# Aggressive signaling among competing species of birds

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14 **Abstract**

15 Aggressive interactions help individuals to gain access to and defend resources, but they can be

16 costly, leading to increased predation risk, injury, or death. Signals involving sounds and color

17 can allow birds to avoid the costs of intraspecific aggressive encounters, but we know less

18 about agonistic signaling between species, where fights can be frequent and just as costly. Here,

19 we review photographic and video evidence of aggressive interactions among species of birds

20 ($N$ = 337 interactions documenting the aggressive signals of 170 different bird species from 121

21 genera and 50 families) to document how individuals signal in aggressive encounters among

22 species, and explore whether these visual signals are similar to those used in aggressive

23 encounters with conspecifics. Despite the diversity of birds examined, most aggressively

24 signaling birds displayed weapons (bills, talons, wings) used in fighting and placed these

25 weapons closest to their heterospecific opponent when signaling. Most species oriented their

26 bodies and heads forward with their bills pointing towards their heterospecific opponent, often

27 highlighting their face, throat, mouth, and bill. Many birds also opened their wings and/or tails,

28 increasing their apparent size in displays, consistent with the importance of body size in

29 determining behavioral dominance among species. Aggressive postures were often similar

30 across species and taxonomic families. Exceptions included Accipitridae and Falconidae, which

31 often highlighted their talons in the air, Columbidae, which often highlighted their underwings

32 from the side, and Trochilidae, which often hovered upright in the air and pointed their fanned

33 tail downward. Most species highlighted bright carotenoid-based colors in their signals, but

34 highlighted colors varied across species and often involved multiple colors in combination (e.g.,

35 black, white, and carotenoid-based colors). Finally, birds tended to use the same visual signals

36 in aggressive encounters with heterospecifics that they use in aggressive encounters with

37 conspecifics, suggesting that selection from aggressive interactions may act on the same

38 signaling traits regardless of competitor identity.

40 **Keywords:** *interspecific aggression, signals, agonistic interactions, dominance hierarchies,*

41 *competition, fighting, color badges*

43   **1 | INTRODUCTION**

44       Aggressive behaviors help individuals to gain access to and defend resources such as

45   food, territories, mates, nesting sites, display sites, and roosting sites. These behaviors,

46   however, can be costly when aggressive encounters escalate to physical battles, which can be

47   energetically demanding (e.g., Riechert 1988; Rovero et al. 2000; deCarvalho et al. 2004; Briffa

48   and Sneddon 2007; Viera et al. 2011) and result in increased predation risk (e.g., Jakobsson et al.

49   1995; Diniz 2020), injury (e.g., Robertson et al. 1986), or death (e.g., Hof and Hazlett 2012;

50   Lowney et al. 2017; Guo and Dukas 2020). Individuals can settle disputes without incurring

51   these costs by instead signaling during aggressive encounters. Such signals commonly broadcast

52   aggressive intent (e.g., Husak 2004; Van Dyk and Evans 2008; Kareklas et al 2015), fighting

53   ability (e.g., Clutton-Brock and Albon 1979; Arnott and Elwood 2009), and dominance status

54   (Senar 2006), allowing competitors to assess their chances of winning a physical battle, and

55   thus resolve a dispute, while minimizing risk.

56       In birds, signals used in aggressive encounters between conspecifics have been well-

57   studied and some generalizations can be drawn. Vocal signals can play a key role in agonistic

58   interactions; specific changes in song can signal step-wise increases in aggressive intent (Searcy

59   and Beecher 2009), and many species signal an impending physical attack by singing soft songs

60   as they approach a competitor (e.g., Dabelsteen et al 1998; Akçay et al 2015). In addition,

61   coloration is often an honest signal of dominance status among conspecific birds, with

62   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). 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. Some studies, however, suggest that vocalizations (e.g., Gorton 1977;

72    Catchpole 1978; Rice 1978; Reed 1982; Martin et al. 1996; Martin and Martin 2001, Jankowski

73    et al. 2010; Sosa-López et al. 2017) and color (e.g., Flack 1976; König 1983; Snow and Snow

74    1984) may signal aggression or dominance in competitive contests among species. Furthermore,

75    several species of birds appear to signal their subordinance to avoid heterospecific aggression

76    from co-occurring dominant species (Gill 1971; Sætre et al. 1993). These examples lead to the

77    general question: what signals do birds use in aggressive contests among species, and how do

78    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

85    sufficient sample sizes, we also used this evidence to compare postures and body regions used

86    by different individuals (3) within species, and (4) among taxonomic families of birds, looking

87    for consistencies and differences.

88

89    **2 | MATERIALS AND METHODS**

90    **2.1 | Signal data**

91        We compiled published videos and photographs of aggressive signaling between

92    different species of birds in the context of competition or defense of resources. The majority of

93    the videos and photographs that we used were available from WikiAves

94    (https://www.wikiaves.com.br/); sources and credit for each item is listed in our data set. Our

95    goal was to find material documenting the signals of diverse groups of birds, and thus we

96    prioritized material representing diverse taxonomic families. We relied on descriptions of the

97    context of the videos or photographs to ensure that we included only media capturing

98    aggressive encounters in our dataset. We did not include direct fights or chases, and instead

99    focused on displays that did not involve contact between focal individuals. In addition, we did

100    not include birds that were retreating from a resource in our dataset. For photographs, we used

101    only images that appeared to capture a full display or signal, although we could not always be

102    sure that the image captured the point of peak intensity.

103        Our dataset is comprised of photographs and videos ($N = 337$ interactions) of 170

104    different bird species from 121 genera, and 50 different families (Gill et al. 2020). It includes a

105    diversity of aggressive interactions, with birds signaling from a perch (53%), the ground (16%),

106    the air (22%), and the water (9%). For each aggressive encounter, we documented details of

107    body orientation and posture, position of the head, wings, shoulders, bill, tail and feet, along

108    with the part of the body positioned closest to the opposite species. We further examined body

109    regions and colors that were most commonly highlighted in aggressive signals.

110

111    **Postures**

112        We examined the postures used during aggressive encounters with heterospecifics by

113    categorizing the posture of each focal bird in our dataset focusing on eight different

114    components (Table 1). We categorized the overall body orientation and the position of six

115    different body regions including head, wing, shoulder, bill, tail, and feet. We also recorded

116    which part of the signaler's body was closest to the receiver (i.e., the heterospecific individual

117    to which the focal individual was signaling). We define each category of posture with photo

118    examples in Table SI.

119

120    **Highlighted body regions**

121        We identified regions of the bird that were most highlighted during the aggressive

122    display, grouping regions by location on the bird and the likelihood of being collectively visible.

123    Some regions typically distinguished in studies of coloration (e.g., lores, forehead, auriculars,

124    chin, throat) were typically visible together, and thus were grouped (e.g., face/throat). We

125    illustrate the regions included in our study in Fig. 1. We defined highlighted regions as those

126    that were most obviously displayed or modified for display to the receiver (e.g., opened mouth,

127  raised crest, flared auriculars), or regions that appeared to highlight contrasting patterns or

128  coloration (e.g., black/white contrasting patches, black throat, bright red crest) that were facing

129  the receiver, often centrally positioned in the display. Distinguishing between these highlighted

130  regions is somewhat subjective; thus, each photograph or video was examined separately by

131  three naïve human observers, who each recorded up to three regions that they perceived as

132  most highlighted in the signal from the positional perspective of the heterospecific opponent.

133  For each image, we considered a body region to be highlighted if it was indicated as highlighted

134  by at least two of the three observers.

135

136  **Highlighted colors**

137      We summarized colors used in interspecific aggressive signaling by recording the colors

138  of focal regions for signaling identified above. The three naïve observers recorded which three

139  colors or color groups were most highlighted in the signal in each image from the positional

140  perspective of the heterospecific opponent, categorizing colors or color groups as: carotenoid

141  (red/orange/pink/yellow), structural (blue/green/violet), black, white, rufous/chestnut,

142  brown/beige, gray, or contrasting black/dark and white. For each image or video, we

143  considered a color or color group to be highlighted if it was indicated as highlighted by at least

144  two of the three observers.

145

146 **Relationship to intraspecific signals**

147      We addressed whether interspecific aggressive signals differed from signals used in

148 intraspecific aggression by comparing the characteristics of interspecific aggressive signals

149 described above (postures, focal regions for signaling) to the characteristics of signals used in

150 within-species aggressive interactions. We did not incorporate color into these comparisons

151 because some species have uniform coloration that would obscure differences in patterns of

152 within- versus among-species signaling. We found information on intraspecific aggressive

153 signals in the literature, or in published photos and video of aggressive interactions (for species

154 less well-known). We described interspecific versus intraspecific aggressive signals as the 'same'

155 if the same postures and highlighted regions were used for both intraspecific and interspecific

156 signaling, 'different' if most (>50%) of the postures and highlighted regions differed, and

157 'similar' if some, but not most, postures, highlighted regions differed. We were unable to obtain

158 information about intraspecific aggressive signals for some species in our dataset ($N$ = 36

159 interactions); for these species we compared observed signals to intraspecific aggressive signals

160 used by their congeners, where possible ($N$ = 6 interactions were designated as 'similar to

161 congener').

162

163 **2.2 | Statistical tests**

164      We conducted all of our statistical analyses and plotting in R (R Core Team, 2020). We

165 provide the R code that we used for our analyses and figures, along with the datasets, as

166 Supporting Information.

167        To describe the postures taken in aggressive encounters, we calculated the proportion

168    of aggressive encounters in which each position was used for all posture components. For each

169    posture component, we included only those aggressive encounters in which the focal body

170    region was visible in our analysis. With the *chisq.test* R function, we used chi-squared goodness-

171    of-fit tests to test whether birds in our dataset were equally likely to use each position for each

172    component of posture. We then used the *binom.test* R function to test whether the majority of

173    birds in our dataset (significantly >50%) used specific positions for each component of posture.

174        To describe the body regions most commonly highlighted in aggressive signals, we

175    calculated the proportion of birds in our dataset which highlighted each body region (as

176    indicated by at least 2/3 naïve observers). We tested whether certain body regions or colors

177    were more likely to be highlighted than others using generalized linear mixed models (glmms)

178    with binomial distributions and a logit link function using the *glmer* function in the *lme4* R

179    package (Bates et al. 2015). To test whether certain body regions were most likely to be

180    highlighted, we used a binary response variable indicating whether the focal body region was

181    highlighted (1 = highlighted; 0 = not highlighted) as the response variable, body region as a

182    categorical predictor variable, and the focal individual as a random effect. We excluded three

183    body regions from our analysis (uppertail coverts, undertail coverts, and tarsal feathers)

184    because they were never identified as the most highlighted body regions in our dataset, and

185    the statistical model could otherwise not converge due to complete separation. To describe the

186    color or color groups most commonly highlighted in aggressive signals, we calculated the

187    proportion of aggressive signals in which each color was highlighted. To test whether certain

188    colors or color groups were most likely to be highlighted, we used a binary response variable

189    indicating whether the focal color was highlighted (1 = highlighted; 0 = not highlighted) as the

190    response variable, color as a categorical predictor variable, and focal interaction as a random

191    effect. We graphically checked model fit for all models (see R code). We calculated confidence

192    intervals for model estimates using the *emmeans* function in the *emmeans* R package (Lenth,

193    2020).

194         We conducted a binomial test using the *binom.test* R function to test whether the

195    majority of birds in our study (>50%) use the same signal (posture and highlighted body

196    regions) during aggressive encounters with heterospecifics as they do with members of their

197    own species. We also used binomial tests to examine the consistency of signals used in

198    aggressive encounters within a species. For species for which we had sufficient data (>6 videos

199    or images) we tested whether the majority of birds in a species (>50%) used certain postures or

200    highlighted certain body regions during aggressive encounters with heterospecifics.

201         We used conditional inference trees to examine how well taxonomic families could be

202    categorized based on their postures, highlighted body regions, or highlighted colors. We

203    included only families that were sufficiently represented (>6 videos or images) in our dataset in

204    this exercise (*N* = 14 families). We used the *ctree* function in the *partykit* R package (Hothorn

205    and Zeileis 2015) to build conditional inference trees, using the family of the focal bird in each

206    video or photograph as the response variable in each tree. To classify families based on posture

207    taken during aggressive encounters, we used all posture components (body orientation, head

208    position, wing position, shoulder position, tail position, feet position, and closest point) as

209    predictors. To classify families based on body regions highlighted in aggressive signals, we used

210    all 17 body regions included in our study (Figure 1) as binary predictor variables (1 = body

211    region highlighted , 0 = body region not highlighted). Similarly, to classify families based on

212    colors highlighted in aggressive signals, we used color or color group (carotenoid, structural,

213    black, white, rufous/chestnut, brown/beige, gray, or contrasting dark and white) as binary

214    predictor variables (1 = color highlighted, 0 = color not highlighted).

215    **3 | RESULTS**

216    **3.1 | Postures taken, and body regions and colors highlighted during aggressive encounters**

217    **with heterospecifics**

218            Birds in our dataset were never equally likely to use each body region position (Table SII).

219    During aggressive interactions with other species, the majority of birds in our dataset had a

220    forward-facing body position (86%; $N$ = 337, $P$ <0.001; Figure 2A), a forward-facing head

221    position (95%; $N$ = 336, $P$ <0.001; Figure 2B), open wings (55%; $N$ = 337, $P$ = 0.025; Figure 2C),

222    open, forward-facing bills (70%; $N$ = 316, $P$ < 0.001; Figure 2E), and trailing tails (71%; $N$ = 295, $P$

223    < 0.001; Figure 2F). The bill of the majority of birds was the closest or one of the closest points

224    to the heterospecific with which they were interacting (88%; $N$ = 337, $P$ < 0.001; Figure 2H).

225    Birds in our dataset had their feet planted on a substrate during most aggressive signals (79%, $N$

226    = 326, $P$ < 0.001; Figure 2G). No one shoulder position was taken in the majority of aggressive

227    signals in our dataset, but most birds had either their underwing forward or their wing closed

228    with their shoulder visible (77%; $N$ = 336, $P$ < 0.001; Figure 2D).

229            Birds in our study were most likely to highlight their face and throat area during

230    aggressive signals directed towards heterospecifics (74%; $N$ = 337, $P$ < 0.001; Figure 3). The

231    mouth (40%; $N$ = 337, $P$ < 0.001; Figure 3), underwings (31%; $N$ = 337, $P$ < 0.001; Figure 3), and

232    bill (31%; $N$ = 337, $P$ < 0.001; Figure 3) were also more commonly highlighted than other body

233    regions. Birds were most likely to highlight carotenoid colors, including red, pink, orange, and

234    yellow, in the aggressive signals captured in our study (50%; $N$ = 337, $P$ < 0.001; Figure 4).

235

236    **3.2 | Similarity to signals used in aggressive encounters with conspecifics**

237    We scored the similarity of 307 of the interactions in our dataset to signals used during

238    aggressive encounters with conspecifics. The majority of birds in our dataset used the same

239    signal (body position and body regions highlighted) during aggressive encounters with

240    heterospecifics that they use in aggressive encounters with conspecifics (82%; $N$ = 307, $P$ <

241    0.001).

242

243    **3.3 | Within-species similarity in signals used in aggressive encounters with heterospecifics**

244    Four species were sufficiently represented in our study to be examined for consistency

245    in the signals that they use during aggressive encounters with heterospecifics. Each of these

246    species had several posture categories that remained consistent across all images or videos.

247    *Columbina talpacoti* (Columbidae) always had their wings raised upward and their feet planted

248    on the substrate ($N$ = 7, $P$ = 0.008). *Eupetomena macroura* (Trochilidae) always had a forward,

249    upright body position, a fanned tail pointed down, and held their bill closest to the

250    heterospecific competitor ($N$ = 7, $P$ = 0.008). Similarly, the bill of *Pitangus sulphuratus*

251    (Tyrannidae) was always one of the body parts closest to the other bird ($N$ = 13, $P$ <0.001).

252    *Thraupis sayaca* (Thraupidae) always had an open, forward-facing bill position, planted feet,

253    and again, held their bill closest to the heterospecific competitor ($N$ = 24, $P$ = <0.001).

254         All four species had at least one body region that was highlighted in the majority of

255    signals in our dataset. All *Columbina talpacoti* individuals observed highlighted their underwings

256    ($N$ = 7, $P$ = 0.008). All *Eupetomena macroura* highlighted their face/throat ($N$ = 7, $P$ = 0.008). The

257    majority of *Pitangus sulphuratus* individuals in our dataset highlighted their face/throat region

258    (77%; $N$ = 13, $P$ = 0.046). Similarly, *Thraupis sayaca* individuals in our dataset tended to

259    highlight their face/throat (96%; $N$ = 24, $P$ = <0.001) and mouth (75%; $N$ = 24, $P$ = 0.01).

260

261    **3.4 | Within- and among-family variation in signals used in aggressive encounters with**

262    **heterospecifics**

263         Wing position is the most important variable for predicting family membership based on

264    a bird's posture during an aggressive encounter ($N$ = 259, $P$ = <0.001; Figure 5). Most of the 14

265    families broadly represented in our study ($N$ = 14 families with seven or more images or videos)

266    most commonly held their wings closed (closed.flat, closed.held.slightly.out,

267    closed.raised.off.back), partially spread, or spread outward, but members of the families

268    Columbidae, Falconidae, Trochilidae, and Tyrannidae more commonly had active wing positions

269    (flapping, raised.upward, soaring.gliding; Figure 5).

270         The mouth was the most important variable for predicting family membership based on

271    which body regions a bird highlighted during an aggressive encounter ($N$ = 259, $P$ <0.001; Figure

272    6). While most families in our dataset showed intra-family variation (Figure 6, Appendix I) in

273    whether the mouth was highlighted in aggressive signals, members of Anatidae always

274    highlighted the mouth, while members of Ardeidae, Columbidae, Falconidae, and Icteridae

275    never did so (Figure 6).

276        Many colors or color groups were highlighted in many different families included in our

277    study (Appendix I), and as a result, the colors most commonly highlighted in aggressive signals

278    to heterospecifics did not accurately predict family membership (Figure 7). We note, however,

279    that in our dataset members of Diomedeidae always highlighted white and members of

280    Spheniscidae always highlighted contrasting dark and white in aggressive signals. Members of

281    Turdidae never highlighted white, contrasting dark and white, or structural colors

282    (blue/green/violet) and Accipitridae and Columbidae never highlighted carotenoid colors

283    (red/orange/pink/yellow).

284    **4 | DISCUSSION**

285        Aggressive interactions among competing species can be costly and dangerous (e.g.,

286    Livezey and Humphrey 1985; Nuechterlein and Storer 1985; Potti et al. 2021), thus favoring the

287    use of signals that allow individuals to avoid the risk of physical fights with other species. Here,

288    we used videos and photographs of aggressive encounters between different species of birds,

289    including 170 different bird species from 121 genera, and 50 different families, to show broad

290    similarities and key differences in signals directed at competing heterospecifics, examining the

291    postures used, and body regions and colors highlighted during these interactions.

292        Despite the diversity of taxa examined, most species of birds in our study highlighted

293    weapons used in fighting (bill, talons, wings) (Figures 3, 6, 8), and held these weapons closest to

294    their heterospecific opponent (Figure 2). In most species, the bill was held closest to, and

295    directed at, the opponent, either opened (e.g., Tyrannidae) or closed (e.g., Trochilidae) (Figure

296    2). For species with well-developed talons used in hunting (Accipitridae, Falconidae), however,

297    the legs, rather than bills, were typically extended outward towards the opponent, with talons

298    opened. These displays required that the birds be positioned in the air; falcons typically

299    achieved these signals while flying with talons dangling, while hawks and related birds either

300    extended their talons while flying, or threw them up towards the opponent from the ground, a

301    perch, or as they approached in the air. Pigeons and doves (Columbidae) stood out as an

302    exception among most birds; they typically lined up sideways to their opponents with one or

303    both wings raised, an underwing closest to the other species. This posture aligns with their

304    unique means of fighting, where they often pound opponents with their wings (e.g., Otis et al.

305    2020).

306          Across birds, many species also spread their wings (e.g., Ardeidae, Diomedeidae) and

307    sometimes their tails (e.g., Trochilidae, Falconidae), augmenting their apparent size to their

308    opponents. Body size is the best predictor of behavioral dominance among aggressively

309    competing species of birds and other animals (Morse 1974; Peters 1983; Robinson and

310    Terborgh 1995; Donadio and Buskirk 2006; Martin and Ghalambor 2014; Miller et al. 2017), and

311    thus extending wings and tails to highlight, or even exaggerate, size could provide an important

312    signal of dominance and threat. Extended wings or tails were not components of the most

313    common signals across all families of birds (Figure 8), but these postures were observed in

314    almost all families. Several species also showed striking color patterns associated with extended

315    wings (e.g., bright or contrasting underwing coverts: Ardeidae, Columbidae; eye spots on

316    upperwings, Eurypygidae). Hummingbirds typically signaled in the air with wings moving

317    extremely rapidly; these species most often faced their opponents with fanned tails that

318    exhibited striking color patterns, shapes, and plumes.

319        The highlighting of similar traits (weapons, size) in aggressive signals among diverse

320    species of birds makes sense from the perspective of the evolution of signals to convey

321    information to other species. A signal of aggression towards another species would be most

322    effective if it could be easily understood by any competitor; a species-specific signal, on the

323    other hand, would require that heterospecifics learn the information conveyed in the signal

324    through costly aggressive contests. Weaponry and size provide information about aggressive

325    intent and fighting ability within most species, and thus serve as a 'shared language' when used

326    as a signal towards other species, including distantly-related competitors such as mammals.

327        The similarities in many aggressive displays across diverse families of birds, and variation

328    in displays within families, made simple distinctions and classification of families by aggressive

329    postures difficult (Figure 5). Only two families commonly used postures that were rarely seen in

330    other families (i.e., where over 70% of individuals using a specific combination of positions were

331    members of the same family). Trochilidae (hummingbirds) often displayed with open or rapidly

332    flapping wings, with a forward orientation, downward facing tails, and closed bills pointing at

333    their opponents. Columbidae (pigeons and doves) often displayed with raised wings and a side

334    orientation. The body regions most highlighted in aggressive displays were also variable within

335    and among families, with similarities among many families (Figure 6). Accipitridae and

336    Falconidae, however, were the two families most likely to highlight their legs and feet during

337    displays (Figure 6).

338     Carotenoid colors were most commonly highlighted in aggressive encounters with

339     heterospecifics across all species of birds (Figure 4). The colors highlighted, however, varied

340     within and among taxonomic families, with some families more likely to highlight white (e.g.,

341     Diomedeidae), black (e.g., Icteridae), or contrasting combinations of dark and white colors (e.g.,

342     Spheniscidae) (Figure 7). Birds commonly highlighted multiple colors in aggressive displays,

343     including rich or warm colors with black and white patches, all in combination (e.g., Figure 8).

344     Aggressive display postures and highlighted colors were fairly consistent within species,

345     with variation in components of the display perhaps reflecting varying intensities of interactions.

346     Even within an extended interaction between two individuals, the displays varied as the birds

347     interacted. For example, video of extended interactions shows birds consistently directing their

348     bills and faces towards the opponent, but their head positions often vary throughout the

349     interaction, as does whether their bills and wings are open (e.g., cranes,

350     https://macaulaylibrary.org/asset/201385401).

351     For most species, aggressive displays towards heterospecific competitors were similar to

352     those directed towards conspecifics (see also Martin and Briskie 2021 for Diomedeidae). This

353     suggests that interactions with other competing species act as a selective pressure on the same

354     displays and traits typically studied from the perspective of intraspecific function (e.g., Figure 9).

355     The broad importance of the bill, face and throat in aggressive signaling with other species

356     (Figure 3) is consistent with previous studies (Dow 1975; Kalinoski 1975; Flack 1976), and

357     suggests that colors and patterns that signal dominance should be more likely to evolve in

358     these regions, and less likely to evolve in regions such as uppertail coverts that were never

359     highlighted in aggressive displays. Nonetheless, some regions involved in aggressive signaling

360    varied among taxonomic groups, suggesting that different regions should be the target of

361    selection for signaling depending on the group. Consistent with this idea, we find brightly

362    colored feet and legs in many falcons and hawks (Brown and Amadon 1968), and bold black,

363    white, and rufous colored underwings in many doves (Goodwin 1970), highlighting these

364    distinct regions in displays. Importantly, studies of aggressive signaling often omit key regions

365    important for signaling, such as the bright mouth linings and underwing patterns that are

366    highlighted in the aggressive displays of many birds.

367            While the aggressive signals used towards conspecifics and heterospecifics appeared

368    superficially similar, we still have much to learn about how birds use signals in conflicts with

369    heterospecifics. For example, birds often use vocalizations in aggressive interactions with

370    competing species, but how they use these sounds can differ from conspecific interactions.

371    Some birds appear to alter their songs or calls to match or mimic the opposing species (Dobkin

372    1979; Veerman 1994; Gorissen et al. 2006; Wilson and Scantlebury 2006), while other species

373    will alter the timing of their singing to sing overtop of the songs of subordinate species – a

374    behavior that is not used when presented with conspecific songs (Martin and Martin 2001).

375    Whether birds use visual signals that are similarly specific to competing heterospecifics remains

376    to be discovered.

377

378    **4.1 | Conclusions**

379    Our review of aggressive signals among competing species of birds highlights similarities and

380    distinctions among diverse species in their postures, highlighted regions, and highlighted colors

381    used in aggressive displays. The results suggest that signals used in aggressive contests within

382   species are also used among species, and that aggressive interactions with heterospecifics likely

383   act as a selective pressure on many of the same traits used in within-species interactions. These

384   same traits are often subject to a diverse suite of selective pressures (inter-sexual selection,

385   predation, parasitism), creating synergistic and conflicting pressures that shape their evolution.

386   Given the importance of heterospecific aggression and interference competition and as a

387   selective pressure on traits (Peiman and Robinson 2010; Grether et al. 2009, 2013, 2017; Drury

388   et al. 2020), we hope that future studies of trait evolution will consider the function of signaling

389   traits as among-species signals mediating competitive interactions, and their role in dominance

390   interactions and hierarchies among species within communities.

391   **DATA ACCESSIBILITY**

392   We have included all of our data and R code as Supporting Information for review, but will

393   archive it for publication.

394

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577 **SUPPORTING INFORMATION**

578

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

580 SUPPORTING INFORMATION

581 TABLE SI: Posture definitions and examples

582 TABLE SII: Posture chi-squared goodness-of-fit test results

583 APPENDIX I: Summary by family

584 Data files:

585 aggressive.signals.csv

586 R code:

587 aggressive.signals.R

588   **Figure Legends**

589   FIGURE 1  Body regions included in our study.

590

591   FIGURE 2  Postures taken during aggressive encounters with heterospecifics: A) body

592   orientation (*N* = 337), B) head position (*N* = 336), C) wing position (*N* = 337), D) shoulder

593   position (*N* = 336), E) bill position (*N* = 316), F) tail position (*N* = 295), G) feet position (*N* = 326),

594   and H) closest point to receiver (*N* = 337).

595

596   FIGURE 3  The face and throat region was most likely body region to be highlighted in

597   aggressive signals (*N* = 337). Gray circles show the raw data (1 = highlighted; 0 = not

598   highlighted), while black points show model estimates back-transformed from log odds, and

599   error bars show 95% confidence intervals.

600

601   FIGURE 4  Carotenoid colors (red, pink, orange, or yellow) were most likely color group to be

602   highlighted in aggressive signals (*N* = 337). Gray circles show the raw data (1 = highlighted; 0 =

603   not highlighted), while black points show model estimates back-transformed from log odds, and

604   error bars show 95% confidence intervals.

605

606   FIGURE 5  Conditional inference tree showing significant associations between postures taken

607   in aggressive encounters and family membership. The box at each terminal node contains *n*

608   values showing the number of birds included in each terminal node. Colored rows below the

609   tree show the percentage of each family that is described by each terminal node.

610

611    FIGURE 6   Conditional inference tree showing significant associations between body regions

612    highlighted in aggressive signals and family membership. Silhouettes along each branch show

613    examples of focal body regions being *highlighted* and *not highlighted*.  The box at each terminal

614    node contains *n* values showing the number of birds included in each terminal node. Colored

615    rows below the tree show the percentage of each family that is described by each terminal

616    node.

617

618    FIGURE 7  Conditional inference tree showing significant associations between colors

619    highlighted in aggressive signals and family membership. Dashed lines indicate branches where

620    the focal color at each node is *not highlighted*, while colored lines indicate branches where the

621    focal color is *highlighted*. The box at each terminal node contains *n* values showing the number

622    of birds included in each terminal node. Colored rows below the tree show the percentage of

623    each family that is described by each terminal node.

624

625    FIGURE 8  Variation in the most common postures used in aggressive signaling towards

626    heterospecifics across the 14 focal families examined in this study. In most families, signaling

627    birds direct their face and point their bill towards the heterospecific opponent. In Columbidae,

628    signaling birds typically line up sideways, with their underwing closest to the heterospecific

629    opponent. In Accipitridae and Falconidae, signaling birds typically extend their legs so that their

630    talons are closest to the heterospecific opponent. Accipitridae, Trochilidae, Falconidae, and

631    Tynrannidae most commonly signaled in the air, while the rest of the families most common

632 signaled from the ground or water. Illustrated species are: *Tadorna tadorna* (Anatidae),

633 *Eupetomena macroura* (Trochilidae), *Columbina talpacoti* (Columbidae), *Pygoscelis papua*

634 (Spheniscidae), *Diomedea antipodensis gibsoni* (Diomedeidae), *Ardea goliath* (Ardeidae),

635 *Haliaeetus pelagicus* (Accipitridae), *Falco femoralis* (Falconidae), *Megarynchus pitangua*

636 (Tyrannidae), *Turdus merula* (Turdidae), *Euphonia chalybea* (Fringillidae), *Tangara (Thraupis)*

637 *cyanoptera* (Thraupidae), *Icterus pyrrhopterus tibialis* (Icteridae), *Eupsittula aurea* (Psittacidae).

638 Paintings illustrate postures from photos and video of interactions.

639

640 FIGURE 9  A male Red-winged Blackbird (*Agelaius phoeniceus*) signals aggressively at a Blue Jay

641 (*Cyanocitta cristata*) at a bird feeder. The study of signaling in Red-winged Blackbirds, and their

642 use of red epaulets, has centered on intraspecific function (Smith 1972; Røskaft and Rohwer

643 1987; Yasukawa and Searcy 2020); however, blackbirds often direct their aggressive displays

644 towards heterospecifics in competitive interactions. Image is a still shot from a Cornell Lab of

645 Ornithology Bird Cam video, available from

646 https://www.youtube.com/watch?v=8QUZEBgeMPk, and reproduced with permission from the

647 Cornell Lab of Ornithology Bird Cams (www.AllAboutBirds.org/Cams).

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.

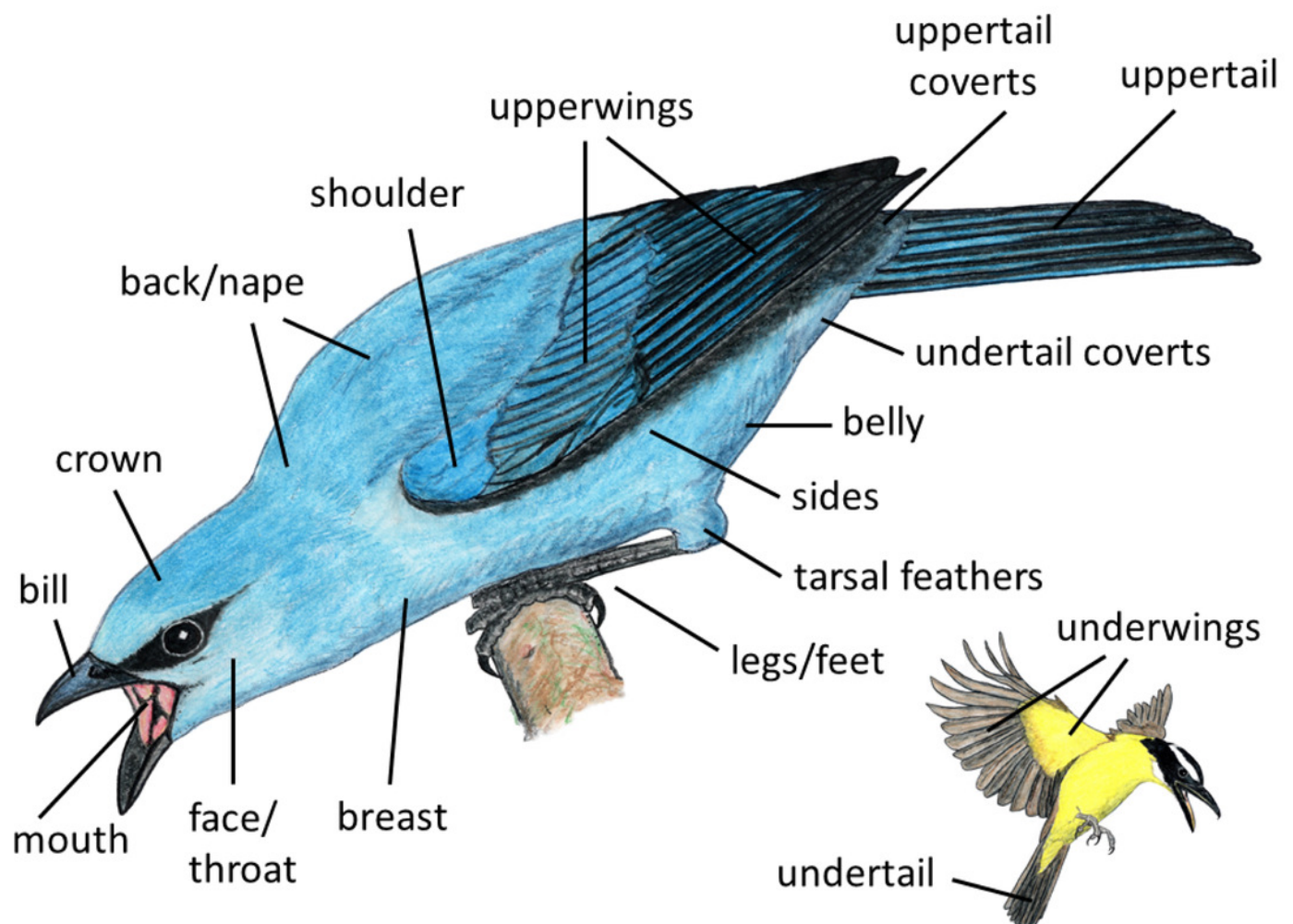
| Posture component | Definition | Position categories |
|---|---|---|
| Body orientation | overall orientation of the signaler's body | forward-upright<br>forward-lowered<br>forward-normal<br>side-oriented<br>feet-forward<br>above the other species<br>upside-down |
| Head position | position of the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

open-downward
open-side
closed-forward
closed-upward
closed-downward
closed-side

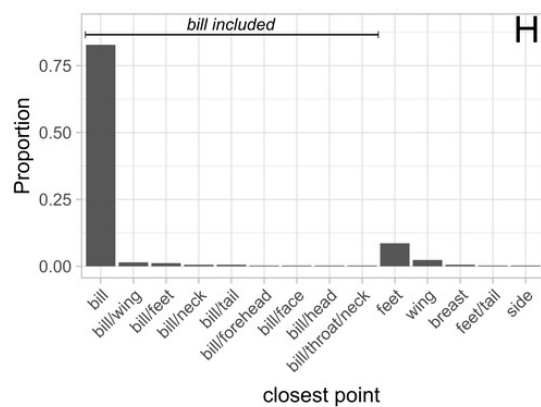
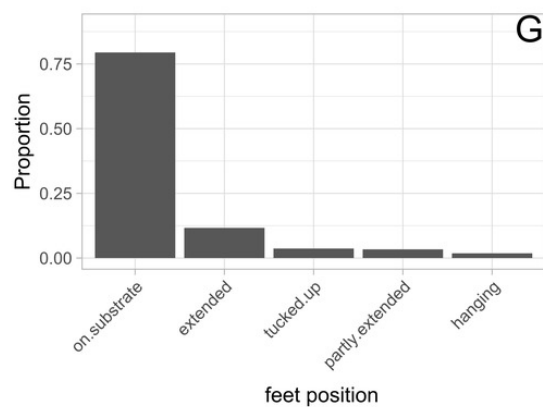
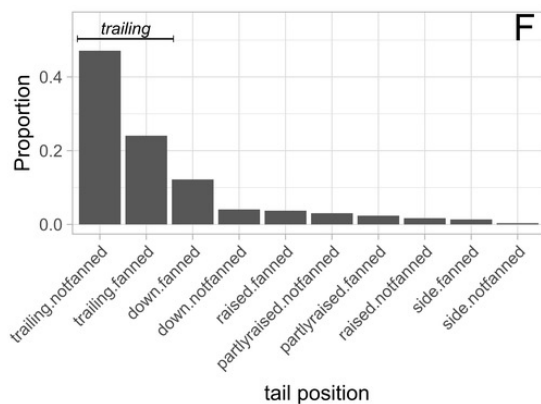
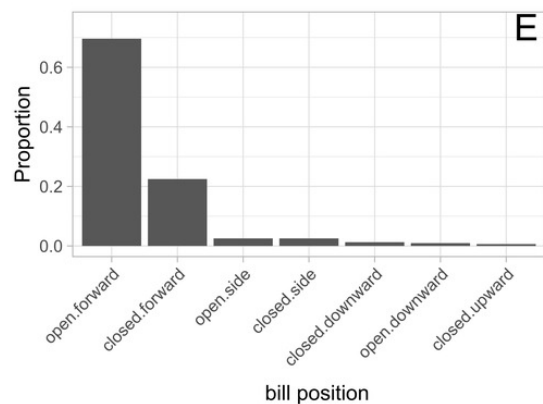
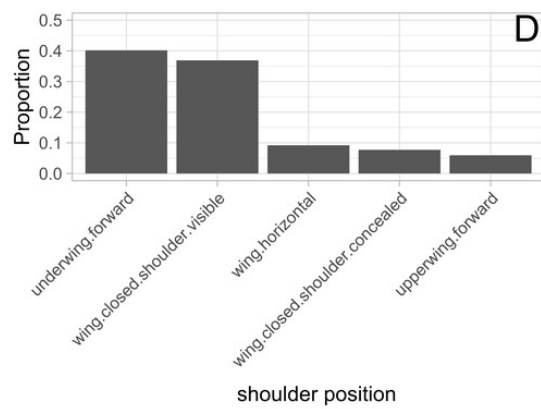
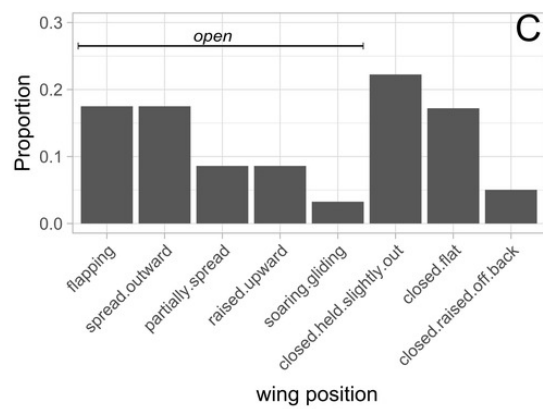
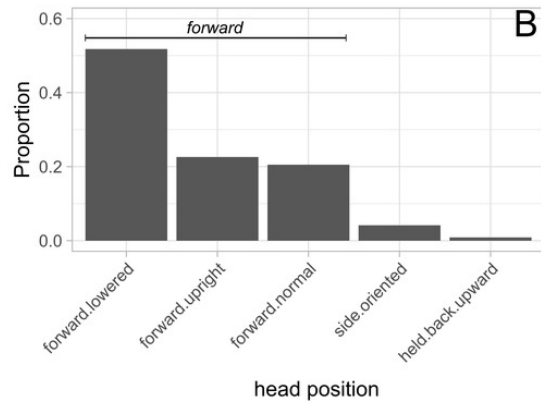
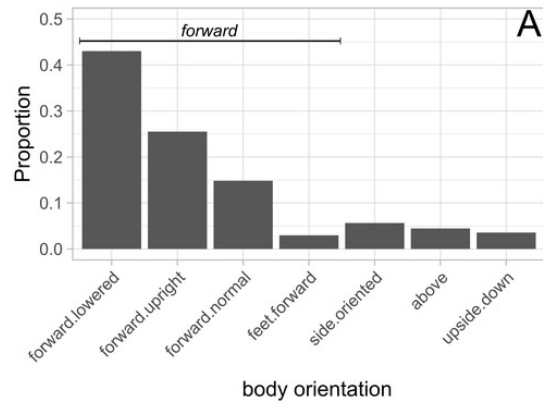
Note: For video segments, we recorded the bill as 'open' if it was
opened at some point during the aggressive signaling.

| 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 |

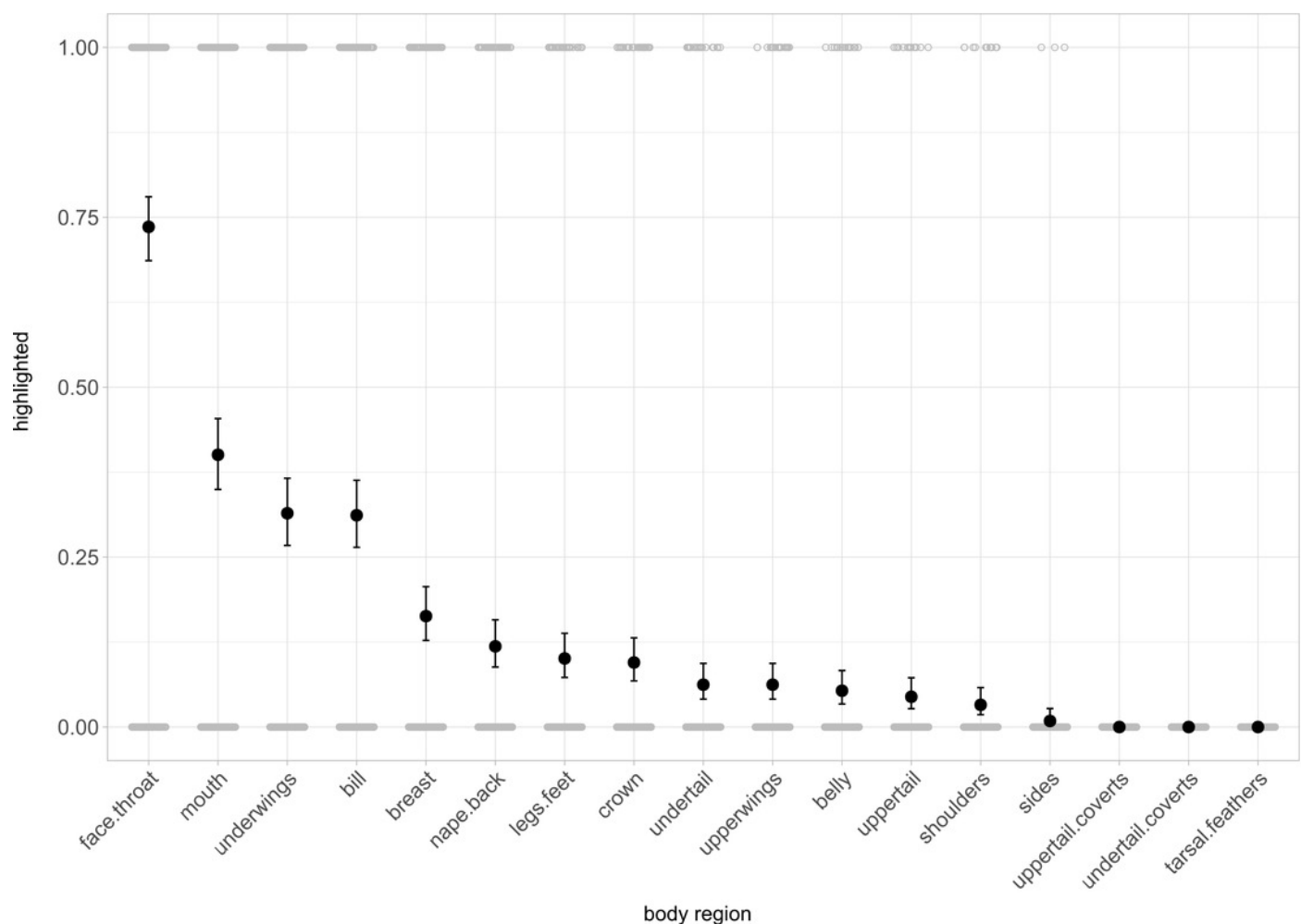
# Figure 1

Body regions included in our study.

# Figure 2

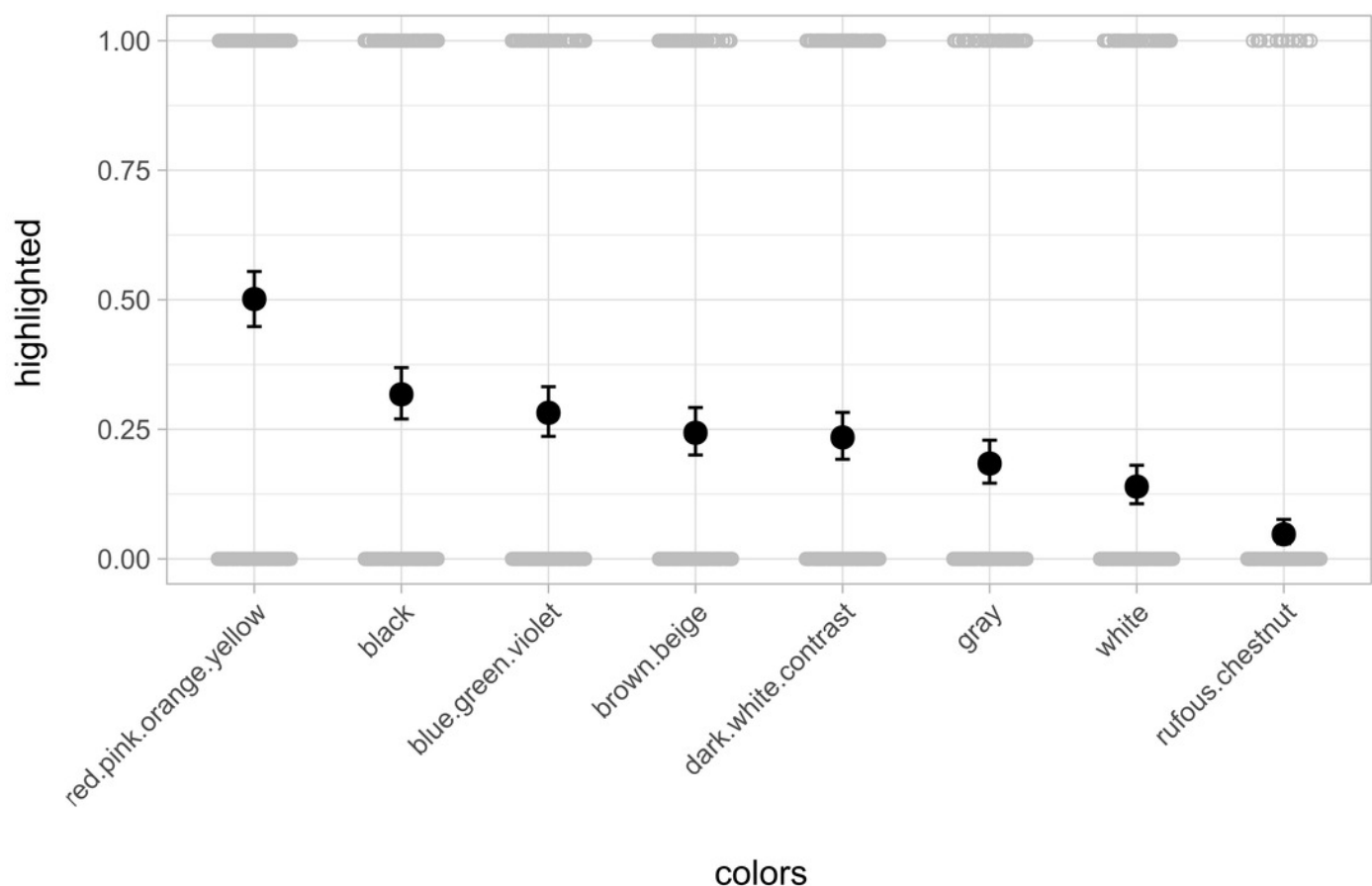
Postures taken during aggressive encounters with heterospecifics:

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).

# Figure 3

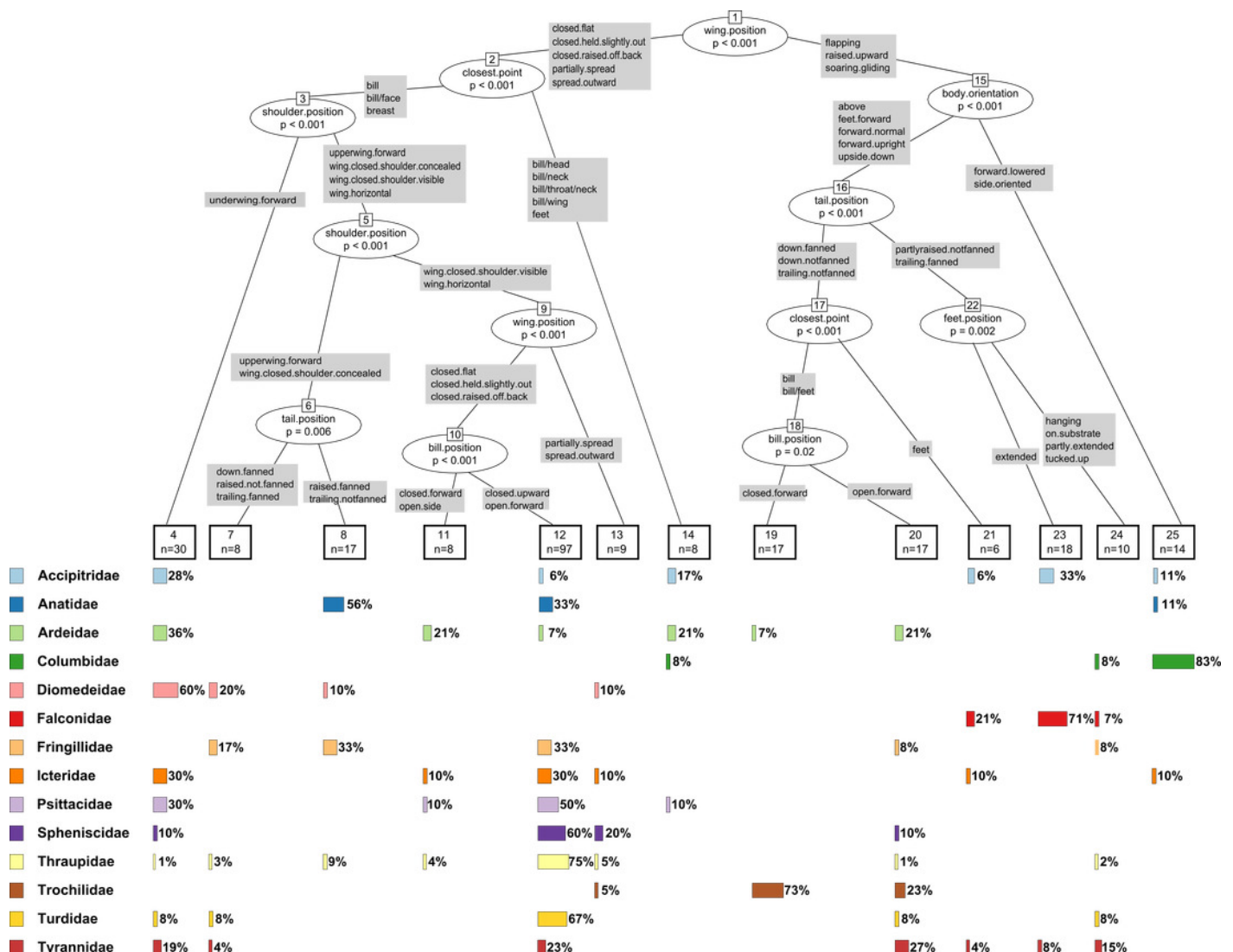
The face and throat region was the most likely body region to be highlighted in aggressive signals (*N* = 337).

Gray circles show the raw data (1 = highlighted; 0 = not highlighted), while black points show model estimates back-transformed from log odds, and error bars show 95% confidence intervals.

# Figure 4

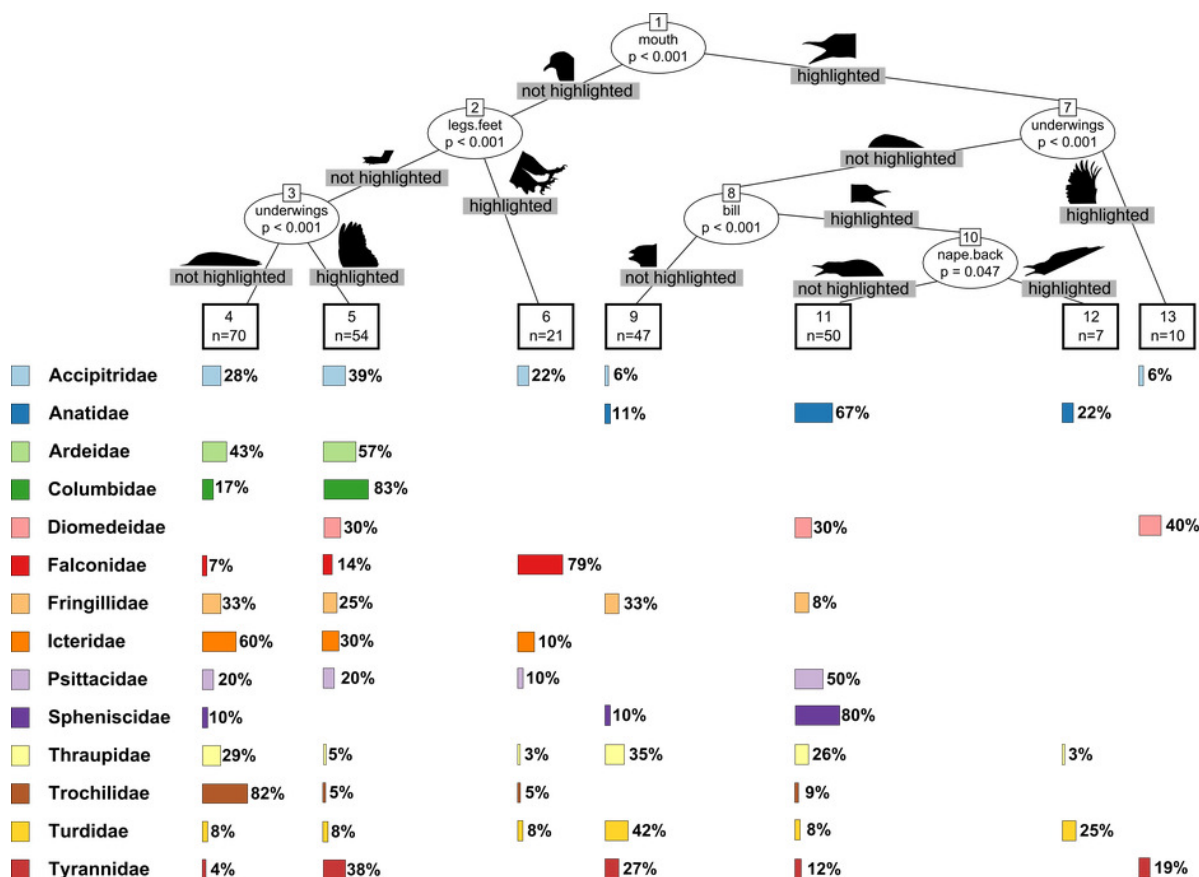
Carotenoid colors (red, pink, orange, or yellow) were the most likely color group to be highlighted in aggressive signals (*N* = 337).

Gray circles show the raw data (1 = highlighted; 0 = not highlighted), while black points show model estimates back-transformed from log odds, and error bars show 95% confidence intervals.

# Figure 5

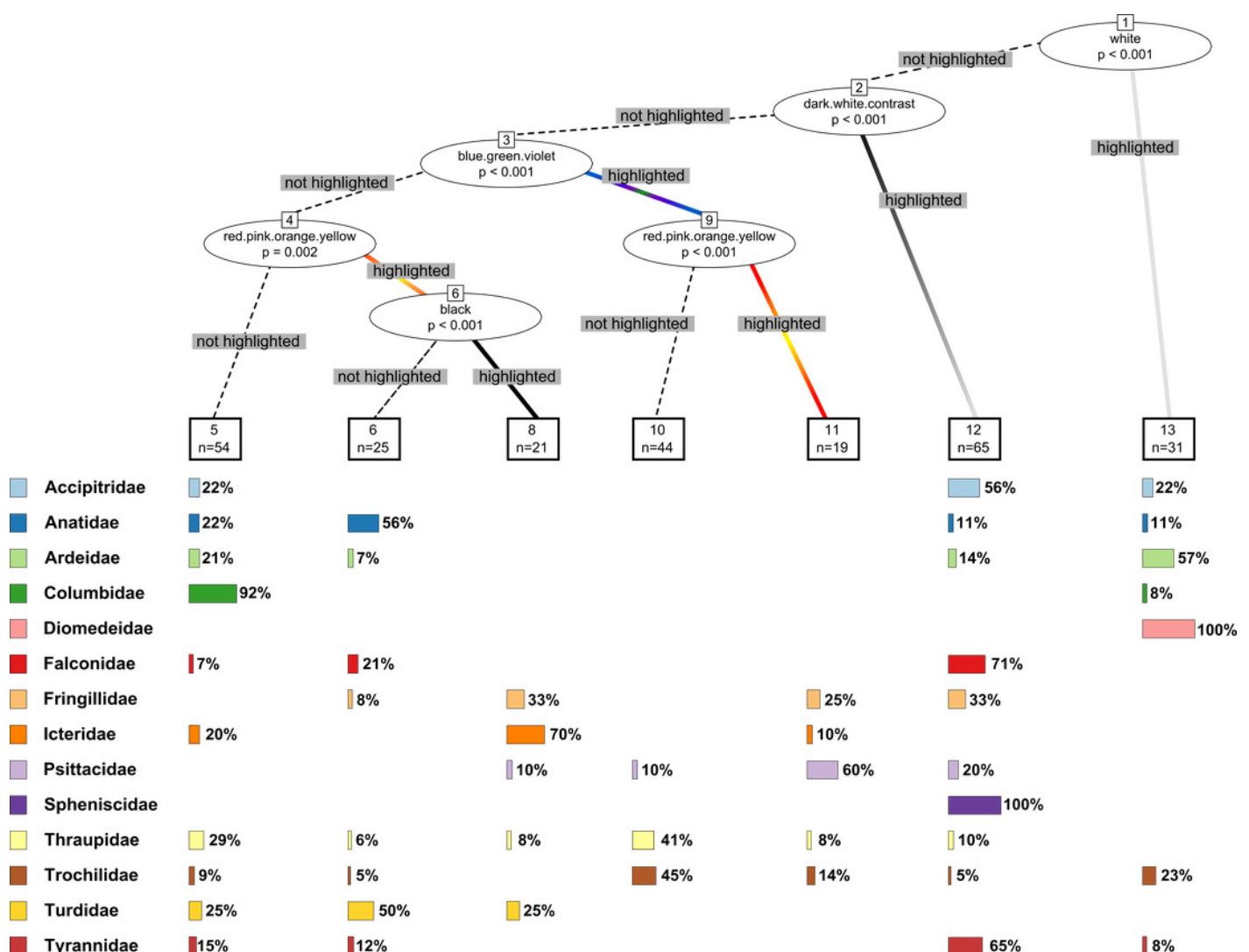
Conditional inference tree showing significant associations between postures taken in aggressive encounters and family membership.

The box at each terminal node contains *n* values showing the number of birds included in each terminal node. Colored rows below the tree show the percentage of each family that is described by each terminal node.

# Figure 6

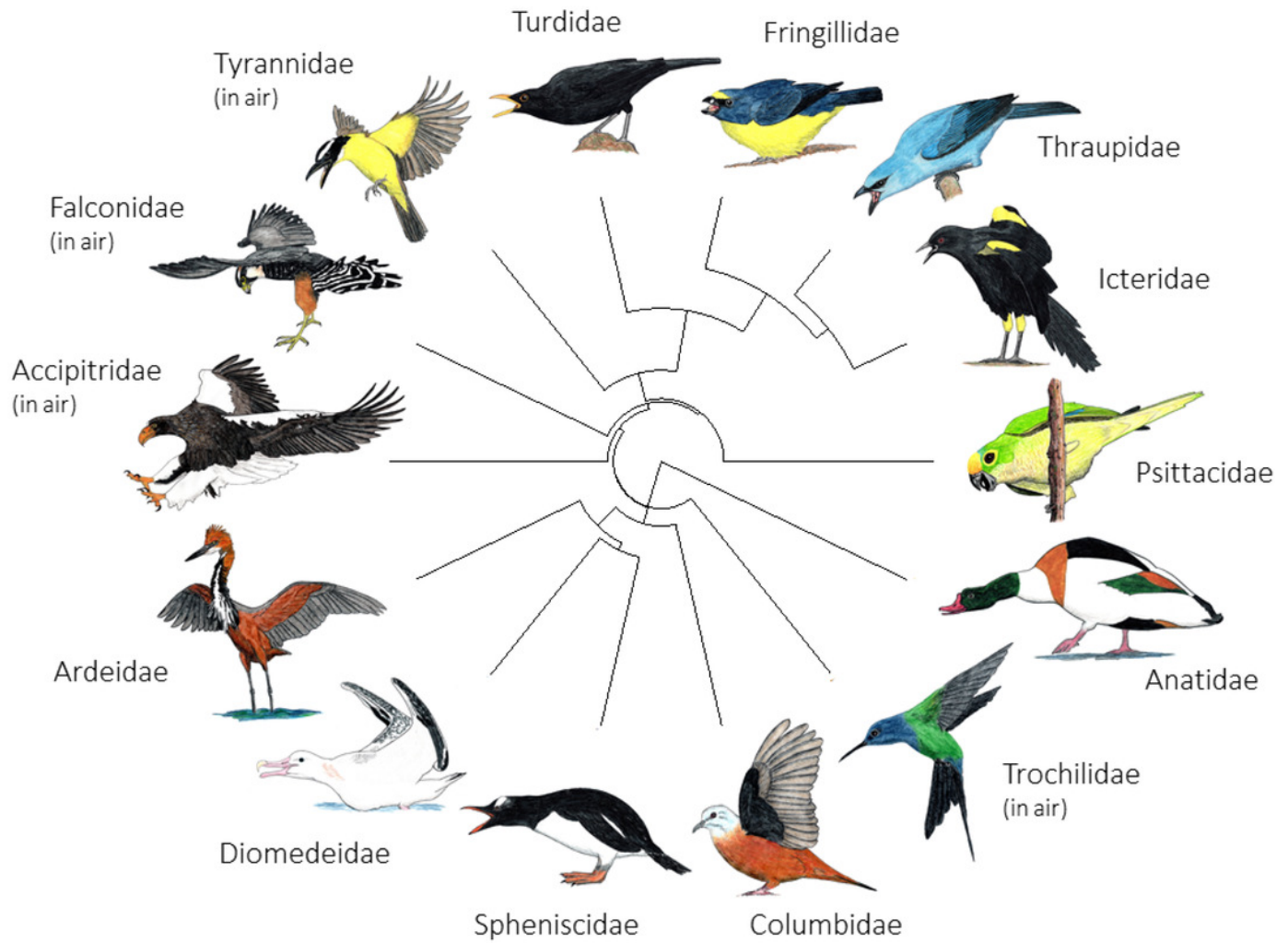
Conditional inference tree showing significant associations between body regions highlighted in aggressive signals and family membership.

Silhouettes along each branch show examples of focal body regions being *highlighted* and *not highlighted*. The box at each terminal node contains *n* values showing the number of birds included in each terminal node. Colored rows below the tree show the percentage of each family that is described by each terminal node.

# Figure 7

Conditional inference tree showing significant associations between colors highlighted in aggressive signals and family membership.

Dashed lines indicate branches where the focal color at each node is *not highlighted*, while colored lines indicate branches where the focal color is *highlighted*. The box at each terminal node contains *n* values showing the number of birds included in each terminal node. Colored rows below the tree show the percentage of each family that is described by each terminal node.

# Figure 8

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.

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

# Figure 9

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).