Aggressive signaling among competing species of birds

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Aggressive interactions help individuals to gain access to and defend resources, but they can be costly, leading to increased predation risk, injury, or death. Signals involving sounds and color can allow birds to avoid the costs of intraspecific aggressive encounters, but we know less about agonistic signaling between species, where fights can be frequent and just as costly. Here, we review photographic and video evidence of aggressive interactions among species of birds (N = 337 interactions documenting the aggressive signals of 164 different bird species from 120 genera, 50 families, and 24 orders) to document how individuals signal in aggressive encounters among species, and explore whether these visual signals are similar to those used in aggressive encounters with conspecifics. Despite the diversity of birds examined, most aggressively signaling birds displayed weapons (bills, talons, wings) used in fighting and placed these weapons closest to their heterospecific opponent when signaling. Most species oriented their bodies and heads forward with their bills pointing towards their heterospecific opponent, often highlighting their face, throat, mouth, and bill. Many birds also opened their wings and/or tails, increasing their apparent size in displays, consistent with the importance of body size in determining behavioral dominance among species. Aggressive postures were often similar across species and taxonomic families. Exceptions included Accipitridae and Falconidae, which often highlighted their talons in the air, Columbidae, which often highlighted their underwings from the side, and Trochilidae, which often hovered upright in the air and pointed their fanned tail downward. Most species highlighted bright carotenoid-based colors in their signals, but highlighted colors varied across species and often involved multiple colors in combination (e.g., black, white, and carotenoid-based colors). Finally, birds tended to use the same visual signals in aggressive encounters with heterospecifics that they use in aggressive encounters with conspecifics, suggesting that selection from aggressive interactions may act on the same signaling traits regardless of competitor identity.

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Abstract

Aggressive interactions help individuals to gain access to and defend resources, but they can be costly, leading to increased predation risk, injury, or death. Signals involving sounds and color can allow birds to avoid the costs of intraspecific aggressive encounters, but we know less about agonistic signaling between species, where fights can be frequent and just as costly. Here, we review photographic and video evidence of aggressive interactions among species of birds (*N* = 337 interactions documenting the aggressive signals of 164 different bird species from 120 genera, 50 families, and 24 orders) to document how individuals signal in aggressive encounters among species, and explore whether these visual signals are similar to those used in aggressive encounters with conspecifics. Despite the diversity of birds examined, most aggressively signaling birds displayed weapons (bills, talons, wings) used in fighting and placed these weapons closest to their heterospecific opponent when signaling. Most species oriented their bodies and heads forward with their bills pointing towards their heterospecific opponent, often highlighting their face, throat, mouth, and bill. Many birds also opened their wings and/or tails, increasing their apparent size in displays, consistent with the importance of body size in determining behavioral dominance among species. Aggressive postures were often similar across species and taxonomic families. Exceptions included Accipitridae and Falconidae, which often highlighted their talons in the air, Columbidae, which often highlighted their underwings from the side, and Trochilidae, which often hovered upright in the air and pointed their fanned tail downward. Most species highlighted bright carotenoid-based colors in their signals, but highlighted colors varied across species and often involved multiple colors in combination (e.g.,

black, white, and carotenoid-based colors). Finally, birds tended to use the same visual signals in aggressive encounters with heterospecifics that they use in aggressive encounters with conspecifics, suggesting that selection from aggressive interactions may act on the same signaling traits regardless of competitor identity.

Keywords: *interspecific aggression, signals, agonistic interactions, dominance hierarchies, competition, fighting, color badges*

1 | INTRODUCTION

Aggressive behaviors help individuals to gain access to and defend resources such as food, territories, mates, nesting sites, display sites, and roosting sites. These behaviors, however, can be costly when aggressive encounters escalate to physical battles, which can be energetically demanding (e.g., Riechert 1988; Rovero et al. 2000; deCarvalho et al. 2004; Briffa and Sneddon 2007; Viera et al. 2011) and result in increased predation risk (e.g., Jakobsson et al. 1995; Diniz 2020), injury (e.g., Robertson et al. 1986), or death (e.g., Hof and Hazlett 2012; Lowney et al. 2017; Guo and Dukas 2020). Individuals can settle disputes without incurring these costs by instead signaling during aggressive encounters. Such signals commonly broadcast aggressive intent (e.g., Husak 2004; Van Dyk and Evans 2008; Kareklas et al. 2015), fighting ability (e.g., Clutton-Brock and Albon 1979; Arnott and Elwood 2009), and dominance status (Senar 2006), allowing competitors to assess their chances of winning a physical battle, and thus resolve a dispute, while minimizing risk.

In birds, signals used in aggressive encounters between conspecifics have been well-studied and some generalizations can be drawn. Vocal signals can play a key role in agonistic interactions; specific changes in song can signal step-wise increases in aggressive intent (Searcy and Beecher 2009), and many species signal an impending physical attack by singing soft songs as they approach a competitor (e.g., Dabelsteen et al. 1998; Akçay et al. 2015). In addition, coloration is often an honest signal of dominance status among conspecific birds, with dominant individuals in many species having larger, and sometimes more intense, badges of

63 status (Senar 2006). These badges often involve melanin pigmentation, but other types of
64 coloration are also used, depending on the species (Senar 2006, Santos et al. 2011).
65 Interference competition, however, does not just occur between conspecifics;
66 aggressive encounters frequently involve members of different species that compete for shared
67 and limiting resources (Peiman and Robinson 2010; Figure 1). Like intraspecific disputes, these
68 interactions can be costly (e.g., Livezey and Humphrey 1985; Nuechterlein and Storer 1985;
69 Potti et al. 2021), suggesting that selection should favor the use of signals among
70 heterospecifics during aggressive contests, but the signals used among competing species
71 remain less explored (Caro and Allen 2017). Some studies, however, suggest that vocalizations
72 (e.g., Gorton 1977; Catchpole 1978; Rice 1978; Reed 1982; Martin et al. 1996; Martin and
73 Martin 2001, Jankowski et al. 2010; Sosa-López et al. 2017) and color (e.g., Flack 1976; König
74 1983; Snow and Snow 1984) may signal aggression or dominance in competitive contests
75 among species. Furthermore, several species of birds appear to signal their subordinance to
76 avoid heterospecific aggression from co-occurring dominant species (Gill 1971; Sætre et al.
77 1993). These examples lead to the general question: what signals do birds use in aggressive
78 contests among species, and how do these signals vary across diverse groups of birds?
79 Here, we review photographic and video evidence of aggressive interactions among
80 species of birds contesting a resource to describe the aggressive signals used by different
81 species and taxonomic groups. Specifically, we reviewed photographs and video of aggressive
82 signaling among species, and used this evidence to (1) identify postures, body regions, and
83 colors used to signal aggression towards competing species, and (2) compare these postures
84 and body regions to those used to signal aggression towards conspecifics. For groups with

sufficient sample sizes, we also used this evidence to assess variation in postures and body regions used by different individuals (3) within species, and (4) among taxonomic families of birds.

2 | MATERIALS AND METHODS

2.1 | Signal data

We compiled published videos and photographs of aggressive signaling between different species of birds in the context of competition or defense of resources. The majority of the videos and photographs (*N*=259) that we used were available from WikiAves (https://www.wikiaves.com.br/), a Brazilian-based website for birdwatching and citizen science, where users can publish photos and recordings in a searchable database focused on Brazil and nearby countries (since 2008). Our goal was to find material documenting the interspecific signals used by diverse groups of birds, and thus we prioritized material representing diverse taxonomic families; the avian biodiversity of South America represented in the WikiAves database provided an excellent foundation for this dataset.

We relied on descriptions of the context of the videos or photographs to ensure that we included only media capturing aggressive encounters in our dataset. In WikiAves, we used the "Advanced Search" tool, filtering under "Main Action" to include only "fighting" interactions, and then used only the resulting images involving interactions among multiple species (database searched July 2019). Similarly, we searched the Internet Bird Collection database (HBW.com, searched July 2019, now available in The Cornell Lab of Ornithology Macaulay

Library: macaulaylibrary.org) for media with captions including the word “fight*” and included only results depicting interspecific interactions in our study. We note that the Macaulay Library – an excellent source for photographs and video – did not have the advanced search options to identify fighting birds, and thus we omitted this data source from our study. We included additional images of interspecific aggressive interactions from other sources (e.g., Martin and Briskie 2020; YouTube.com: searched July 2019 for specific taxa and the search term “fight”) for certain groups that were underrepresented in our dataset to increase the taxonomic breadth of our study. Sources and credit for each item are listed in our data set.

We further refined our dataset to focus only on signals used in aggressive interactions between heterospecifics. We did not include photographs or video segments that depicted direct fights (i.e., physical contact between competitors) or chases, and instead focused on displays that did not involve contact between focal individuals. We note that signals used during direct fights and chases were thus omitted from our study, and could be different from those used in aggressive signaling without contact. In addition, we did not include birds that were retreating from a resource or interaction in our dataset because we wished to characterize aggressive signals; retreating from a resource or interaction meant that the focal bird was no longer aggressively challenging other species. Retreating birds may signal submission to aggressive heterospecifics (see also Gill 1971; Sætre et al. 1993); however, our study was not designed to identify such signals. We considered a bird as retreating from a resource or interaction when it appeared to be actively moving away from the resource or aggressively signaling heterospecific, respectively (e.g., beginning to fly or move away). For

127 photographs, we used only images that appeared to capture a full display or signal, although
128 we could not always be sure that the image captured the point of peak intensity.
129 Our dataset is comprised of photographs and videos (*N* = 337 interactions) of 164
130 different bird species from 120 genera, 50 families, and 24 orders, following the IOC World Bird
131 List taxonomy (Gill et al. 2020). It includes a diversity of aggressive interactions, with birds
132 signaling from a perch (53%), the ground (16%), the air (22%), and the water (9%). While
133 interactions from South America comprise the majority of our dataset (*N*=259), we also include
134 interactions from Africa (*N*=17), Europe (*N*=15), North America (*N*=14), Oceania (*N*=12), Asia
135 (*N*=9), and Antarctica (*N*=7). For each aggressive encounter, we documented details of the
136 signaler's posture, and the body regions and colors that were highlighted in the signal.
137

138 **Postures**

139 We examined the postures used during aggressive encounters with heterospecifics by
140 categorizing the posture of each focal bird in our dataset focusing on eight different
141 components (Table 1). We categorized the overall body orientation and the position of six
142 different body regions including head, wing, shoulder, bill, tail, and feet. We also recorded
143 which part of the signaler's body was closest to the receiver (i.e., the heterospecific individual
144 to which the focal individual was signaling). We define each category of posture with photo
145 examples in Table SI.
146

147 **Body regions highlighted by signaling birds**

148 We identified body regions that focal individuals featured most prominently (i.e.,
149 highlighted) in aggressive displays, grouping regions by location on the bird and their likelihood
150 of being collectively visible. Some regions that are typically examined separately in studies of
151 coloration (e.g., lores, forehead, auriculars, chin, throat) tended to be visible together, and thus
152 we grouped them for our analyses (e.g., face/throat). We illustrate the regions included in our
153 study in Figure 3a. We defined highlighted regions as those that were most obviously displayed
154 or modified for display to the receiver (e.g., opened mouth, raised crest, flared auriculars),
155 often centrally positioned in the display. Distinguishing between these highlighted regions is
156 somewhat subjective; thus, each photograph or video was examined separately by three naïve
157 human observers, who each recorded up to three regions that they perceived as most
158 highlighted by the signaler from the positional perspective of the heterospecific receiver. For
159 our analyses, we considered a body region to be highlighted in an interaction if it was indicated
160 as highlighted by at least two of the three observers.

161

162 **Colors highlighted by signaling birds**

163 We summarized the colors used in interspecific aggressive signaling by recording the
164 colors that focal birds most commonly highlighted in aggressive signals towards other species.
165 The three naïve observers recorded which three colors or color groups were most prominently
166 featured (i.e., highlighted) by the signaler in each interaction from the positional perspective of
167 the heterospecific receiver, categorizing colors or color groups as: carotenoid
168 (red/orange/pink/yellow), structural (blue/green/violet), black, white, rufous/chestnut,

169 brown/beige, gray, or contrasting black/dark and white. For our analyses, we considered a color
170 or color group to be highlighted in an interaction if it was indicated as highlighted by at least
171 two of the three observers. We note that in most signals these are the colors of the body
172 regions that were identified as highlighted, or parts thereof, but in others these may be the
173 colors of different body regions or a single body region.
174 To differentiate between colors that were present in a signaling species, but were not
175 highlighted, and those that were not present, we consulted written descriptions of the
176 coloration of each species in our study. We relied on color descriptions from Birds of the World
177 (Billerman et al. 2020) for all species, except for one species (*Leptoptilos crumenifer*), which was
178 missing a complete color description in this source; we thus consulted another source for a
179 complete color description for this species (Neudamm 1900). References for the color
180 descriptions that we used for all species in our study are available in our dataset. For each
181 species, focal colors or color groups that are present, but not highlighted in a focal interaction
182 are indicated by 0 in our dataset, and focal colors or color groups that are not present in the
183 focal species are indicated by NA, and thereby excluded from the analysis. Appendix III provides
184 more information about the color names considered to be part of each focal color category.

185 **Relationship to intraspecific signals**

186 We addressed whether interspecific aggressive signals differed from signals used in
187 intraspecific aggression by comparing the characteristics of interspecific aggressive signals
188 described above (postures, focal regions for signaling) to the characteristics of signals used in
189 within-species aggressive interactions. We did not incorporate color into these comparisons
190 because some species have uniform coloration and are thus uninformative with respect to

patterns of within- versus among-species signaling. For species already included in our dataset, we found information on intraspecific aggressive signals in published photographs and videos of aggressive interactions (*N* = 141 species). For these species, we also incorporated descriptions of intraspecific aggressive signals from the literature, where available (i.e., for better-studied species: *N* = 20 of the 141 species included in this component of the study). We described the degree of similarity between interspecific and intraspecific aggressive signals as the 'same' if the same postures and highlighted regions were used for both intraspecific and interspecific signaling, 'different' if most (>50%) of the postures and highlighted regions differed, and 'similar' if some, but not most, postures, highlighted regions differed. We were unable to obtain information about intraspecific aggressive signals for some species in our dataset (*N* = 36 interactions); for these species we compared observed signals to intraspecific aggressive signals used by their congeners, where possible (*N* = 6 interactions were designated as 'similar to congener').

2.2 | Statistical tests

We conducted all of our statistical analyses and plotting in R (R Core Team 2020). We provide the R code that we used for our analyses and figures, along with our dataset, as Supporting Information.

We used Bayesian phylogenetic mixed-effects models using the *MCMCglmm* function in the *MCMCglmm* R package (version 2.32; Hadfield 2010) to test whether birds were more likely to use specific postures, highlight specific body regions or colors, or use the same signals as in intraspecific interactions in aggressive encounters with heterospecifics. This allowed us to

incorporate the effects of phylogeny in our analyses; we obtained a phylogeny for the signaling species in our dataset from Jetz et al. (2012; birdtree.org; maximum clade credibility tree of 1,000 Hackett all-species trees; Figure S1). We included the phylogeny and *focal.interaction* as random effects in each model. We did not specify priors for fixed effects so that all variance parameters were estimated (Hadfield 2018), but specified priors where V=1 and nu=2 for both R and G structures (Hadfield 2010, 2018). We used a categorical (i.e., binomial) distribution and ran simulations for 1,000,000 iterations (burnin = 10,000 iterations, thinning interval = 1). We provide details about model diagnostics in the Supporting Information. We used the *pairs* function in the *emmeans* R package, v. 1.5.3 (Lenth 2020) to conduct post hoc Tukey's contrasts between categorical predictors in our models, testing whether the pairwise differences between estimated likelihoods differ significantly from zero.

We used a separate model for each component of posture (i.e., body orientation, head position, etc.) to test whether different positions of each component (e.g., forward.lowered, forward.upright, etc.) were equally likely to be assumed in interspecific aggressive interactions. We used a binary response variable indicating whether each position was assumed (1 = position assumed; 0 = position not assumed) as the response variable, and position as a categorical predictor variable. To describe the body regions most commonly highlighted in aggressive signals, we examined the proportion of interactions in our dataset which highlighted each body region (as indicated by at least 2/3 naïve observers). To test whether certain body regions were most likely to be highlighted, we used a binary response variable indicating whether the focal body region was highlighted (1 = highlighted; 0 = not highlighted) as the response variable and body region as a categorical predictor variable. We excluded three body regions from our

analysis (uppertail coverts, undertail coverts, and tarsal feathers) because they were never identified as the most highlighted body regions in our dataset.

Similarly, to describe the color or color groups most commonly highlighted in aggressive signals, we calculated the proportion of interactions in our dataset which highlighted each color or color group (as indicated by at least 2/3 naïve observers). To test whether certain colors or color groups were most likely to be highlighted, we used a binary response variable indicating whether the focal color was highlighted (1 = highlighted; 0 = not highlighted) as the response variable and color as a categorical predictor variable. Colors or color groups that were not present in the signaling species in each focal interaction were excluded from this analysis.

To understand whether birds use the same signals in aggressive encounters with heterospecifics as in aggressive encounters with members of their own species, we calculated the proportion of interactions in our dataset in which the signal had each degree of similarity (*same*, *similar*, *similar to congener*, or *different*). We used a binary response variable indicating whether each degree of similarity was assumed (1 = yes; 0 = no) as the response variable and degree of similarity as a categorical predictor variable.

To ensure that source format (photo vs video) did not have a large influence on our results, we repeated all MCMCglmm models with the subset of the dataset captured in photographs (*N*=289 interactions; see Appendices VI, VIII, and IX in Supporting Information).

We used binomial tests using the *binom.test* R function to examine the consistency of signals used in aggressive encounters within a species. For species for which we had sufficient data (>6 videos or images) we tested whether the majority of birds in a species (>50%) used

certain postures or highlighted certain body regions during aggressive encounters with heterospecifics.

Finally, to examine how the signals used in interspecific aggressive interactions vary among families, we examined the proportions of each family that used each posture, and highlighted each body region and color. We included only families that were sufficiently represented (>6 videos or images) in our dataset in this exercise (*N* = 14 families).

3 | RESULTS

3.1 | Postures assumed, and body regions and colors highlighted during aggressive encounters with heterospecifics

Birds in our dataset were never equally likely to use each body region position (Figure 2; Table S3). During aggressive interactions with other species, birds in our dataset were most likely to assume a forward-facing, lowered body position (42%; *N* = 337, *P* <0.001; Table S3; Figure 2a), with a forward-facing, lowered head (52%; *N* = 336, *P* <0.001; Table S3; Figure 2b), open wings (57%; *N* = 337, *P* = 0.004; Table S3; Figure 2c), open, forward-facing bills (68%; *N* = 316, *P* < 0.001; Table S3; Figure 2e), and trailing, unfanned tails (39%; *N* = 295, *P* < 0.001; Table S3; Figure 2f). The bill of the majority of birds was the body region held closest to the heterospecific receiver (87%; *N* = 337, *P* < 0.001; Table S3; Figure 2h). Birds in our dataset had their feet planted on a substrate during most aggressive signals (81%, *N* = 326, *P* < 0.001; Table S3; Figure 2g) and were most likely to assume a shoulder position with either their underwing forward (38%), or their wing closed with their shoulder visible (34%; *N* = 336, *P* < 0.001; Table S3; Figure 2d).

277 Birds in our study were most likely to highlight their face and throat area during
278 aggressive signals directed towards heterospecifics (77%; *N* = 337, *P* < 0.001; Figure 3b, 4; Table
279 S6a). The mouth (37%; *N* = 337, *P* < 0.001; Figure 3b, 4; Table S6a), underwings (27%; *N* = 337, *P*
280 < 0.001; Figure 3b, 4; Table S6a), and bill (27%; *N* = 337, *P* < 0.001; Figure 3b, 4; Table S6a) were
281 also more commonly highlighted than other body regions. Birds were most likely to highlight
282 carotenoid colors, including red, pink, orange, and yellow, in the aggressive signals captured in
283 our study (55%; *N* = 337, *P* = 0.02; Figure 3c, 5; Table S6b).
284 Model results for postures, highlighted body regions, and highlighted colors remained
285 similar when run using only the subset of the data obtained from photographs (Appendices VI,
286 VIII), indicating that the source format had little influence on our results.
287

288 **3.2 | Similarity to signals used in aggressive encounters with conspecifics**

289 We scored the similarity of 307 of the interactions in our dataset to signals used during
290 aggressive encounters with conspecifics. The majority of birds in our dataset used the same
291 signal (body position and body regions highlighted) during aggressive encounters with
292 heterospecifics that they use in aggressive encounters with conspecifics (87%; *N* = 307, *P* <
293 0.001; Table S10). Model results remained similar when run using only the subset of the data
294 obtained from photographs (Appendix X), indicating that the source format had little influence
295 on our results.
296

297 **3.3 | Within-species similarity in signals used in aggressive encounters with heterospecifics**

298 Four species were sufficiently represented in our study to be examined for consistency
299 in the signals that they use during aggressive encounters with heterospecifics. Each of these
300 species had several posture categories that remained consistent across all images or videos.
301 *Columbina talpacoti* (Columbidae) always had their wings raised upward and their feet planted
302 on the substrate (N = 7, P = 0.008). *Eupetomena macroura* (Trochilidae) always had a forward,
303 upright body position, a fanned tail pointed down, and held their bill closest to the
304 heterospecific competitor (N = 7, P = 0.008). Similarly, the bill of *Pitangus sulphuratus*
305 (Tyrannidae) was always one of the body parts closest to the other bird (N = 13, P <0.001).
306 *Thraupis sayaca* (Thraupidae) always had an open, forward-facing bill position, planted feet,
307 and again, held their bill closest to the heterospecific competitor (N = 24, P = <0.001).
308 All four species had at least one body region that was highlighted in the majority of
309 signals in our dataset. All *Columbina talpacoti* individuals observed highlighted their underwings
310 (N = 7, P = 0.008). All *Eupetomena macroura* highlighted their face/throat (N = 7, P = 0.008). The
311 majority of *Pitangus sulphuratus* individuals in our dataset highlighted their face/throat region
312 (77%; N = 13, P = 0.046). Similarly, *Thraupis sayaca* individuals in our dataset tended to
313 highlight their face/throat (96%; N = 24, P = <0.001) and mouth (75%; N = 24, P = 0.01).
314

315 **3.4 | Within- and among-family variation in signals used in aggressive encounters with**
316 **heterospecifics**

317 Many birds in our study showed some aspects of their posture that were fairly
318 stereotyped across interspecific aggressive signals by members of their family, and some

postures were fairly unique to a specific family (Figure 6). Members of Falconidae always assumed an underwing.forward shoulder position and typically extended their feet (92%; Table S13). Anatidae and Spheniscidae always positioned their bill forward and open, and had a trailing, unfanned tail (Table S13). Fringillidae and Turdidae also always held their bill open and forward (Table S13). Columbidae was the only family in which most birds in our dataset did not have a forward-oriented body orientation (75% side oriented; Table S13) or head position (58% side oriented; Table S13). Columbidae, Falconidae, and Trochilidae always had open wing positions (i.e., flapping, spread.outward, partially.spread, raised.upward, soaring.gliding; Figure 6; Table S13). While most families in our study positioned their bill closest to their competitor, the bill was not involved in the majority of interspecific aggressive signals by members of Accipitridae (50% feet; Table S13), Columbidae (50% wing; Table S13) or Falconidae (86% feet; Table S13).

Most families in our dataset showed intra-family variation in which body regions were most likely to be highlighted in interspecific aggressive signals (Table S14). Members of Anatidae, however, always highlighted the mouth, while members of Ardeidae, Columbidae, Falconidae, and Icteridae never did so (Figure 4; Table S14). Falconidae was the only family in which most members were most likely to highlight their legs and feet (Figures 4,6; Table S14).

Many colors or color groups were highlighted in many different families included in our study, but we observed some differences among families in the signals commonly used in aggressive interactions with heterospecifics (Figure 5; Table S15). In our dataset members of Diomedeidae always highlighted white and members of Spheniscidae always highlighted contrasting dark and white in aggressive signals. Despite carotenoid colors being commonly

highlighted in most families in our dataset, Columbidae never highlighted red, pink, orange, or yellow, and instead were most likely to highlight gray in aggressive interspecific interactions (Figure 5; Table S15). We note that rufous and chestnut were never the most commonly highlighted colors in any family widely represented in our study, while all families had some representatives that highlighted black (Figure 5; Table S15).

4 | DISCUSSION

Aggressive interactions among competing species can be costly and dangerous (e.g., Livezey and Humphrey 1985; Nuechterlein and Storer 1985; Potti et al. 2021), thus favoring the use of signals that allow individuals to avoid the risk of physical fights with other species (Caro and Allen 2017). Here, we used publicly available videos and photographs of aggressive encounters between different species of birds. Our study includes 164 different bird species from 121 genera, 50 families, and 24 different orders to show broad similarities and key differences in signals directed at competing heterospecifics, examining the postures used, and body regions and colors highlighted during these interactions.

Despite the diversity of taxa examined, most species of birds in our study highlighted weapons used in fighting (bill, talons, wings) (Figure 3b), and held these weapons closest to their heterospecific opponent (Figure 2h). In most species, the bill was directed at the opponent (i.e., oriented forward and held closest to the opponent), either opened (e.g., Anatidae) or closed (e.g., Trochilidae) (Figure 2). We note that the bill may be the closest point to a competitor when a bird is in a neutral position but facing a competitor; however, many birds in our study assumed a forward, lowered body position, which thrusts the bill closer to a

competitor (Figure 2). For species with well-developed talons used in hunting (Accipitridae, Falconidae), the legs, rather than bills, were typically extended outward towards the opponent, with talons opened. These displays required that the birds be positioned in the air; falcons typically achieved these signals while flying with talons dangling, while hawks and related birds either extended their talons while flying, or threw them up towards the opponent from the ground, a perch, or as they approached in the air. Pigeons and doves (Columbidae) stood out as an exception among most birds; they typically lined up sideways to their opponents with one or both wings raised, an underwing closest to the other species. This posture aligns with their unique means of fighting, where they often pound opponents with their wings (e.g., Otis et al. 2020).

Across birds, many species also spread their wings (e.g., Ardeidae, Diomedeidae) and sometimes their tails (e.g., Trochilidae, Falconidae), augmenting their apparent size to their opponents. Body size is the best predictor of behavioral dominance among aggressively competing species of birds and other animals (Morse 1974; Peters 1983; Robinson and Terborgh 1995; Donadio and Buskirk 2006; Martin and Ghalambor 2014; Miller et al. 2017), and thus extending wings and tails to highlight, or even exaggerate, size could provide an important signal of dominance and threat. Spread wings or tails were not components of the most common signals across all families of birds (Figure 6), but these postures were observed in most families in our dataset. Several species also showed striking color patterns associated with extended wings (e.g., bright or contrasting underwing coverts: Ardeidae, Columbidae; eye spots on upperwings, Eurypygidae). Hummingbirds typically signaled in the air with wings moving extremely rapidly; these species most often faced their opponents with fanned tails that

384 exhibited striking color patterns, shapes, and plumes.

385 The highlighting of similar traits (weapons, size) in aggressive signals among diverse
386 species of birds makes sense from the perspective of the evolution of signals to convey
387 information to other species. A signal of aggression towards another species would be most
388 effective if it could be easily understood by any competitor; a species-specific signal, on the
389 other hand, would require that heterospecifics learn the information conveyed in the signal
390 through costly aggressive contests. Weaponry and size provide information about aggressive
391 intent and fighting ability within most species, and thus serve as a 'shared language' when used
392 as a signal towards other species, including distantly-related competitors such as mammals
393 (Kruuk 1967).

394 Few families in our study used postures in aggressive displays that were unique relative
395 to other families (Figure 6). This is in part due to the similarities in many aggressive displays
396 across diverse families of birds (Figures 4, 5), which suggests that our results may be broadly
397 applied. Only two families commonly used postures that were rarely seen in other families (i.e.,
398 where over 70% of individuals using a specific combination of positions were members of the
399 same family). Trochilidae (hummingbirds) often displayed with open or rapidly flapping wings,
400 with a forward orientation, downward facing tails, and closed bills pointing at their opponents.
401 Columbidae (pigeons and doves) often displayed with raised wings and a side orientation. The
402 body regions most highlighted in aggressive displays were also variable within and among
403 families, with similarities among many families (Table S14). Accipitridae and Falconidae,
404 however, were the two families most likely to highlight their legs and feet during displays (Table
405 S14).

406 Carotenoid colors were most commonly highlighted in aggressive encounters with
407 heterospecifics across all species of birds, when they were present (Figure 3c). This may suggest
408 the use of carotenoids to signal dominance or quality in intraspecific interactions seen in some
409 groups (Senar 2006) extends to interspecific interactions. The colors highlighted, however,
410 varied within and among taxonomic families, with some families being instead more likely to
411 highlight white (e.g., Diomedeidae), black (e.g., Icteridae), or contrasting combinations of dark
412 and white colors (e.g., Spheniscidae) (Figures 5, 6, Table S15). Birds commonly highlighted
413 multiple colors in aggressive displays, including rich or warm colors with black and white
414 patches, all in combination (e.g., Figure 5, 6).
415 Aggressive display postures and highlighted colors were fairly consistent within species,
416 with variation in components of the display perhaps reflecting varying intensities of interactions.
417 Even within an extended interaction between two individuals, the displays varied as the birds
418 interacted. For example, video of extended interactions shows birds consistently directing their
419 bills and faces towards the opponent, but their head positions often vary throughout the
420 interaction, as does whether their bills and wings are open (e.g., cranes,
421 https://macaulaylibrary.org/asset/201385401).
422 For most species, aggressive displays towards heterospecific competitors were similar to
423 those directed towards conspecifics (see also Martin and Briskie 2021 for Diomedeidae). This
424 suggests that interactions with other competing species act as a selective pressure on the same
425 displays and traits typically studied from the perspective of intraspecific function (e.g., Figure 1).
426 The broad importance of the bill, face and throat in aggressive signaling with other species
427 (Figure 2h, 3b) is consistent with previous studies (Dow 1975; Kalinoski 1975; Flack 1976), and

suggests that colors and patterns that signal dominance should be more likely to evolve in these regions, and less likely to evolve in regions such as uppertail coverts that were never highlighted in aggressive displays. Nonetheless, some regions involved in aggressive signaling varied among taxonomic groups, suggesting that different regions should be the target of selection for signaling depending on the group. Consistent with this idea, we find brightly colored feet and legs in many falcons and hawks (Brown and Amadon 1968), and bold black, white, and rufous colored underwings in many doves (Goodwin 1970), highlighting these distinct regions in displays. Importantly, we find that certain areas that have been omitted from studies of aggressive signaling (including both those conducted on museum specimens: e.g., Shultz et al. 2017, Cooney et al. 2019; and those using other methods: Martin et al. 2015, Drury et al. 2020), such as bright mouth linings and underwing patterns, are in fact frequently emphasized in the aggressive displays of many bird species.

While the aggressive signals used towards conspecifics and heterospecifics appeared superficially similar, we still have much to learn about how birds use signals in conflicts with heterospecifics. We have compared visual signals used in conspecific and heterospecific interactions at a fairly coarse scale, but more subtle differences may exist. For example, birds often use vocalizations in aggressive interactions with competing species, but how they use these sounds can differ from conspecific interactions. Some birds appear to alter their songs or calls to match or mimic the opposing species (Dobkin 1979; Veerman 1994; Gorissen et al. 2006; Wilson and Scantlebury 2006), while other species will alter the timing of their singing to sing overtop of the songs of subordinate species – a behavior that is not used when presented with conspecific songs (Martin and Martin 2001). Whether birds similarly alter their visual

450 signals in response to competing heterospecifics, perhaps by modifying the frequency or
451 intensity of their displays, remains to be explored.

452 Our study would not have been possible without the resources provided by
453 birdwatchers and community scientists, and in particular, the Brazilian online resource
454 WikiAves. While aggressive interactions among species are common and important for the
455 structure of ecological communities (Peiman and Robinson 2010), aggressive signals are fleeting
456 and difficult to observe. Compilations of photos and videos from many independent observers
457 allowed us a unique opportunity to document aggressive signals on a broader taxonomic scale,
458 illustrating the importance of community science datasets for understanding the intersection
459 between behavioral and community ecology.
460

461 **4.1 | Conclusions**

462 Our review of aggressive signals among competing species of birds explores similarities and
463 differences among diverse species in the postures, and the body regions and colors that they
464 highlight in aggressive displays. The results suggest that signals used in aggressive contests
465 within species are also used among species, and that aggressive interactions with
466 heterospecifics likely act as a selective pressure on many of the same traits used in within-
467 species interactions. These same traits are often subject to a diverse suite of selective pressures
468 (inter-sexual selection, predation, parasitism), creating synergistic and conflicting pressures that
469 shape their evolution. Given the importance of heterospecific aggression and interference
470 competition and as a selective pressure on traits (Peiman and Robinson 2010; Grether et al.

2009, 2013, 2017; Drury et al. 2020), we hope that future studies of trait evolution will consider the function of signaling traits as among-species signals mediating competitive interactions, and their role in dominance interactions and hierarchies among species within communities.

DATA ACCESSIBILITY

We have included all of our data and R code as Supporting Information for review, but will archive it for publication.

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682 **SUPPORTING INFORMATION**

683

684 The following Supporting Information is available for this article online:

685 SUPPORTING INFORMATION

686

687 APPENDIX I: Position categories for each component of posture in our dataset

688 APPENDIX II: Instructions for naïve observers examining images for body regions and

689 colours most highlighted in interspecific aggressive signals

690 APPENDIX III: Color names considered to be synonymous with each focal color or color

691 group

692 APPENDIX IV: Phylogeny of species included in dataset

693 APPENDIX V: Posture model results and diagnostics

694 APPENDIX VI: Posture model results from subset of data obtained from photographs

695 APPENDIX VII: Highlighted body regions and highlighted colors model results and

696 diagnostics

697 APPENDIX VIII: Highlighted body regions and colors model results from subset of data

698 obtained from photographs

699 APPENDIX IX: Degree of similarity to intraspecific aggressive signal model results and

700 diagnostics

701 APPENDIX X: Degree of similarity to intraspecific aggressive signal model results from

702 subset of data obtained from photographs

703 APPENDIX XI: Signals used in aggressive interspecific interactions by family

APPENDIX XII: Supporting Information References

Data files:

aggressive.signals.csv

R code:

aggressive.signals.R

710 **Figure Legends**

711 **FIGURE 1** A male Red-winged Blackbird (*Agelaius phoeniceus*) signals aggressively at a Blue Jay
712 (*Cyanocitta cristata*) at a bird feeder. The study of signaling in Red-winged Blackbirds, and their
713 use of red epaulets, has centered on intraspecific function (Smith 1972; Røskaft and Rohwer
714 1987; Yasukawa and Searcy 2020); however, blackbirds often direct their aggressive displays
715 towards heterospecifics in competitive interactions. Image is a still shot from a Cornell Lab of
716 Ornithology Bird Cam video, available from
717 https://www.youtube.com/watch?v=8QUZEBgeMPk, and reproduced with permission from the
718 Cornell Lab of Ornithology Bird Cams (www.AllAboutBirds.org/Cams). This interaction is an
719 example of one of the interactions included in our dataset.

720

721 **FIGURE 2** Postures assumed during aggressive encounters with heterospecifics: a) body
722 orientation (*N* = 337), b) head position (*N* = 336), c) wing position (*N* = 337), d) shoulder position
723 (*N* = 336), e) bill position (*N* = 316), f) tail position (*N* = 295), g) feet position (*N* = 326), and h)
724 closest point to receiver (*N* = 337). Gray circles show the raw data jittered (1 = posture assumed
725 in focal interaction; 0 = posture not assumed in focal interaction), black points show model
726 estimates back-transformed from log odds, and error bars show 95% credible intervals. Letters
727 in each panel indicate differences between estimates for each posture category; estimates with
728 the same letter are not significantly different from one another.

729

730 **FIGURE 3** Body regions and colors highlighted in aggressive interactions with heterospecifics. a)
731 Body regions included in our study; paintings by Paul R. Martin. b) The face and throat region

732 was the most likely body region to be highlighted in aggressive signals (*N* = 337). c) Carotenoid
733 colors (red, pink, orange, or yellow) were the most likely color group to be highlighted in
734 aggressive signals (carotenoids: *N*=316; blue/green/violet: *N*=189; dark-white contrast: *N*=294;
735 black: *N*=329; brown/beige: *N*=303; gray: *N*=308; white: *N*=299; rufous/chestnut: *N*=132). Gray
736 circles show the jittered raw data (1 = highlighted; 0 = not highlighted), black points show
737 model estimates back-transformed from log odds, and error bars show 95% credible intervals.
738 Letters in each panel indicate differences between estimates for categorical predictors;
739 estimates with the same letter are not significantly different from one another.
740
741 **FIGURE 4** Phylogeny of all species in our dataset and the body regions most commonly
742 highlighted by each species. Each column corresponds to one body region: black bars in a
743 column indicate a region that is highlighted by the focal species in at least half of the
744 interactions in our dataset in which the focal species is the signaler; bars filled with light gray
745 indicate a region that is not highlighted by the focal species (i.e., highlighted in less than half of
746 the interactions in our dataset in which it is the focal species is the signaler). Numbers along the
747 x-axis are branch lengths.
748
749 **FIGURE 5** Phylogeny of all species in our dataset and the colors most likely to be highlighted by
750 each species. Each column corresponds to one color group: darkly filled bars in a column
751 indicate a color/color group that is highlighted by the focal species in at least half of the
752 interactions in our dataset in which the focal species is the signaler (red for
753 red.pink.orange.yellow, blue for blue.green.violet, dark gray for dark.white.contrast, black for

754 black, brown for brown, beige, gray for gray, gray for white, rufous for rufous chestnut); bars
755 filled with light gray indicate a color/color group that is not highlighted by the focal species (i.e.,
756 highlighted in less than half of the interactions in our dataset in which it is the focal species is
757 the signaler); blank spaces indicate colors that are not present in the focal species. Numbers
758 along the x-axis are branch lengths.
759
760 **FIGURE 6** Variation in the most common postures used in aggressive signaling towards
761 heterospecifics across the 14 focal families examined in this study. In most families, signaling
762 birds direct their face and point their bill towards the heterospecific opponent. In Columbidae,
763 signaling birds typically line up sideways, with their underwing closest to the heterospecific
764 opponent. In Accipitridae and Falconidae, signaling birds typically extend their legs so that their
765 talons are closest to the heterospecific opponent. Accipitridae, Trochilidae, Falconidae, and
766 Tynrannidae most commonly signaled in the air, while the rest of the families most common
767 signaled from the ground or water. Illustrated species are: *Tadorna tadorna* (Anatidae),
768 *Eupetomena macroura* (Trochilidae), *Columbina talpacoti* (Columbidae), *Pygoscelis papua*
769 (Spheniscidae), *Diomedea antipodensis gibsoni* (Diomedeidae), *Ardea goliath* (Ardeidae),
770 *Haliaeetus pelagicus* (Accipitridae), *Falco femoralis* (Falconidae), *Megarynchus pitangua*
771 (Tyrannidae), *Turdus merula* (Turdidae), *Euphonia chalybea* (Fringillidae), *Tangara (Thraupis)*
772 *cyanoptera* (Thraupidae), *Icterus pyrrhopterus tibialis* (Icteridae), *Eupsittula aurea* (Psittacidae).
773 Paintings illustrate postures from photos and video of interactions. Paintings by Paul R. Martin.
774
775

776

Table 1(on next page)

Categories used to describe the position of eight different components of a bird's posture.

We define each category of posture with photo examples in Table SI.

Table 1. Categories used to describe the position of eight different components of a bird's posture. We define each category of posture with photo examples in Table SI.

Posture component	Definition	Position categories
Body orientation	overall orientation of the signaler's body	forward-upright forward-lowered forward-normal side-oriented feet-forward above the other species upside-down
Head position	position of the signaler's head relative to their body	forward-upright forward-lowered forward-normal side-oriented held-back-and-upwards
Wing position	position of the signaler's wings relative to their body	flapping (for birds actively flapping or hovering in the air) soaring-gliding spread-outward raised-upward partially-spread closed-flat closed-held-slightly-out closed-raised-off-back
Shoulder position	position of the shoulders (including underwing/upperwing) relative to the receiver	underwing-forward upperwing-forward wing-horizontal (i.e., shoulder forward, flight feathers trailing) wing closed with shoulder visible wing closed with shoulder concealed
Bill position	position of the bill relative to the receiver, and whether it is open or closed	open-forward open-upward

		open-downward open-side closed-forward closed-upward closed-downward closed-side Note: For video segments, we recorded the bill as 'open' if it was opened at some point during the aggressive signaling.
Tail position	position of the tail relative to the body and receiver, and whether or not the tail was fanned	trailing-fanned trailing-not fanned raised-fanned raised-not fanned down-fanned down-not fanned partly raised-fanned partly raised-not fanned side-oriented-fanned side-oriented-not fanned
Feet position	position of the feet	on-substrate (including ground, water or perch) tucked-up extended partially extended hanging
Closest point	closest part of the signaler's body to the receiver	bill feet wing tail breast

1

Figure 1

A male Red-winged Blackbird (*Agelaius phoeniceus*) signals aggressively at a Blue Jay (*Cyanocitta cristata*) at a bird feeder.

The study of signaling in Red-winged Blackbirds, and their use of red epaulets, has centered on intraspecific function (Smith 1972; Røskaft and Rohwer 1987; Yasukawa and Searcy 2020); however, blackbirds often direct their aggressive displays towards heterospecifics in competitive interactions. Image is a still shot from a Cornell Lab of Ornithology Bird Cam video, available from https://www.youtube.com/watch?v=8QUZEBgeMPk, and reproduced with permission from the Cornell Lab of Ornithology Bird Cams (www.AllAboutBirds.org/Cams). This interaction is an example of one of the interactions included in our dataset.

Figure 2

Postures assumed during aggressive encounters with heterospecifics:

a) body orientation (N = 337), b) head position (N = 336), c) wing position (N = 337), d) shoulder position (N = 336), e) bill position (N = 316), f) tail position (N = 295), g) feet position (N = 326), and h) closest point to receiver (N = 337). Gray circles show the raw data jittered (1 = posture assumed in focal interaction; 0 = posture not assumed in focal interaction), black points show model estimates back-transformed from log odds, and error bars show 95% credible intervals. Letters in each panel indicate differences between estimates for each posture category; estimates with the same letter are not significantly different from one another.

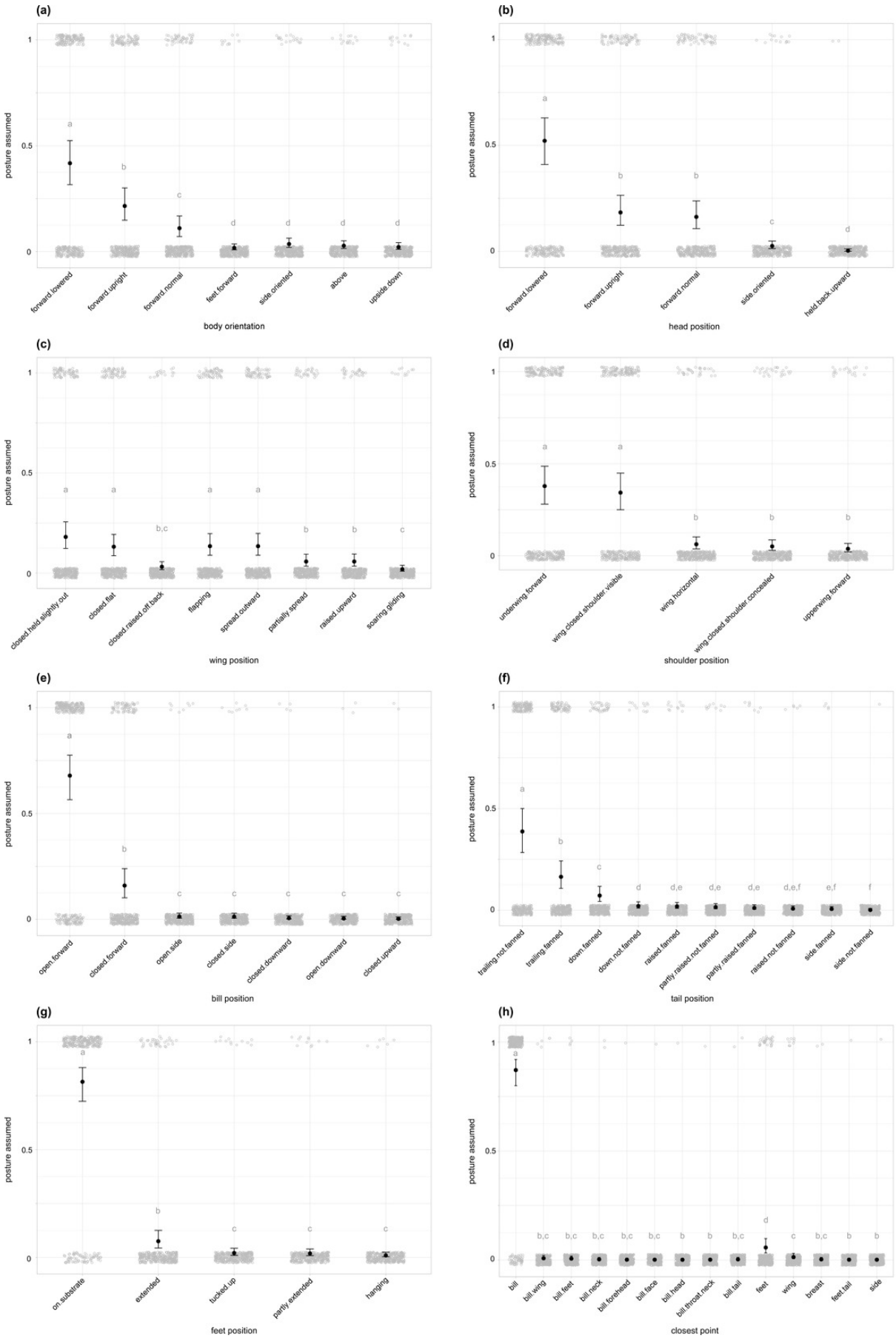
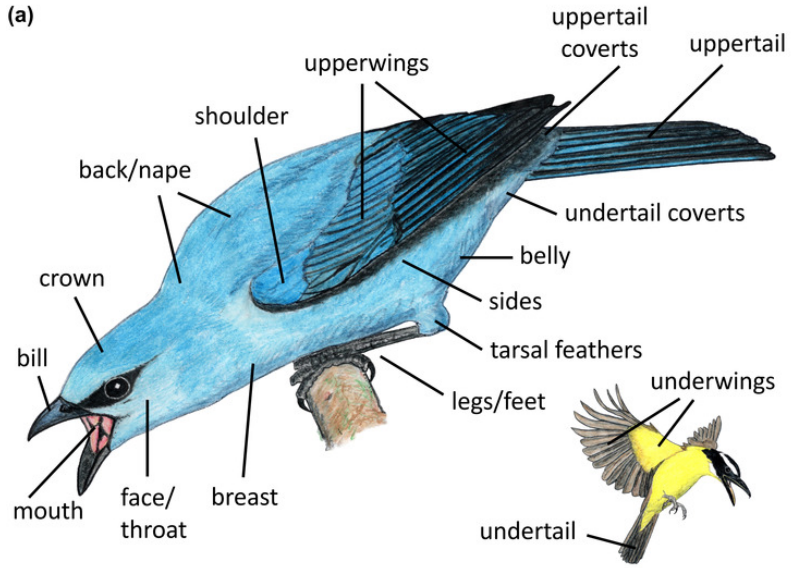
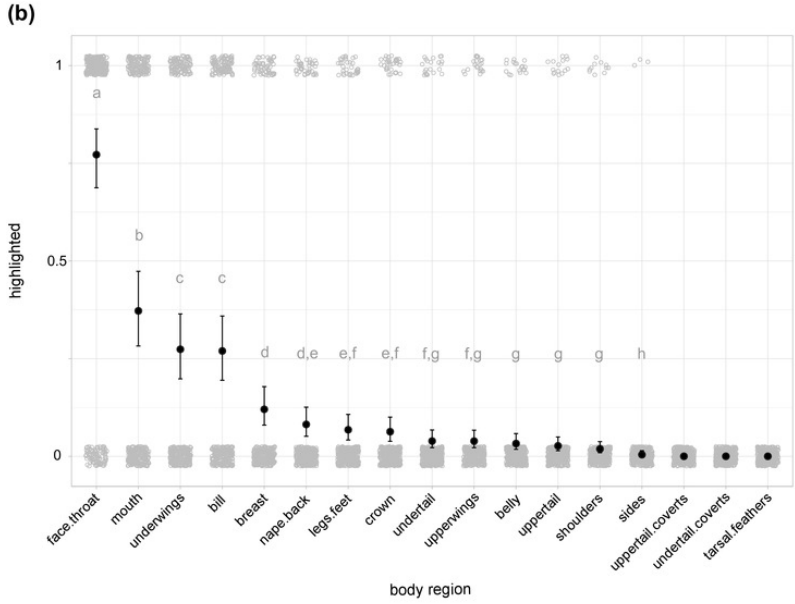

(a)
posture assumed
body orientation
forward.lowered
forward.upright
forward.normal
feet.forward
side.oriented
above
upside.down
(b)
posture assumed
head position
forward.lowered
forward.upright
forward.normal
side.oriented
held.back.upward
(c)
posture assumed
wing position
closed.held.slightly.out
closed.flat
closed.raised.off.back
flapping
spread.outward
partially.spread
raised.upward
soaring.gliding
(d)
posture assumed
shoulder position
underwing.forward
wing.closed.shoulder.visible
wing.horizontal
wing.closed.shoulder.concealed
upperwing.forward
(e)
posture assumed
bill position
open.forward
closed.forward
open.side
closed.side
closed.downward
open.downward
closed.upward
(f)
posture assumed
tail position
trailing.not.fanned
trailing.fanned
down.fanned
down.not.fanned
raised.fanned
partly.raised.not.fanned
partly.raised.fanned
raised.not.fanned
side.fanned
side.not.fanned
(g)
posture assumed
feet position
on.substrate
extended
tucked.up
partly.extended
hanging
(h)
posture assumed
closest point
bill
bill.wing
bill.feet
bill.neck
bill.forehead
bill.face
bill.head
bill.throat.neck
bill.tail
feet
wing
breast
feet.tail
side

Figure 3

Body regions and colors highlighted in aggressive interactions with heterospecifics.

a) Body regions included in our study; paintings by Paul R. Martin. b) The face and throat region was the most likely body region to be highlighted in aggressive signals (N = 337). c) Carotenoid colors (red, pink, orange, or yellow) were the most likely color group to be highlighted in aggressive signals (carotenoids: N=316; blue/green/violet: N=189; dark-white contrast: N=294; black: N=329; brown/beige: N=303; gray: N=308; white: N=299; rufous/chestnut: N=132). Gray circles show the jittered raw data (1 = highlighted; 0 = not highlighted), black points show model estimates back-transformed from log odds, and error bars show 95% credible intervals. Letters in each panel indicate differences between estimates for categorical predictors; estimates with the same letter are not significantly different from one another.


(a)
uppertail coverts
uppertail
upperwings
shoulder
back/nape
undertail coverts
belly
crown
sides
bill
tarsal feathers
underwings
legs/feet
mouth
face/ throat
breast
undertail


(b)
highlighted
1
0.5
0
a
b
c
c
d
d,e
e,f
e,f
f,g
f,g
g
g
g
h
face.throat
mouth
underwings
bill
breast
nape.back
legs.feet
crown
undertail
upperwings
belly
uppertail
shoulders
sides
uppertail.coverts
undertail.coverts
tarsal.feathers
body region

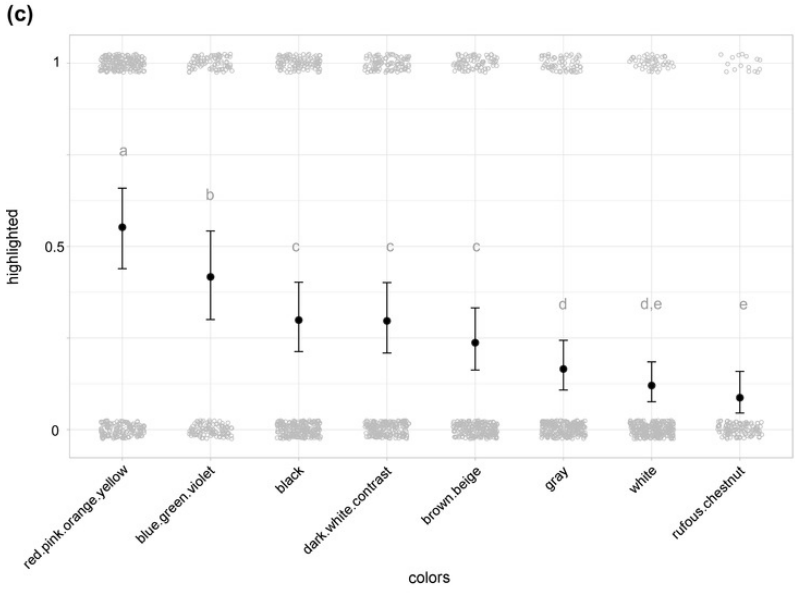

(c)
highlighted
1
0.5
0
a
b
c
c
c
d
d,e
e
red.pink.orange.yellow
blue.green.violet
black
dark.white.contrast
brown.beige
gray
white
rufous.chestnut
colors

Figure 4

Phylogeny of all species in our dataset and the body regions most commonly highlighted by each species.

Each column corresponds to one body region: black bars in a column indicate a region that is highlighted by the focal species in at least half of the interactions in our dataset in which the focal species is the signaler; bars filled with light gray indicate a region that is not highlighted by the focal species (i.e., highlighted in less than half of the interactions in our dataset in which it is the focal species is the signaler). Numbers along the x-axis are branch lengths.

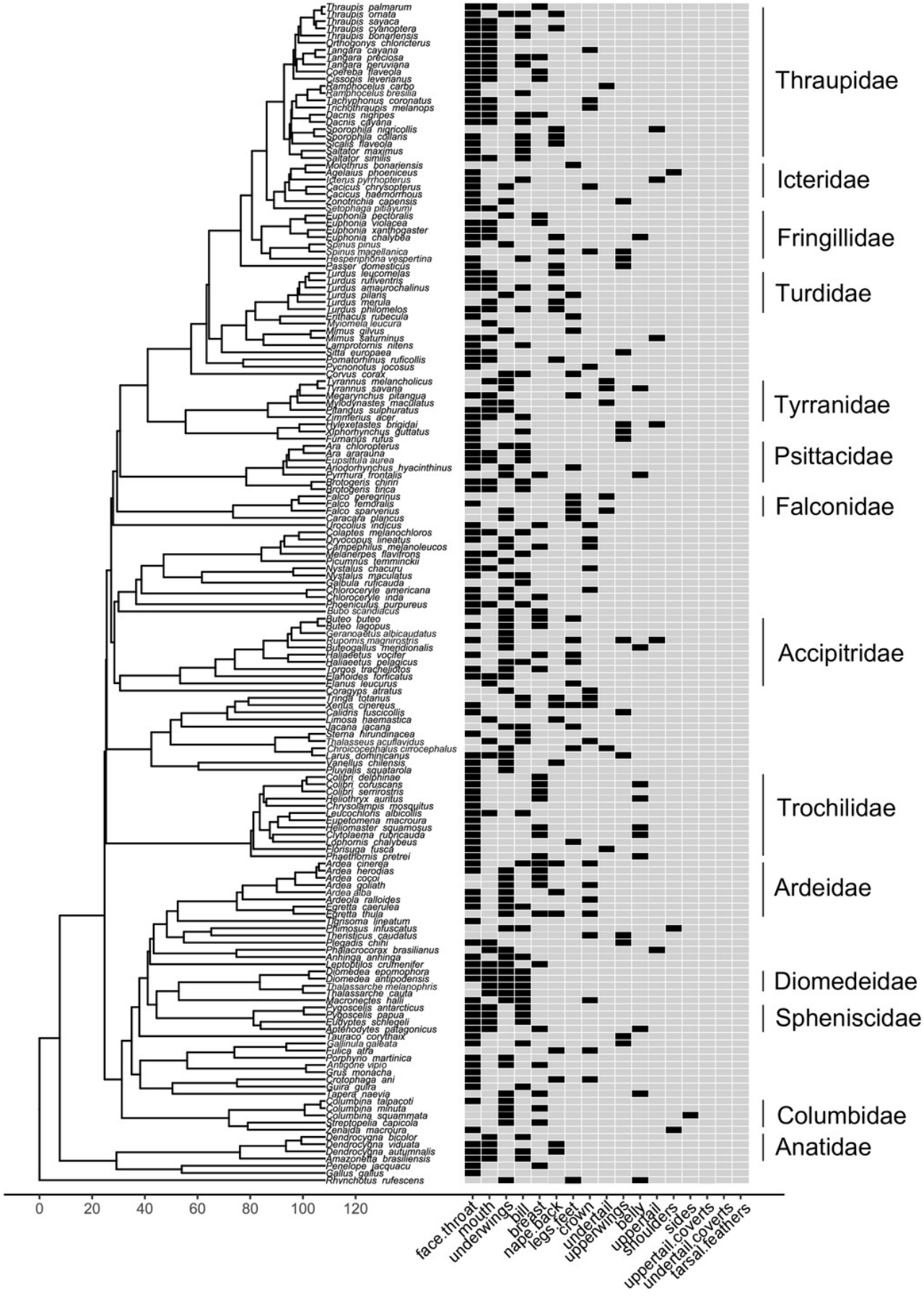

Thraupidae
Icteridae
Fringillidae
Turdidae
Tyrranidae
Psittacidae
Falconidae
Accipitridae
Trochilidae
Ardeidae
Diomedeidae
Spheniscidae
Columbidae
Anatidae
0
20
40
60
80
100
120
face.throat
mouth
underwings
bill
breast
nape.back
legs.feet
crown
undertail
upperwings
belly
uppertail
shoulders
uppertail.sides
undertail.coverts
tarsal.feathers

Figure 5

Phylogeny of all species in our dataset and the colors most likely to be highlighted by each species.

Each column corresponds to one color group: darkly filled bars in a column indicate a color/color group that is highlighted by the focal species in at least half of the interactions in our dataset in which the focal species is the signaler (red for red.pink.orange.yellow, blue for blue.green.violet, dark gray for dark.white.contrast, black for black, brown for brown, beige, gray for gray, gray for white, rufous for rufous chestnut); bars filled with light gray indicate a color/color group that is not highlighted by the focal species (i.e., highlighted in less than half of the interactions in our dataset in which it is the focal species is the signaler); blank spaces indicate colors that are not present in the focal species. Numbers along the x-axis are branch lengths.

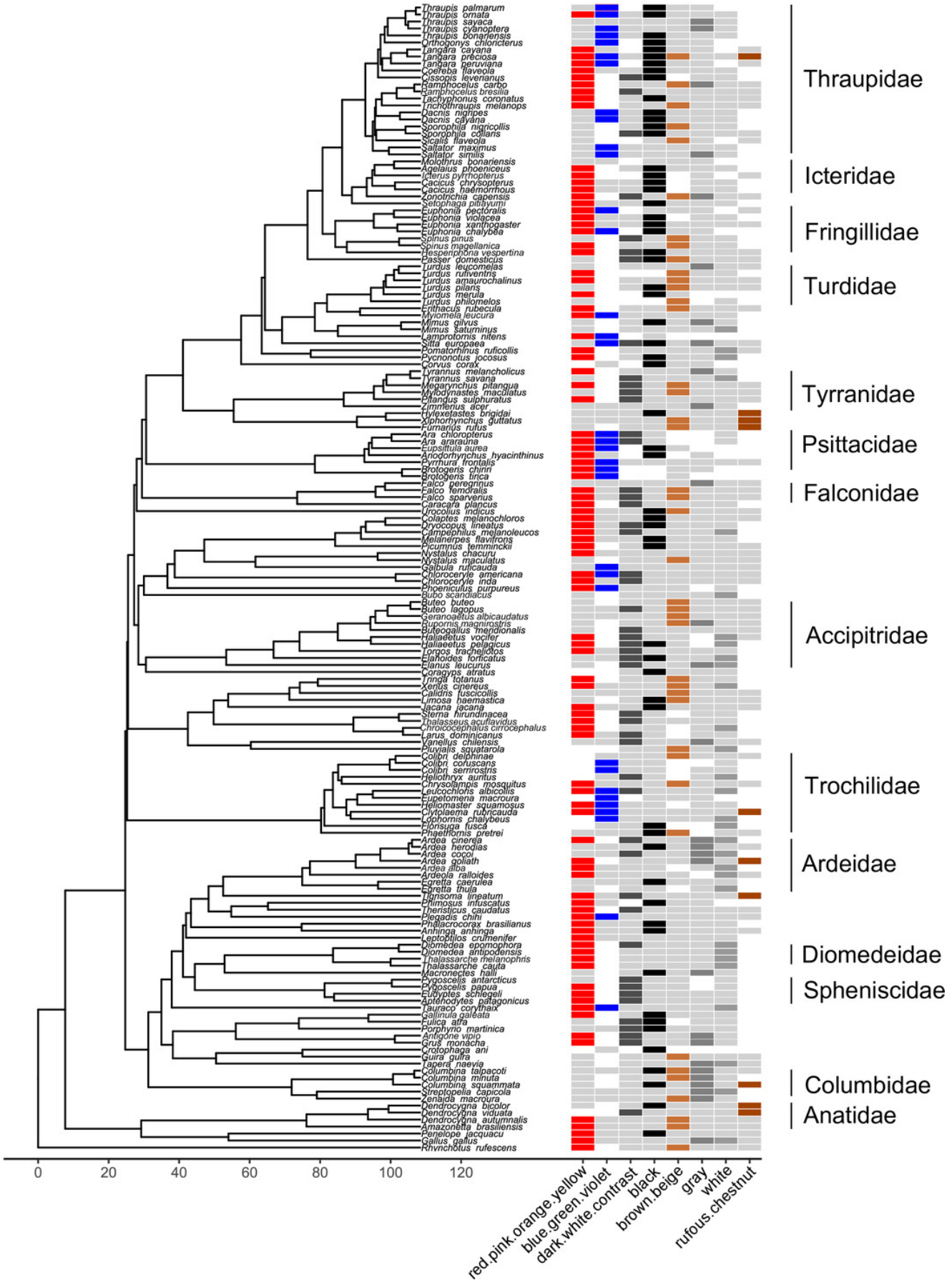
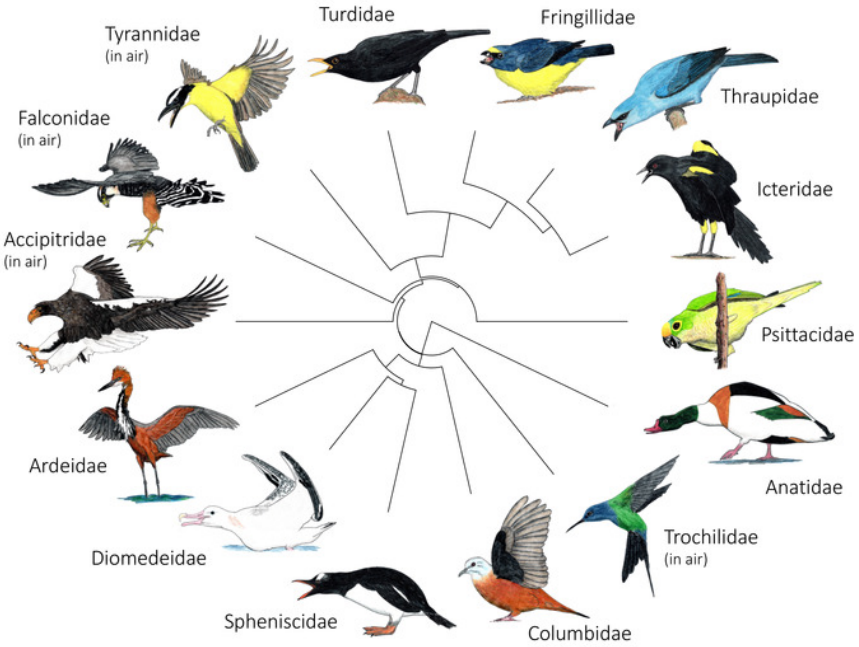

Thraupis palmarum
Thraupis ornata
Thraupis sayaca
Thraupis cyanoptera
Thraupis bonariensis
Orthogonys chloricterus
Tangara cayana
Tangara preciosa
Tangara peruviana
Coereba flaveola
Cissopis leverianus
Ramphocelus carbo
Ramphocelus bresilia
Tachyphonus coronatus
Trichothraupis melanops
Dacnis nigripes
Dacnis cayana
Sporophila nigricollis
Sporophila collaris
Sicalis flaveola
Saltator maximus
Saltator similis
Molothrus bonariensis
Agelaius phoeniceus
Icterus pyrrhopterus
Cacicus chrysopterus
Cacicus haemorrhous
Zonotrichia capensis
Setophaga pitiayumi
Euphonia pectoralis
Euphonia violacea
Euphonia xanthogaster
Euphonia chalybea
Spinus pinus
Spinus magellanica
Hesperiphona vespertina
Passer domesticus
Turdus leucomelas
Turdus rufiventris
Turdus amaurochalinus
Turdus pilaris
Turdus merula
Turdus philomelos
Erithacus rubecula
Myiomela leucura
Mimus gilvus
Mimus saturninus
Lamprotornis nitens
Sitta europaea
Pomatorhinus ruficollis
Pycnonotus jocosus
Corvus corax
Tyrannus melancholicus
Tyrannus savana
Megarynchus pitangua
Myiodynastes maculatus
Pitangus sulphuratus
Zimmerius acer
Hylexetastes brigidai
Xiphorhynchus guttatus
Furnarius rufus
Ara chloropterus
Ara ararauna
Eupsittula aurea
Anodorhynchus hyacinthinus
Pyrrhura frontalis
Brotogeris chiriri
Brotogeris tirica
Falco peregrinus
Falco femoralis
Falco sparverius
Caracara plancus
Urocolius indicus
Colaptes melanochloros
Dryocopus lineatus
Campephilus melanoleucos
Melanerpes flavifrons
Picumnus temminckii
Nystalus chacuru
Nystalus maculatus
Galbula ruficauda
Chloroceryle americana
Chloroceryle inda
Phoeniculus purpureus
Bubo scandiacus
Buteo buteo
Buteo lagopus
Geranoaetus albicaudatus
Rupornis magnirostris
Buteogallus meridionalis
Haliaeetus vocifer
Haliaeetus pelagicus
Lorgos trachelotos
Elanoides forficatus
Elanus leucurus
Coragyps atratus
Tringa totanus
Xenus cinereus
Calidris fuscicollis
Limosa haemastica
Jacana jacana
Sterna hirundinacea
Thalasseus acuflavidus
Chroicocephalus cirrocephalus
Larus dominicanus
Vanellus chilensis
Pluvialis squatarola
Colibri delphinae
Colibri coruscans
Colibri serrirostris
Heliothryx auritus
Chrysolampis mosquitus
Leucochloris albicollis
Eupetomena macroura
Heliomaster squamosus
Clytolaema rubricauda
Lophornis chalybeus
Florisuga fusca
Phaethornis pretrei
Ardea cinerea
Ardea herodias
Ardea cocoi
Ardea goliath
Ardea alba
Ardeola ralloides
Egretta caerulea
Egretta thula
Tigrisoma lineatum
Phimosus infuscatus
Theristicus caudatus
Plegadis chihi
Phalacrocorax brasilianus
Anhinga anhinga
Leptodontos crumenifer
Diomedea epomophora
Diomedea antipodensis
Thalassarche melanophris
Thalassarche cauta
Macronectes halli
Pygoscelis antarcticus
Pygoscelis papua
Eudyptes schlegeli
Aptenodytes patagonicus
Tauraco corythaix
Gallinula galeata
Fulica atra
Porphyrio martinica
Antigone vipio
Grus monacha
Crotophaga ani
Guira guira
Taperá naevia
Columbina talpacoti
Columbina minuta
Columbina squammata
Streptopelia capicola
Zenaida macroura
Dendrocygna bicolor
Dendrocygna viduata
Dendrocygna autumnalis
Amazonetta brasiliensis
Penelope jacquacu
Gallus gallus
Rhynchotus rufescens
Thraupidae
Icteridae
Fringillidae
Turdidae
Tyrranidae
Psittacidae
Falconidae
Accipitridae
Trochilidae
Ardeidae
Diomedeidae
Spheniscidae
Columbidae
Anatidae
0
20
40
60
80
100
120
red.pink.orange.yellow
blue.green.violet
dark.white.contrast
black
brown.beige
gray
white
rufous.chestnut

Figure 6

Variation in the most common postures used in aggressive signaling towards heterospecifics across the 14 focal families examined in this study.

In most families, signaling birds direct their face and point their bill towards the heterospecific opponent. In Columbidae, signaling birds typically line up sideways, with their underwing closest to the heterospecific opponent. In Accipitridae and Falconidae, signaling birds typically extend their legs so that their talons are closest to the heterospecific opponent. Accipitridae, Trochilidae, Falconidae, and Tynrannidae most commonly signaled in the air, while the rest of the families most common signaled from the ground or water. Illustrated species are: *Tadorna tadorna* (Anatidae), *Eupetomena macroura* (Trochilidae), *Columbina talpacoti* (Columbidae), *Pygoscelis papua* (Spheniscidae), *Diomedea antipodensis gibsoni* (Diomedeidae), *Ardea goliath* (Ardeidae), *Haliaeetus pelagicus* (Accipitridae), *Falco femoralis* (Falconidae), *Megarynchus pitangua* (Tyrannidae), *Turdus merula* (Turdidae), *Euphonia chalybea* (Fringillidae), *Tangara (Thraupis) cyanoptera* (Thraupidae), *Icterus pyrrhopterus tibialis* (Icteridae), *Eupsittula aurea* (Psittacidae). Paintings illustrate postures from photos and video of interactions. Paintings by Paul R. Martin.


Turdidae
Fringillidae
Tyrannidae
(in air)
Thraupidae
Falconidae
(in air)
Icteridae
Accipitridae
(in air)
Psittacidae
Anatidae
Ardeidae
Trochilidae
(in air)
Diomedeidae
Spheniscidae
Columbidae