1 **Climate, crypsis and Gloger's rule in a large family of tropical passerine birds**

2 **(Furnariidae)**

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14 Running head: Climate and habitat type in Gloger's rule

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49 **Abstract**

50   Gloger's rule predicts endothermic animals should have darker colors under warm and

51 rainy climates, but empirical studies have typically found that animals tend to be darker under

52 cool and rainy climates. Moreover, Gloger's rule has rarely been tested jointly with the

53 prediction that animals occupying dark habitats should have darker colors to enhance crypsis.

54 We aimed to disentangle the effects of climate and light environments (habitat type) as correlates

55 of plumage brightness in a large Neotropical passerine family. We found that cooler and rainier

56 climates are associated with darker plumage, even after accounting for habitat types, and that

57 darker habitats are associated with darker plumage, even after accounting climate. There was an

58 important interaction between precipitation and temperature, whereby the negative effect of

59 temperature on brightness becomes stronger under cooler temperatures. Climate and light

60 environments have separate but complementary effects in driving macroevolutionary patterns of

61 plumage color variation in birds.

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72   Ecogeographic rules describe correlations between organismal phenotypes and features

73   of their environment. Their repeated observation across taxa and space is *prima facie* evidence

74   that they are driven by common selective pressures (Mayr 1963, James 1991, VanderWerf 2011).

75   Gloger's rule (Gloger 1833, Rensch 1929) is a longstanding ecogeographic rule describing a

76   correlation between the colors of mammals and birds and the climatic conditions they occupy.

77   Recent interpretations of Gloger's rule (Delhey 2019, Marcondes et al. in review) have divided it

78   into two versions: one "simple" and the other "complex". The simple version relates to variation

79   in overall melanin content, with greater amounts of melanin making feathers and fur darker

80   (McGraw et al. 2005). This version of Gloger's rule predicts that animals tend to be darker in

81   rainy and warm climates and brighter in dry and cool climates (Gloger 1833). The complex

82   version of Gloger's rule concerns variation specifically in pheomelanin content (Delhey 2019),

83   with greater amounts of pheomelanin making feathers and fur more brown or reddish-brown

84   (McGraw et al. 2005). This paper concerns only the simple version of Gloger's rule, which

85   historically has been the only version most investigators have recognized (Delhey 2019).

86   Gloger's rule has been investigated mostly at the intraspecific level, where evidence is

87   abundant (Zink and Remsen 1986, Delhey 2019). Well-studied examples of species that have

88   been found to be darker in more humid climates come from a broad variety of bird clades and

89   include, but are not limited to, the Barn Owl *Tyto alba* (Roulin and Randin 2015, Romano et al.

90   2019), Black Sparrowhawk *Accipiter melanoleucos* (Tate and Amar 2017), Song Sparrow

91   *Melospiza melodia* (Burtt and Ichida 2004) and Variable Antshrike *Thamnophilus caerulescens*

92   (Marcondes et al. in review).

93   In contrast, Gloger's (1833) prediction that animals should be darker in warmer climates

94   has rarely been supported (Delhey 2019). More often, it has been found that populations

95   inhabiting warmer climates tend to be lighter than their counterparts from cooler locales, a

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96   pattern dubbed Bogert's rule and often attributed to thermoregulatory advantages (Clusella-

97   Trullas et al. 2007, Rising et al. 2009, Delhey 2019).

98   Mayr (1956) argued that ecogeographic rules typically apply only to variation between

99   populations within species, but Gloger's rule has also been considered—and widely confirmed—

100   at the interspecific level. In fact, interspecific comparative analyses are crucial to revealing how

101   evolutionary processes operating within species can be generalized across macroevolutionary

102   scales (Meiri 2011, Stoddard et al. 2019). The predicted negative correlation between brightness

103   and humidity has been supported in phylogenetic comparative studies of the world's primates

104   (Kamilar and Bradley 2011), a large clade of Holarctic shrews (Stanchak and Santana 2018), the

105   entire Australian avifauna (Delhey 2018), the world's woodpeckers (Miller et al. 2019), and the

106   world's passerine birds (Delhey et al. 2019). The latter two studies also supported the prediction

107   of Bogert's rule that animals are lighter in warmer regions.

108   Beyond climate, another major ecological axis to consider when investigating the causes

109   of variation in animal color, particularly brightness, is habitat type, or light environment. Endler

110   (1993) predicted that, to enhance crypsis, animals inhabiting dark light environments (*e.g.* the

111   interior of dense forests) should be darker than those inhabiting open areas with bright light

112   conditions (*e.g.*, savannas), a prediction that has received wide support from comparative studies

113   on birds (McNaught and Owens 2002, Gomez and Thery 2004, Dunn et al. 2015, Maia et al.

114   2016, Shultz and Burns 2017, Marcondes and Brumfield 2019). Because forests, particularly

115   tropical rainforests, are more prevalent in rainier climates, this raises the possibility that the

116   tendency for birds to be darker in more humid places (Gloger's rule) is confounded by a need for

117   crypsis in darker environments.

118   The passerine family Furnariidae (the woodcreepers, ovenbirds, foliage-gleaners and

119   allies) is well-suited for investigating the relative roles of climate and light environments in

120   driving interspecific variation in plumage brightness. Throughout the Neotropics, furnariids

121   occupy virtually every terrestrial biome and habitat type (here construed to mean the spatial

122   vegetation structure and density typically occupied by each bird species). They are found at the

123   extremes of both precipitation and temperature in the Neotropics, from the warm and rainy

124   Amazonian rainforests to warm and arid Chaco savannas, and from cool and dry high-elevation

125   puna grasslands to the cool and rainy Andean cloud forests (Remsen 2003). Moreover, even

126   under the same climatic conditions at a single geographic locality, species in this family

127   specialize in such different habitat types as, for example, the lower strata of tropical rainforests,

128   the forest canopy, and patches of open vegetation. They therefore experience dramatically

129   different light environments, from the dim forest understory to intensely sun-lit fields and

130   savannahs. Despite this ecological diversity, furnariids are virtually all festooned exclusively in

131   innumerous shades of brown and rufous that vary relatively little in hue, but greatly in

132   brightness. For example, furnariid colors range from light and creamy brown in the puna- and

133   desert-inhabiting *Ochetorhynchus* earth-creepers to dark and rich brown in some species of

134   tropical rainforest-dwelling *Xiphorhynchus* woodcreepers.

135   If Gloger's rule is driven primarily by climate, species inhabiting rainy and warm

136   climatic regimes are predicted to be darker than those from dry and cool regimes, regardless of

137   their habitat preference. In contrast, if Gloger's rule is mainly a result of birds adapting to be

138   darker in darker (forest) habitats, bird species occupying forest habitats are predicted to be darker

139   than their nonforest-based relatives, even if they inhabit similar climatic regimes. Marcondes and

140   Brumfield (2019) previously demonstrated that furnariid species have evolved to be darker in

141   darker habitats, consistent with Endler's (1993) predictions for crypsis. Here, we sought to

142   investigate the interacting roles of climate and habitat type in driving interspecific variation in

143   plumage brightness in the Furnariidae.

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145   **Methods**

146   **Color data**

147   We used the color dataset previously described in Marcondes and Brumfield (2019) and

148   deposited on the Dryad digital repository under DOI 10.5061/dryad.s86434s (embargoed until

149   July 16, 2021). Briefly, this dataset includes reflectance data for 250 (84%) furnariid species,

150   with an average of 6.4 specimens per species (range: 1-8). For each specimen, this dataset

151   includes reflectance spectra from seven plumage patches divided into a dorsal (crown, back,

152   rump and tail) and a ventral (belly, breast and belly) set. We calculated plumage brightness

153   (percentage of reflected white light) and averaged it across all specimens of each species.

154   Because the Furnariidae are sexually monochromatic with no evidence of cryptic sexual

155   dichromatism (Remsen 2003; Tobias et al. 2012; Diniz et al. 2016; Marcondes and Brumfield

156   2019), we considered the sexes together in our analyses. Finally, we used principal component

157   analysis (PCA) to reduce our dataset to one principal component for the venter and one for the

158   dorsum. The first principal components of dorsal and ventral PCAs were both loaded in the same

159   direction by brightness in all plumage patches, thus representing overall brightness of that body

160   surface; subsequent principal components captured various aspects of contrasts between plumage

161   patches within each body surface (Marcondes and Brumfield 2019). Our final color dataset thus

162   consisted of the first principal component score of brightness for each body surface (hereafter,

163   simply "dorsal brightness" and "ventral brightness") for each species.

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165   **Habitat and climatic data**

166   We used Marcondes and Brumfield's (2019) categorization scheme for habitat types,

167   which was based on Endler's (1993) discussion of natural light environments. In brief, each of

168   the 250 furnariid species we analyzed was assigned to one habitat type, in decreasing order of

169   ambient light intensity: nonforest, intermediate and forest. The forest category includes only

170   species that occupy the dimly-lit middle and lower strata of rainforests; we assigned canopy and

171   edge species to the intermediate category because these areas are more intensely illuminated than

172   the forest interior (Endler 1993, Marcondes and Brumfield 2019).

173   To obtain climatic data for each furnariid species we used the georeferenced locality

174   records dataset of Seeholzer et al. (2017). This extensively-vetted dataset contains 23,588

175   occurrence records (average=70.4 records/species) gathered from museum specimens, audio

176   recordings and observational records. For each locality in this dataset, we obtained mean annual

177   temperature and mean annual precipitation from the BioClim database (Hijmans et al. 2005) and,

178   for each species, we took the median of temperature and precipitation across all its occurrence

179   localities. Because of their different magnitudes and units (°C for temperature and mm/year for

180   precipitation), before fitting any statistical models (see below), at this stage we scaled each

181   climatic variable to have a mean of 0 and a standard deviation of 1.

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183   **Statistical analyses**

184   To test the two hypotheses regarding the effects of climate and habitat on plumage

185   brightness in the Furnariidae, we fit a series of phylogenetic Bayesian multilevel linear models

186   using the modeling software Stan (Carpenter et al. 2017) as implemented in the R library *brms*

187   (Bürkner 2017). All R scripts used for the analyses are available at https://github.com/jonnations.

188   The multilevel model framework allowed us to fit linear models with multiple predictor variables

189   while including group-level effects that account for statistical non-independence of species data

190   due to shared phylogenetic history.

191   First, we tested the hypothesis that Gloger's rule is primarily driven by climate, and

192   species in wetter and warmer localities are darker than those from drier and cooler localities,

193   regardless of habitat preference (forest, intermediate or nonforest). Under this hypothesis, we

194   expect that species occupying wet and warm locales will be darker than those from dry and cool

195   locales even when comparing nonforest species in the former to forest species in the latter. We

196   fit two identical phylogenetic multivariate linear regression models, one with dorsal brightness as

197   our response variable (Dorsal Model 1) and the other with ventral brightness as our response

198   variable (Ventral Model 1). These models use precipitation, temperature, and the interaction

199   between precipitation and temperature as the predictor variables. We used a species level matrix

200   of scaled phylogenetic branch lengths (*i.e.*, the phylogenetic correlation matrix; Bürkner 2017)

201   from the phylogeny of Harvey et al. (in review) as a group-level effect (de Villemereuil et al.

202   2012) to account for correlations due to phylogenetic relatedness of species. These models test

203   the Gloger's rule prediction that birds occupying warm and rainy regions should be darker than

204   those occupying cool and dry regions (Gloger 1833, Rensch 1929). A nonzero, negative effect of

205   precipitation on brightness would be consistent with Gloger's rule, and a nonzero, positive effect

206   would contradict it; likewise for the effect of temperature on brightness. Dorsal and Ventral

207   Models 1 also estimate the interaction parameter of temperature and precipitation, which allows

208   us to explicitly test whether wetter and warmer habitats result in darker plumage, and drier,

209   cooler habitats result in brighter plumage. As both the dorsal and ventral brightness data had a

210   slight positive skew, we used the skew-normal distribution family to describe the response

211   variable rather than a simple Gaussian distribution. This distribution family estimates an

212   additional parameter, alpha, which describes the direction and the strength of the skew. We fit

213   regularizing priors on the group-level effects to prevent MCMC chains from occasionally

214   searching very large, unreasonable values of model space (Gelman 2006; McElreath 2016). Each

215   of the models included 4 chains run for 10000 generations with 5000 generations of warm-up

216   and 5000 chains of sampling. We assessed chain convergence using the Gelman-Rubin

217   diagnostic $\hat{R}$, and chain efficiency using effective sample size (ESS). $\hat{R} < 1.01$ and ESS > 500

218   represent acceptable convergence and mixing.

219   We also tested the alternative hypothesis that Gloger's rule is related to light

220   environments regardless of climatic variables. Under this hypothesis, we expect species

221   occupying forested habitats to be darker than those inhabiting nonforest habitats, even if the

222   nonforest species are in rainier and warmer climates. Specifically, we separated the effects of

223   habitat from the effects of climate by fitting a phylogenetic multiple regression linear model with

224   dorsal brightness (Dorsal Model 2) or ventral brightness (Ventral Model 2) as our response and

225   temperature, precipitation, and our categorical habitat as predictor variables. As in Dorsal and

226   Ventral Models 1, we included our phylogenetic correlation matrix as a group level effect.

227   Dorsal and Ventral Models 2 have three predictor variables, generating three population-level

228   outcomes: 1) The effect of precipitation on brightness, corrected for the influence of temperature,

229   habitat, and phylogeny, 2) the effect of temperature on brightness, corrected for precipitation,

230   habitat, and phylogeny, and 3) a posterior distribution of the mean brightness values of each

231   habitat conditioned on the phylogenetic relationships, and corrected for the effects of

232   precipitation and temperature. The estimated mean brightness values can directly address our

233   question about whether species in darker habitats have darker plumage regardless of their

234   climatic regimes. For categorical predictors, *brms* assigns a random category (habitat type in our

235   case) as a dummy variable to use as the intercept value, so we removed the intercept parameter

236   from the model to directly generate posterior distributions for each habitat. We used these

237   posterior distributions of the mean brightness for each habitat to determine if species in different

238   habitats differ in their brightness. To determine if the posterior distributions of the mean

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239   brightness for each habitat are different from one another, we calculated the distributions of the

240   differences of each habitat's brightness estimates, *i.e.* contrasts (nonforest-intermediate,

241   nonforest-forest, intermediate-forest) (McElreath 2016; Roycroft et al. 2019) using the

242   *compare_levels* function in the R library *tidybayes* (Kay 2019). If the 95% credible interval of

243   these difference distributions does not overlap zero, then we can credibly say that brightness is

244   different between those habitats. This method of calculating the differences between posterior

245   distributions is analogous to the "Bayesian T-Test" of Kruschke (2013). As in Model 1, we used

246   regularizing priors and ran 4 chains of 10,000 generations and checked for convergence with $\hat{R}$

247   and ESS.

248   As a null model, we also fit an intercept-only phylogenetic multilevel model for

249   brightness. This model has no predictor variables and only estimates the intercept of the group

250   level-effect, in our case the phylogenetic correlation matrix. For each plumage surface (dorsal

251   and ventral), we performed model comparison of our three models using the difference in

252   expected log predictive density (ELPD) from the widely applicable information criteria (WAIC,

253   Wantanabe 2010) using the *waic* function in the R package *loo* (Vehtari et al 2018), which

254   calculates the ELPD and the standard error of the estimate. WAIC is appropriate for Bayesian

255   inference with non-Gaussian posterior distributions (Gelman, Hwang, and Vehtari 2013); lower

256   WAIC values represent greater support for a model. Comparing against the null allowed us to

257   verify that precipitation, temperature, and habitat improved the predictive ability of our model

258   rather than phylogeny alone explaining differences in brightness. WAIC also allowed us to

259   assess whether the climate interaction model or the climate + habitat model was a better

260   predictor of our brightness data.

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262   **Results**

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263   All of our Bayesian multilevel models properly converged, and all parameters had $\hat{R} <$

264   1.01 and ESS > 500. Results of Model 1 for the dorsal plumage showed a strong negative effect

265   of precipitation on dorsal plumage brightness (Table 1, Figure 1), indicating that as precipitation

266   increases, plumage gets darker, as predicted by Gloger's rule. Model 1 also showed a strong

267   positive effect of temperature on dorsal plumage (Table 1, Figure 1), demonstrating that as

268   temperature increases, dorsal plumage gets brighter, *contra* Gloger's rule but consistent with

269   Bogert's rule. We also found a positive interaction between precipitation and temperature (Table

270   1, Figures 1 and 2). This interaction indicates that the negative effect of precipitation on

271   brightness decreases with increasing temperature. In other words, Gloger's rule is more notable

272   when comparing species that vary in the amount of precipitation they receive but all occupy

273   similarly cool environments, rather than when comparing species that vary in precipitation but

274   which all occupy similarly warm environments.

275   We found similar results for the ventral plumage. Precipitation had a negative effect on

276   ventral plumage brightness (Table 1, Figure 1). Temperature had an uncertain positive effect on

277   ventral brightness (95% credible interval overlapping 0), demonstrating that temperature has less

278   importance on ventral plumage than on dorsal plumage. We found a weak positive effect of the

279   interaction between precipitation and temperature on the ventral plumage (Table 1, Figures 1 and

280   2).

281   There was a subtle difference between the venter and the dorsum in effects of the

282   interaction of precipitation and temperature and brightness (Figure 2). Both plumage surfaces

283   tended to be darkest for species in cool/rainy climates and brightest in cool/dry climates. But

284   whereas temperature seemed to have little effect on dorsal brightness in dry climates, ventral

285   plumages tended to be darker under warm/dry conditions than under cool/dry conditions. In other

286   words, there is little change in dorsal brightness when comparing species from cool/dry and

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287   warm/dry conditions, but ventral brightness is higher (lighter) in species from cool/dry than

288   warm/dry conditions.

289   Our Dorsal and Ventral Models 2, in which we removed the interaction between

290   precipitation and temperature and added habitat as a predictor, showed a similar negative effect

291   of precipitation on both dorsal plumage and ventral plumage (Table 2). We also found positive

292   effects of temperature on dorsal, and an uncertain effect of temperature on ventral plumage

293   (Table 2). This model also estimated the posterior distributions of mean plumage brightness for

294   each habitat, conditioned on phylogenetic effects and the climatic variables (Figure 3). We then

295   calculated the differences of those distributions (Figure 3). For the dorsal plumage we found that

296   intermediate and nonforest species are credibly brighter than forest species but not

297   distinguishable from each other, because the difference in their posterior distributions overlapped

298   zero (Figure 3). Results were similar for ventral plumage, except that the difference between

299   intermediate and forest species slightly overlapped zero. Therefore, we found that birds in forest

300   habitats are darker than birds from intermediate or nonforest habitats, even after accounting for

301   differences in temperature and precipitation.

302   We used the ELPD scores of the WAIC analysis to compare Models 1 and 2 to the null.

303   We found that both predicted dorsal plumage brightness better than the null model (Table 3).

304   However, the standard error of the ELPD scores of Models 1 and 2 overlapped, so that we are

305   unable to conclude which of these two models better predicted dorsal plumage brightness. For

306   the ventral plumage, Models 1 and 2 also better predicted ventral brightness than the null model,

307   but in this case Model 2, which included habitat, was a better predictor of ventral plumage

308   brightness than Model 1, which did not include habitat.

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310   **Discussion**

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311   Gloger's rule is a longstanding ecogeographic principle predicting that birds and

312   mammals that inhabit rainier and warmer climates tend to have darker plumage and pelage color

313   than their counterparts (intra- as well as interspecific) from drier and cooler places (Gloger 1833,

314   Rensch 1929, Mayr 1942, 1963, Delhey 2017, 2019). Here, we found strong support in the

315   Furnariidae for the predicted relationship between brightness and precipitation. In contrast, we

316   found that furnariid species tended to be darker in cooler climates, contrary to the second

317   prediction of Gloger's rule, but consistent with a pattern dubbed Bogert's rule or thermal

318   melanism, which is often observed in ectothermic animals (Clusella-Trullas et al. 2018). We also

319   found a credible positive interaction between precipitation and brightness, meaning that the

320   negative relationship between precipitation and plumage brightness becomes stronger in cooler

321   climates (Figures 1 and 2). Finally, forest-based lineages tended to have darker plumage than

322   nonforest-based lineages (Figure 3), consistent with a previous study on furnariids and other

323   closely-related families (Marcondes and Brumfield 2019). But, here, we expanded on that

324   previous finding by showing that that tendency for birds to have darker plumage in darker

325   habitats persists even after accounting for the effects of climate. This indicates that climate and

326   light environments have separate but complementary effects in driving macroevolutionary

327   patterns of plumage color variation in birds.

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329   **Gloger's rule, precipitation and temperature**

330   Gloger (1833) wrote that "melanins [...] increase with higher temperature and humidity"

331   (translation from the German from Delhey 2019), implicating both climatic variables in the rule

332   that would become his namesake. But Rensch (1936), in the first major discussion of Gloger's

333   rule in English, downplayed the role of temperature, placing more importance on humidity

334   (reviewed by Delhey 2019).

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335   The test of time—and of modern quantitative techniques—have validated Rensch's

336   (1936) emphasis on humidity. Intra- (e.g., Rising et al. 2009, Amar et al. 2014, Marcondes et al.

337   in review) and interspecific (e.g., Delhey 2018, Delhey et al. 2019) comparisons, including this

338   study, have consistently failed to find support for a tendency for birds to be darker in warmer

339   places. Our Models 1 and 2 showed a positive effect of temperature on brightness, particularly in

340   rainy climates (see below). This is diametrically opposite to Gloger's (1833) formulation, but in

341   accordance with intraspecific findings in the Black Sparrowhawk *Accipiter melanogaster* (Amar

342   et al. 2014), Savannah Sparrow *Passerculus sandwichensis* (Rising et al. 2009) and Variable

343   Antshrike *Thamnophilus caerulescens* (Marcondes et al. in review), as well as comparative

344   results from analyses of the Australian avifauna (Delhey 2018) and the world's passerines

345   (Delhey et al. 2019). These findings are consistent with Bogert's rule, a lesser known

346   ecogeographical rule usually considered to apply only to ectothermic animals (Clusella-Trullas et

347   al. 2018, Delhey 2018, 2019). This rule predicts animals should be darker in cooler climates to

348   enhance thermoregulation. The consistency of results showing the same pattern in birds suggests

349   that Bogert's rule may be applicable to endothermic animals as well, although we lack an

350   understanding of its mechanistic underpinnings in that case. Experimental work would be better

351   suited to advance our knowledge in that regard (Delhey 2018).

352   Our models showed a strong interaction between precipitation and temperature (Figures 1

353   and 2). In cooler temperatures, the correlation between greater precipitation and lower brightness

354   was stronger than in warmer temperatures. For illustration, consider four species of furnariids,

355   each occupying a different climatic regime (Figure 2): the Peruvian Recurvebill *Syndactyla*

356   *ucayalae* (warm/rainy), the Necklaced Spinetail *Synallaxis stictothorax* (warm/dry), the Itatiaia

357   Spinetail *Asthenes moreirae* (cool/rainy), and the Cream-rumped Miner *Geositta isabellina*

358   (cool/dry). Our results suggest that the two species inhabiting dry climates are expected to be

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359   brighter than the two species inhabiting rainy climates. But the difference in brightness between

360   the species inhabiting a cool/dry and a cool/rainy climate should be greater than the difference in

361   brightness between the species inhabiting a warm/dry and a warm/rainy climate. This is indeed

362   what our data show. The difference in the first principal component of dorsal brightness between

363   *Geositta isabellina* (cool/dry) and *Asthenes moreirae* (cool/rainy) was 0.3328, whereas the

364   difference in the first principal component of dorsal brightness between *Synallaxis stictothorax*

365   (warm/dry) and *Syndactyla ucayalae* (warm/rainy) was 0.1544.

366   These results can be contrasted with those of Delhey et al. (2019), who, like us, found

367   support for Gloger's rule for precipitation and Bogert's rule for temperature across the world's

368   passerines, but did not test for their interaction. Delhey et al. (2019) proposed a general

369   framework whereby the effect of temperature on plumage brightness has a quadratic shape, with

370   birds being brighter at low and high temperatures and darker in intermediate temperatures, given

371   the same levels of precipitation. Due to the credible interaction effect we found, our results do

372   not conform to that framework. Instead, they suggest a more nuanced scenario: birds are lighter

373   in cool and dry climates, especially for the ventral plumage, but in cool and rainier climates the

374   effect of precipitation becomes more prevalent, leading to darker plumage (Figure 2). The

375   difference between ours and Delhey et al.'s (2019) conclusions highlights how findings at a more

376   broadly inclusive level (all passerines) may not be directly translatable to a more restricted clade

377   (Furnariidae). This may be because the furnariids include proportionally fewer species occupying

378   very cold climates relative to the passerines as a whole. The minimum temperature in our dataset

379   was 1.7°C, whereas in Delhey et al.'s dataset it was lower than -10°C. Those species from very

380   cold climates, which are also usually dry climates, could be driving the results observed when

381   considering all passerines.

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383   **Gloger's rule, precipitation and habitat type**

384   Numerous studies have shown that bird species of dark light environments (*e.g.* forests)

385   tend to be darker than their relatives from open habitats, a pattern attributed to natural selection

386   for crypsis (Endler 1993, McNaught and Owens 2002, Gomez and Thery 2004, Dunn et al. 2015,

387   Maia et al. 2016, Shultz and Burns 2017, Marcondes and Brumfield 2019), but these studies have

388   been conducted largely separately from investigations of Gloger's rule (*e.g.*, Delhey 2018,

389   Delhey et al. 2019). We used a model with temperature, precipitation and habitat type as

390   predictors of brightness to calculate contrasts between the posterior distributions of the

391   phylogenetic mean of brightness in each habitat, while controlling for differences in the climatic

392   variables. These contrasts showed that species from bright light environments (nonforest) are

393   credibly brighter, ventrally, than those from intermediate light environments (forest edge and

394   canopy), followed by species occupying the forest interior (Figure 3). Results were similar for

395   the dorsal plumage, except that there was no difference between nonforest and intermediate

396   habitats (Figure 3).

397   Zink and Remsen (1986) suggested background matching as the main adaptive

398   mechanism responsible for Gloger's rule. The aforementioned comparative work and our results

399   corroborate this. Birds tend to be darker in darker (forested) habitats. Because forest habitats also

400   tend to receive more precipitation (for example, precipitation in our dataset, mean±sd: forest

401   species, 2009±611 mm/year; intermediate habitat, 1597±700 mm/year; nonforest 852±631

402   mm/year), the correlation between brightness and habitat could be spuriously driven by climate.

403   Our results show that is not the case. The difference in brightness across habitats persists even

404   after controlling for climatic variables, demonstrating that they have separate effects on the

405   evolution of plumage brightness.

406   Zink and Remsen (1986) also suggested that "humidity per se presumably has little direct

407   influence". Because our Model 2 showed negative correlations between brightness and

408   precipitation, even while including habitat as a predictor, we disagree. Higher precipitation, by

409   itself, does correlate with darker birds. A potential explanation for this is protection against

410   feather-degrading bacteria. It is well-documented that increased melanization makes feathers

411   more resistant to feather-degrading bacteria (Goldstein et al. 2004, Gunderson et al. 2008), and

412   that these bacteria are common on plumages of wild birds (Burtt and Ichida 1999, 2004, Kent

413   and Burtt 2016). However, before it can be conclusively said that feather-degrading bacteria

414   drive increased pigmentation in birds living in rainier habitats, evidence is needed that these

415   bacteria are in fact more abundant in more rainy habitats.

416

417   **Gloger's rule and vegetation density**

418   Delhey (2018) used remote sensing data to show that, in Australia, birds tend to be darker

419   in more heavily-vegetated areas. This is similar to, and consistent with, our findings. But our

420   analyses based on habitat preference offer further insight, because bird species occupy habitat

421   types differentially even within the same locality, a pattern that cannot be captured by remote

422   sensing-based metrics of vegetation cover. For example, at a typically used resolution, remote

423   sensing data may show that a 30 m x 30 m cell is covered in very dense, tall vegetation

424   (rainforest). But different species of furnariids occupying that cell may experience diverse light

425   environments. For example, in western Amazonia that cell may be occupied by the Orange-

426   fronted Plushcrown *Metopothrix aurantiaca* in the intensely sun-lit forest canopy and the

427   Tawny-throated Leaftosser *Sclerurus mexicanus* in undergrowth vegetation near the forest floor

428   in the dim forest interior.

18

429   Remote sensing analyses may also be complicated by the fact they are often based on

430   museum specimens collected up to a few decades ago, before recent intense anthropogenic

431   landscape change that will be reflected in remote sensing data. The landscape where a bird was

432   collected many years ago may have little resemblance to the landscape at the same locality today.

433   Nevertheless, vegetation density by itself might also favor increased pigmentation,

434   because greater melanin content makes feathers harder and more resistant to abrasion

435   (Barrowclough and Sibley 1980, Burtt 1986, Bonser 1995). This is often considered in the

436   context of abrasion from airborne particles, but it is conceivable that abrasion from vegetation

437   might also be an important selective factor favoring heavier plumage pigmentation (Kale 1966,

438   Burtt 1986, Surmacki et al. 2011, Kroodsma and Verner 2013), although this demands further

439   empirical study.

440

441   **Conclusion**

442   Gloger's rule is a classic ecogeographic principle predicting animals should be darker in

443   wetter and warmer regions. We have shown, based on comparative analyses of the Furnariidae, a

444   family of >200 Neotropical passerine species, that the prediction related to precipitation is borne

445   out in our data, but the prediction related to temperature is not. In fact, we found that furnariids

446   tend to be darker in cooler regions. We also found a previously undescribed credible interaction

447   of precipitation and temperature, whereby the negative effect of precipitation on plumage

448   brightness becomes stronger under cool temperatures. Furthermore, we also showed that species

449   in this family tend to be darker in darker light environments and that this effect persists even

450   after controlling for the effects of climate.

451   Based on ours and previous results, we suggest that the pattern encapsulated by Gloger's

452   rule is produced by a combination of the partially correlated effects of habitat type, precipitation,

453 and vegetation density. The effect of habitat type is driven by natural selection for enhanced

454 crypsis in darker light environments (Zink and Remsen 1986, Endler 1993, McNaught and

455 Owens 2002, Gomez and Thery 2004, Dunn et al. 2015, Maia et al. 2016, Shultz and Burns

456 2017, Marcondes and Brumfield 2019), whereas the effect of precipitation may be due to feather-

457 degrading bacteria (Burtt and Ichida 1999, 2004, Goldstein et al. 2004, Gunderson et al. 2008,

458 Kent and Burtt 2016), and the effect of vegetation density may be related to feather abrasion

459 (Kale 1966, Burtt 1986, Surmacki et al. 2011, Kroodsma and Verner 2013), though the latter two

460 effects still demand further empirical work to be conclusively demonstrated. It is also still

461 unclear how the effects of temperature fit into this scenario.

462

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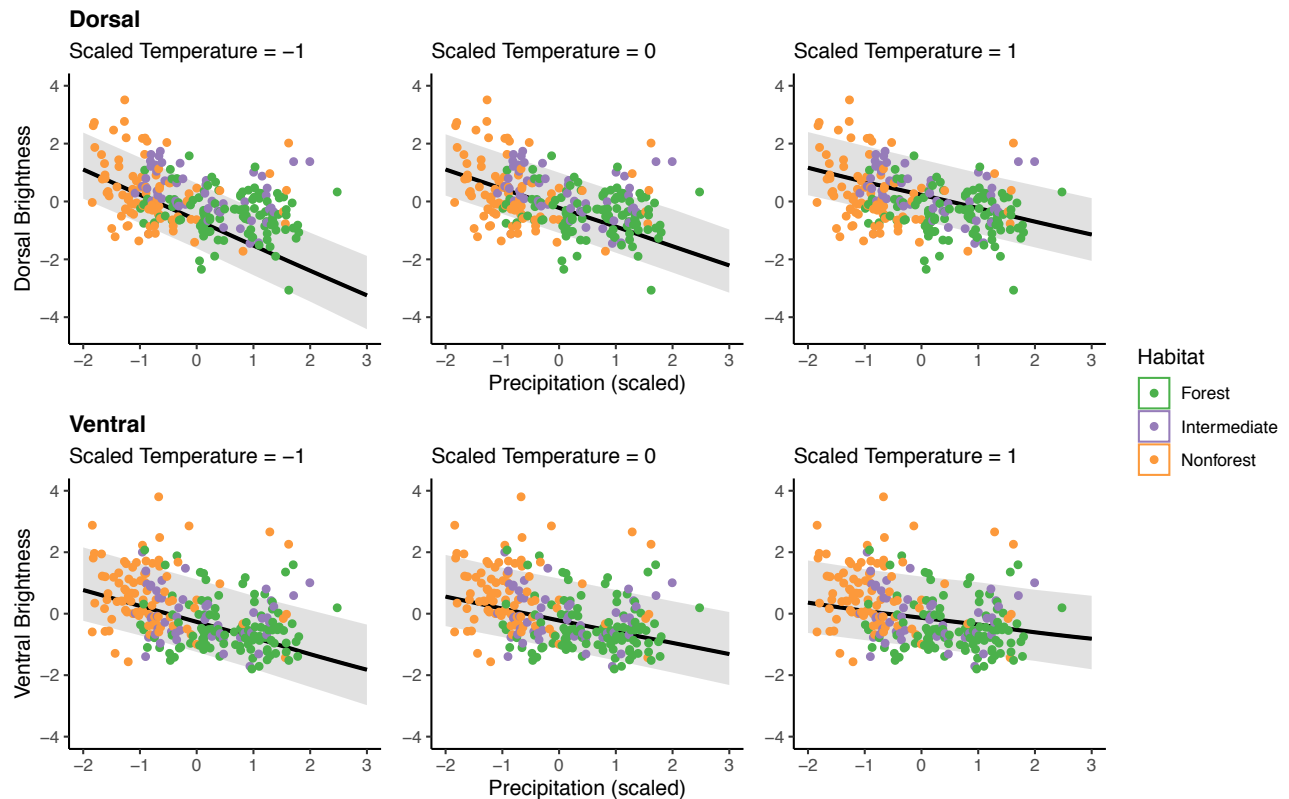
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595   Figure 1. The slope of the negative relationship between temperature and brightness increases as

596   temperature decreases (from Model 1). Plots in the left-hand column show the effect of

597   precipitation on brightness when scaled temperature is -1 (mean – 1 standard deviation); the

598   middle column shows the effect of precipitation on brightness when scaled temperature is zero
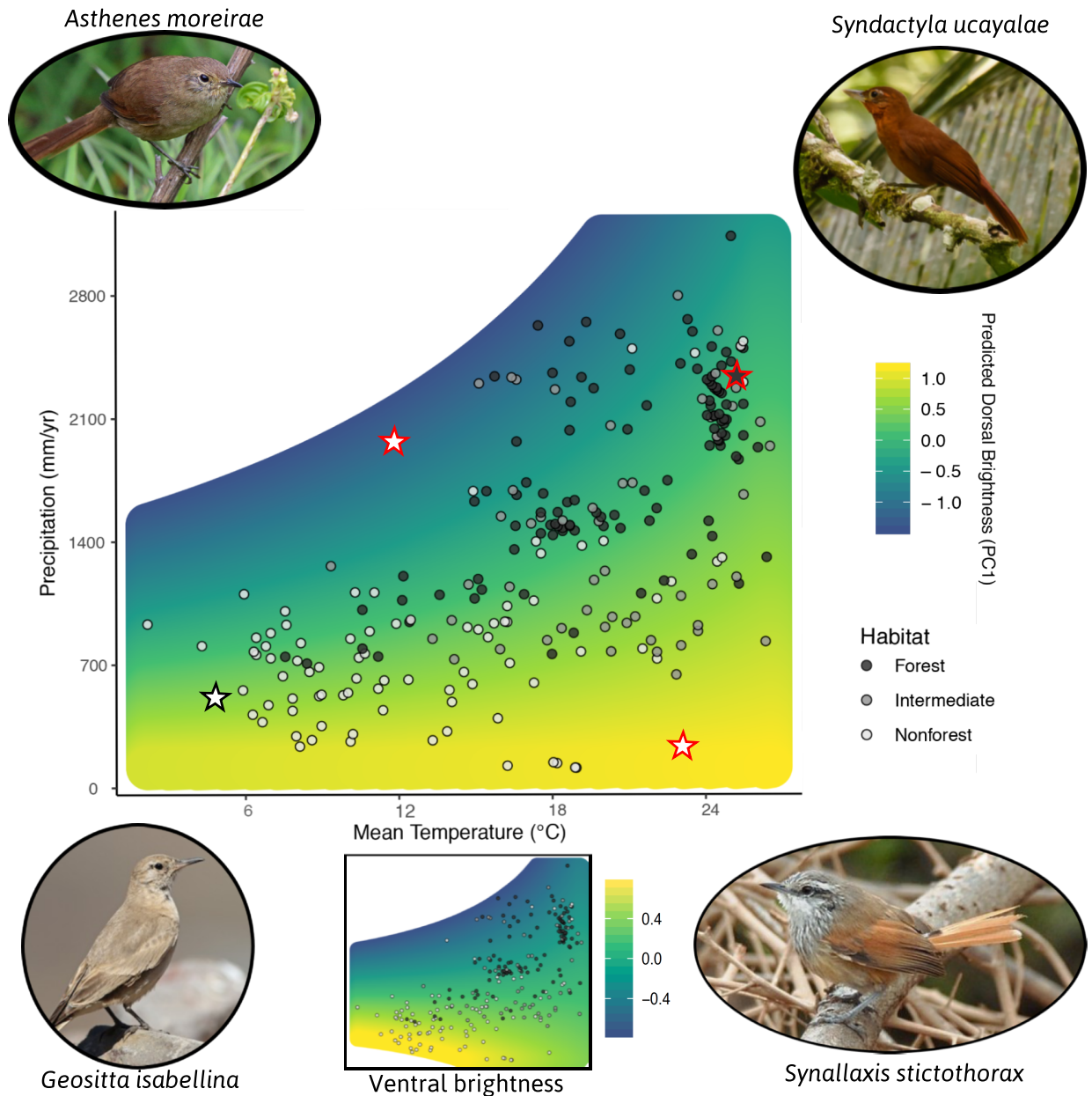
599   (the mean), and the right-hand column shows the effect of precipitation on brightness when

600   scaled temperature is 1 (mean + 1 SD).

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605   Figure 2. A complex interaction between precipitation and temperature predicts dorsal (main

606   panel) and ventral (inset at bottom) brightness in the Furnariidae. The colors in the heatmap

607   represent brightness as predicted by Model 1, which includes precipitation, temperature and their

608   interaction as predictors. Stars represent the depicted species they are closest to. Photograph

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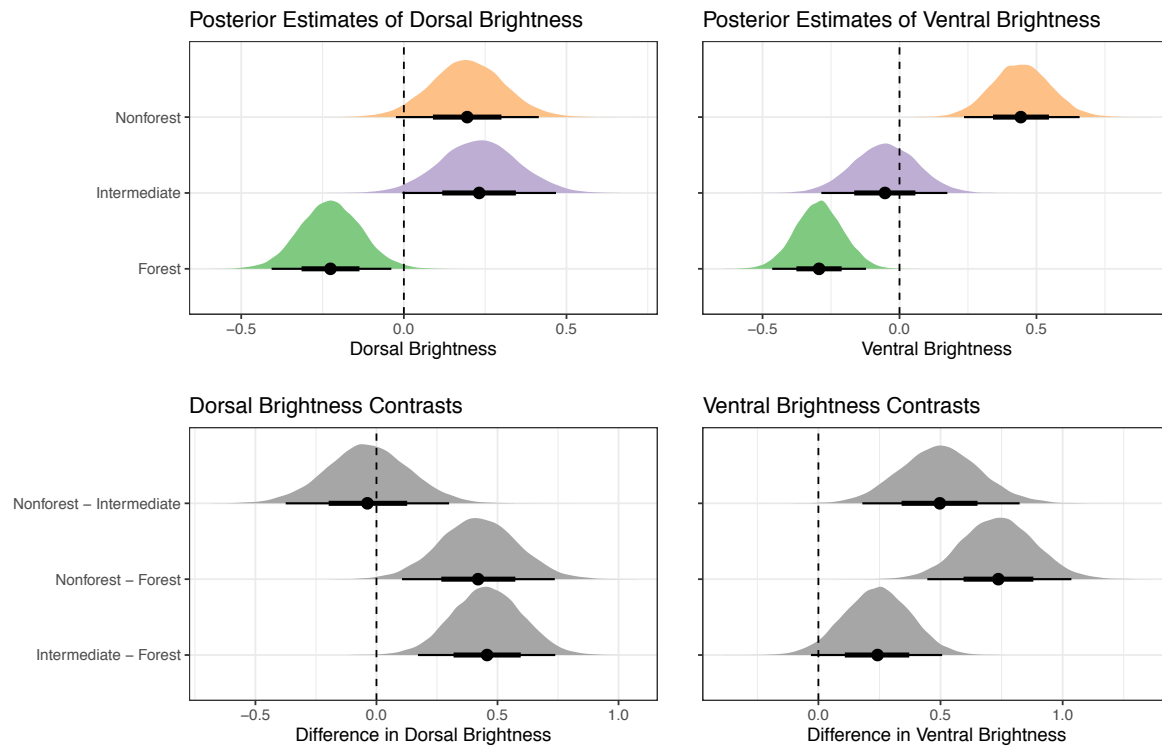614

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Figure 3. Differences in mean plumage brightness across light environments persist even after accounting for climatic variation. Top row: posterior distributions of the mean brightness value, conditioned on temperature, precipitation, and the phylogenetic correlation matrix, for the effects of climate. Bottom row: contrasts between the phylogenetic means of each habitat. If the contrast overlaps zero (dotted line), then there is no credible difference between the brightness of the two habitats. The black circle represents the mean and the horizontal bars the 66% (thick bar) and 95% (thin bar) credible intervals of the distribution.

Dorsal Model 1

Population-Level Effects	α mean	α 95% CI	β mean	β 95% CI
Intercept	-0.12	(-0.26, 0.02)	-	-
Temperature	-	-	0.44	(0.08, 0.28)
Precipitation	-	-	-0.66	(-0.82, -0.51)
Temperature * Precipitation			0.21	(0.07, 0.35)
Family Parameters	**Estimate**	**95% CI**		
Sigma	0.83	(0.66, 0.95)	-	-
Alpha	2.76	(1.93, 3.74)	-	-
Group-Level Effects	**Estimate**	**95% CI**		
Phylogenetic Error (sd)	0.26	(0.01, 0.54)	-	-

Ventral Model 1

Population-Level Effects	α mean	α 95% CI	β mean	β 95% CI
Intercept	-0.08	(-0.23, 0.07)	-	-
Temperature	-	-	0.08	(-0.08, 0.23)
Precipitation			-0.38	(-0.53, -0.23)
Temperature * Precipitation			0.14	(0.00, 0.29)
Family Parameters	**Estimate**	**95% CI**		
Sigma	0.91	(0.81, 1.00)	-	-
Alpha	3.21	(2.42, 4.04)	-	-
Group-Level Effects	**Estimate**	**95% CI**		
Phylogenetic Error (sd)	0.14	(0.01, .036)		

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642

643   Table 1: Results from Dorsal Model and Ventral Model 1, where plumage brightness is predicted

644   by temperature, precipitation, and their interaction. α represents the intercept and β represents

645   the regression coefficient conditioned on the phylogenetic correlation matrix. Population-Level

646   Effects are the climatic parameters, Sigma is the residual error in the model, Alpha is the skew

647   parameter in the skew-normal distribution, and Phylogenetic Error is the error in the model

648   attributed to the phylogenetic correlation matrix.

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Dorsal Model 2

Population-Level Effects	β mean	β 95% CI
Precipitation	-0.48	(-0.64, -0.32)
Temperature	0.35	(0.20, 0.50)
Forest Habitat	-0.23	(-0.41, -0.04)
Intermediate Habitat	0.23	(0.00, 0.47)
Nonforest Habitat	0.20	(-0.02, .041)
Family Parameters	**Estimate**	**95% CI**
Sigma	0.81	(0.65, 0.94)
Alpha	2.70	(1.86, 3.69)
Group-Level Effects	**Estimate**	**95% CI**
Phylogenetic Error (sd)	0.29	(0.02, 0.55)

Ventral Model 2

Population-Level Effects	β mean	β 95% CI
Precipitation	-0.19	(-0.34, -0.04)
Temperature	0.10	(-0.05, 0.25)
Forest Habitat	-0.29	(-0.46, -0.12)
Intermediate Habitat	-0.05	(-0.29, 0.17)
Nonforest Habitat	0.44	(0.24, 0.66)
Family Parameters	**Estimate**	**95% CI**
Sigma	0.86	(0.76, 0.96)
Alpha	3.09	(2.31, 3.93)

Group-Level Effects	Estimate	95% CI
Phylogenetic Error (sd)	0.16	(0.01, .039)

666

667 Table 2: Results from Dorsal Model and Ventral Model 2, where brightness is predicted by

668 temperature, precipitation and habitat type. β represents the regression coefficient, conditioned

669 on the phylogenetic correlation matrix. Population-Level Effects are climatic parameters and the

670 brightness estimates for each habitat. Sigma is the residual error in the model, Alpha is the skew

671 parameter in the skew-normal distribution, and Phylogenetic Error is the error in the model

672 attributed to the phylogenetic correlation matrix.

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Model Comparison	WAIC (se)	ELPD (se)	ELPD Difference
Dorsal Null Model	693.7 (30.8)	-348.8 (15.4)	-34.4 (9.2)
Dorsal Model 1*	**629.3 (26.2)**	**-314.6 (13.1)**	**-2.2 (4.0)**
Dorsal Model 2*	**624.9 (27.5)**	**-312.4 (13.7)**	**0**
Ventral Null Model	676.8 (22.3)	-338.4 (11.2)	-23.8 (7.6
Ventral Model 1	648.4 (24.8)	-324.2 (12.4)	-9.5 (5.0)
Ventral Model 2*	**629.3 (24.9)**	**-314.6 (12.4)**	**0**

689

690 Table 3: Model comparison for Dorsal Models and Ventral Models. The first column shows the

691 Widely Applicable Information Criterion (WAIC) score with the standard error of the estimate in

692 parentheses. The second model shows the Estimated Log-Predictive Density (ELPD), or the

693 difference in the model's predictive accuracy, with standard error in parentheses. The third

694 column provides the difference between the ELPD scores and the model with the highest

695 predictive accuracy. In Model 1, brightness is predicted by temperature, precipittaion and their

696 interaction. In Model 2, brightness is predicted by temperature, precipitation and habitat type.

697 For both venter and dorsum, Models 2 (in bold) have the highest predictive accuracy for the

698 given data, and the null models have the lowest predictive accuracy. In the Dorsal models, the

699 standard error of the ELPD difference for Models 1 and 2 overlaps, which means we cannot

700 determine which of the two models has the highest ELPD score.

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