.1. https://mc-stan.org/loo/.

Wacker, C. B., B. M. McAllan, G. Körtner, and F. Geiser. 2016. The functional requirements of mammalian hair: a compromise between crypsis and thermoregulation? Science of Nature 103:53.

Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. Journal of Machine Learning Research 11:3571–3594.

Zink, R. M., and J. V. Remsen Jr. 1986. Evolutionary processes and patterns of geographic variation in birds. Pages 1–69 *in* R. F. Johnston, ed. Current ornithology. Plenum, New York.

Associate Editor: Rebecca J. Safran
Editor: Daniel I. Bolnick

"*Paradisea apoda*, the great paradise bird, has become a familiar object of admiration in museums of natural history and collections. In no other bird is the coloring so rich and the blending of browns, purple, green and orange so alluringly beautiful. Add to this the long, curving fall of plumes behind, and one of the most entrancing spectacles animate nature has to show is vouchsafed." Figured (from top to bottom): *Paradisea apoda*, *Parotia sefilata*, and *Cicinnurus regius*. From "Some Birds of Paradise from New Guinea" by Geo. S. Mead (*The American Naturalist*, 1894, 28:915–920).