The outcomes of most aggressive interactions among closely related bird species are asymmetric

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Aggressive interactions among closely related species are common. These can play an important role as a selective pressure shaping species, traits and assemblages. The nature of this selective pressure depends on whether the outcomes of aggressive contests are asymmetric between species (i.e., one species is consistently dominant), yet few studies have estimated the prevalence of asymmetric versus symmetric outcomes to aggressive contests. Here we use previously published data involving 26,656 interactions between 270 species pairs of birds from 26 taxonomic families to address the question: How often are aggressive interactions among closely related bird species asymmetric? We define asymmetry using (i) the proportion of contests won by one species, and (ii) statistical tests for asymmetric outcomes of aggressive contests. We calculate these asymmetries using data summed across different sites for each species pair, and compare results to asymmetries calculated using data separated by location. We find that 80% of species pairs had aggressive outcomes where one species won 80% or more of aggressive contests. We also find that the majority of aggressive interactions among closely related species show statistically significant asymmetries, and above a sample size of 52 interactions, all outcomes are asymmetric following binomial tests. Results using data partitioned by location showed similar patterns. Species pairs with dominance data from multiple sites showed the same dominance relationship across locations in 93% of the species pairs. Overall, our results suggest that the outcome of aggressive interactions among closely related species are usually consistent and asymmetric, and should thus favor ecological and evolutionary strategies specific to the position of a species within a dominance hierarchy.

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20 Abstract

21 Aggressive interactions among closely related species are common, and can play an

22 important role as a selective pressure shaping species traits and assemblages. The nature

23 of this selective pressure depends on whether the outcomes of aggressive contests are

24 asymmetric between species (i.e., one species is consistently dominant), yet few studies

25 have estimated the prevalence of asymmetric versus symmetric outcomes to aggressive

26 contests. Here we use previously published data involving 26,656 interactions between

27 270 species pairs of birds from 26 taxonomic families to address the question: How often

28 are aggressive interactions among closely related bird species asymmetric? We define

29 asymmetry using (i) the proportion of contests won by one species, and (ii) statistical

30 tests for asymmetric outcomes of aggressive contests. We calculate these asymmetries

31 using data summed across different sites for each species pair, and compare results to

32 asymmetries calculated using data separated by location. We find that 80% of species

33 pairs had aggressive outcomes where one species won 80% or more of aggressive

34 contests. We also find that the majority of aggressive interactions among closely related

35 species show statistically significant asymmetries, and above a sample size of 52

36 interactions, all outcomes are asymmetric following binomial tests. Results using data

37 partitioned by location showed similar patterns. Species pairs with dominance data from

38 multiple sites showed the same dominance relationship across locations in 93% of the

39 species pairs. Overall, our results suggest that the outcome of aggressive interactions

40 among closely related species are usually consistent and asymmetric, and should thus

41 favor ecological and evolutionary strategies specific to the position of a species within a

42 dominance hierarchy.

43

INTRODUCTION

Aggressive interactions commonly occur among closely related species (*Kruuk, 1976*; *Feinsinger, 1976*; *Willis & Oniki, 1978*; *Robinson & Terborgh, 1995*). Such direct interspecific interactions have been shown to play an important role in interference competition for resources, including habitat, food, nest sites, and roost sites (*Chappell, 1978*; *Dhondt & Eyckerman, 1980*; *Robertson & Gaines, 1986*; *Alatalo & Moreno, 1987*; *Wallace, Collier & Sydeman, 1992*; *Dhondt, 2012*). Aggressive interactions may also influence indirect ecological interactions (*Martin, 1988*; *Martin & Martin, 2001a*; *Martin & Martin, 2001b*) by reducing the fitness costs manifested through density-dependent responses of predators and parasites that prey or infect closely related species (often called "apparent competition"; *Holt, 1977*; *Holt & Kotler, 1987*; *Holt & Lawton, 1994*). Although it has been suggested that aggressive interactions occur among closely related species due to misplaced aggression (*Murray, 1976*; *Murray, 1981*; *Murray, 1988*; *Jones et al., 2016*), sexual selection for aggressive displays (*Nuechterlein & Storer, 1985*), or as a means of practicing for intraspecific contests (*Nuechterlein & Storer, 1985*), evidence to date suggests that many aggressive interactions reflect adaptive responses to reduce ecological costs for one or both species (*Robinson & Terborgh, 1995*; *Martin & Martin, 2001b*; *Leisler, 1988*; *Palomares & Caro, 1999*; *Peiman & Robinson, 2010*; *Blowes et al., 2013*; *Losin et al., 2016*).

Given the ecological importance of aggressive interactions among closely related species, such interactions may have broad consequences for species assemblages and trait evolution (*Morse, 1974*; *Grether et al., 2009*; *Grether et al., 2013*; *Freshwater, Ghalambor & Martin, 2014*; *Martin & Ghalambor, 2014*). The nature of these

67   consequences, however, depends on whether the outcome of aggressive interactions

68   between species are symmetric, with both species regularly winning aggressive contests,

69   or asymmetric, with one species winning the majority of aggressive contests. For

70   example, if the outcomes of aggressive interactions are asymmetric, then selection may

71   favor traits in the dominant species that enhance fighting abilities (*Young, 2003*; *Owen-*

72   *Ashley & Butler, 2004*; *Donadio & Buskirk, 2006*) or that signal dominance to other

73   species (*Dow, 1975*; *Flack, 1976*; *König, 1983*; *Snow & Snow, 1984*). Asymmetric

74   interactions may also favor traits in the subordinate species that reduce the likelihood of

75   heterospecific aggression, such as traits that reduce ecological overlap with dominant

76   species (*Feinsinger, 1976*; *Willis & Oniki, 1978*; *Morse, 1974*; *König, 1983*) or that

77   reduce aggression from dominant species (e.g., the loss of signals that induce aggression

78   from the dominant species, or the evolution of signals that mimic the dominant or other

79   dangerous species; *Gill, 1971*; *Feinsinger & Chaplin, 1975*; *Feinsinger & Colwell, 1978*;

80   *Rainey & Grether, 2007*; *Prum & Samuelson, 2012*; *Prum, 2014*). Conversely, if

81   aggressive interspecific interactions are typically symmetric, then selection may act

82   similarly on the interacting species, potentially favoring traits such as interspecific

83   territoriality (*Orians & Willson, 1964*). Thus, selection should shape the evolution of

84   species' traits differently if aggressive interactions are symmetric versus asymmetric.

85   Despite the importance of understanding the prevalence of asymmetric relationships

86   among interacting species, relatively little is known about how common such patterns are

87   in nature.

88   In this paper, we ask: how often are aggressive interactions among closely related

89   species asymmetric? Although the outcomes of many aggressive contests among species

90   are asymmetric (*Morse, 1974*; *Lawton & Hassell, 1981*; *Persson, 1985*), few studies have

91   compared the frequency of asymmetric versus symmetric relationships between

92   aggressively interacting species. The studies that have examined this question have found

93   asymmetric interactions to be common: 1) a study of 13 species of surgeonfish

94   (Acanthuridae) on a barrier reef at Aldabra, Indian Ocean, found evidence for asymmetric

95   interactions among 26 of the 27 species pairs that interacted aggressively (*Robertson &*

96   *Gaines, 1986*), 2) a study of closely related species of birds in Amazonian Peru found that

97   9 of the 12 focal species pairs exhibiting interspecific aggression also showed statistically

98   significant asymmetries in their response to playback of heterospecific songs (*Robinson*

99   *& Terborgh, 1995*), 3) a comparative study of interspecific killing among carnivorous

100   mammals found asymmetric killing (i.e., only one species was known to kill the other,

101   rather than both killing each other) in 18 of 19 species pairs that were within the same

102   taxonomic families (excluding domesticated species; *Palomares & Caro, 1999*), and 4)

103   our own comparative study of ecological traits of dominant and subordinate species of

104   North American birds found evidence that 64 of 65 congeneric species pairs had

105   asymmetric outcomes to aggressive interactions (*Freshwater, Ghalambor & Martin,*

106   *2014*).

107   Here, we compile published, quantitative data on the outcomes of aggressive

108   interactions among species within the same taxonomic families, focusing on birds where

109   interaction data are common. We estimate asymmetries in interactions among species

110   using statistical tests for asymmetries and the proportion of aggressive contests won by

111   each species. Although statistical tests provide an accepted method for identifying

112   asymmetries in the outcomes of interactions (*Crawley, 2013*), these tests may not be the

113   optimal method for estimating their magnitude, prevalence, or biological importance. For

114   example, a lack of statistically significant dominance asymmetries may simply reflect

115   small sample sizes; in other cases, large sample sizes may result in statistically significant

116   asymmetries of small biological effect (e.g., 55:45 splits in the outcomes of aggressive

117   interactions). Thus, we also estimated the prevalence of asymmetric interactions by

118   calculating the proportion of aggressive contests won by each species, providing a view

119   of their biological importance that has not been highlighted in other studies to date (e.g.,

120   *Freshwater, Ghalambor & Martin 2014*). The outcome of aggressive contests, including

121   which species is behaviorally dominant, may also vary across different habitats or

122   geographic locales (*Altshuler, 2006*; *Carstensen et al., 2011*), but the frequency of such

123   variation has not previously been explored. To test how common asymmetric aggressive

124   interactions are in birds, we examined the outcome of contests across diverse groups of

125   birds, including vultures feeding at carcasses, hummingbirds feeding at nectar sources,

126   antbirds and woodcreepers feeding on prey fleeing from army ant swarms, and a broad

127   collection of North American congeners. Where possible, we also examined if the

128   outcome of aggressive interactions between the same species pairs changed between

129   different geographic locations. Collectively, we present results from data representing

130   270 interacting pairs of species from 26 families, and including the outcomes of 26,656

131   interactions.

132

133   **MATERIALS & METHODS**

134   **Interaction data**

135   We used published data from *Freshwater, Ghalambor & Martin (2014)* and *Martin &*

136   *Ghalambor (2014)*, supplemented with additional quantitative data, including published

137   data for interactions that had been excluded from *Martin & Ghalambor (2014)* because of

138   a lack of genetic or mass data for the interacting species. This study did not require

139   vertebrate ethics approvals because we used published data in a comparative test

140   supplemented with a few additional natural history observations. For data on North

141   American congeners, we included only the youngest phylogenetically-independent

142   species pair for which we had quantitative data on the outcomes of aggressive

143   interactions (following *Freshwater, Ghalambor & Martin 2014*). The complete datasets

144   and sources for all of the data are included with this submission as supplementary files

145   Data S1-S3. Overall, we created two different datasets: (1) all of the data combined,

146   including data for species interactions that were gathered from multiple sites and summed

147   together for each species pair (Data S2), and (2) the same data entered for each individual

148   location separately, and where each location had at least 6 observations per species pair

149   (Data S3). We included data separated by location to address the potential effects of

150   lumping data across geographic locations on our results. Separating data by location also

151   allowed us to test for geographic variation in dominance relationships among species

152   using the cases where the same species pairs had interaction data from multiple locations.

153   For all datasets, we included only species pairs (Data S2) or locations (Data S3) that had

154   at least 6 interactions with clear outcomes (i.e., one species clearly won the interaction).

155   Following the previous work, we included chases, supplants and displacements,

156   kleptoparasitism, and physical attacks as aggressive interactions (see *Freshwater,*

157   *Ghalambor & Martin 2014* for definitions of these terms). We excluded observations that

158   involved the defense of eggs or young and avoided interactions involving more than one

159   individual of each species (following *Freshwater, Ghalambor & Martin 2014*; *Martin &*

160   *Ghalambor, 2014*). We included observations related to competition for nest sites,

161   because many birds compete aggressively with other species for nesting sites (e.g.,

162   *Wallace, Collier & Sydeman, 1992*).

163

164   **Statistical tests of asymmetry**

165   We tested for asymmetries in the outcomes of aggressive contests between pairs of

166   species using binomial tests in the statistical program R (*R Core Team, 2014*). We ran

167   binomial tests on aggressive interaction data for each species pair in our analysis, and

168   again on our dataset partitioned by location within each species pair. The likelihood of

169   detecting a significant ($P < 0.05$) asymmetry in the outcome of aggressive interactions

170   among species increases with the number of interactions observed (i.e., sample size;

171   *Crawley, 2013*), so we plotted *P*-values as a function of sample size for all species pairs.

172

173   **Proportion of interactions won**

174   We also tested for asymmetries in the outcomes of aggressive contests between pairs of

175   species by examining the proportion of interactions won by one species. We know of no

176   cut-off for designating interactions as asymmetric, so we plotted the cumulative number

177   of species pairs showing asymmetric outcomes to their interactions, varying the definition

178   of asymmetric from >60% to 100% of the interactions won by the dominant. As before,

179   we plotted these relationships for data summarized by species pairs, and again for data

180   partitioned by location within each species pair.

181

182   **Variation in dominance among locations**

183   For species pairs with dominance data from multiple locations (each location with greater

184   than 6 interactions per species pair), we looked at the frequency with which dominance

185   status switched between species among locations, and tested for differences in the

186   proportion of aggressive contests won by each species between sites using Chi-squared

187   tests in R (*R Core Team, 2014*).

188

189   **RESULTS**

190   **Statistical tests of asymmetry**

191   Overall, 223 of 270 species pairs (82.6%) showed statistically significant ($P < 0.05$)

192   asymmetries in the outcomes of aggressive contests. Above a sample size of 52, all

193   aggressive interactions among species were statistically significant ($P < 0.05$) (Fig. 1).

194   Data partitioned by location within species pairs revealed similar results: 235 of 287

195   comparisons (81.9%) showed statistically significant ($P < 0.05$) asymmetries in the

196   outcomes of aggressive contests.

197

198   **Proportion of interactions won**

199   For data summarized by species pair, 79.6% of species pairs had dominant species that

200   won >80% of the aggressive contests (range across groups: 72.2% for vultures to 86.4%

201   for antbirds and woodcreepers; Fig. 2). In contrast, 97.0% of species pairs had dominant

202   species that won >60% of the aggressive contests (range across groups: 95.6% for

203   hummingbirds to 100.0% for vultures), while 48.1% of species pairs had dominant

204   species that won 100% of the aggressive contests (range across groups: 27.8% for

205   vultures to 65.2% for antbirds and woodcreepers) (Fig. 2). Data partitioned by location

206   within species pairs revealed similar results: 79.8% of species pairs had dominant species

207   that won >80% of the aggressive contests (range across groups: 72.0% for vultures to

208   89.1% for antbirds and woodcreepers), 96.2% of species pairs had dominant species that

209   won >60% of the aggressive contests (range across groups: 88.0% for vultures to 98.4%

210   for antbirds and woodcreepers), and 50.5% of species pairs had dominant species that

211   won 100% of the aggressive contests (range across groups: 32.0% for vultures to 70.3%

212   for antbirds and woodcreepers).

213

214   **Variation in dominance among locations**

215   Across all species pairs, 30 had aggressive interaction data from more than one location

216   (with over 6 interactions observed from each location); 23 species pairs had data for 2

217   locations, 7 species pairs had data for 3 locations. Of the 30 species pairs with data from

218   different geographic locations, 12 species pairs had data from different countries, 13

219   species pairs had data from different states or provinces within the same countries, and 5

220   species pairs had data from different geographic locales within the same state or province.

221   Dominance relationships within species pairs were consistent across sites (i.e., the

222   same species won the majority of the interactions at both or all three locations) in 28 of

223   the 30 species pairs (93.3%). The 2 species pairs whose dominance relationship flipped

224   between locations included one pair of vultures (Accipitridae: Rüppell's Vulture, *Gyps*

225   *rueppellii*—White-backed Vulture, *Gyps africanus*, Amboseli National Park, Kenya and

226   Serengeti National Park, Tanzania) and one pair of hummingbirds (Trochilidae:

227   Glittering-bellied Emerald, *Chlorostilbon lucidus*— Ruby-topaz Hummingbird,

228   *Chrysolampis mosquitus*, Serra do Pará, Pernambuco, Brazil and Cadeia do Espinhaço,

229   Bahia, Brazil). For 6 of the 30 species pairs (20.0%; including the 2 for which dominance

230   relationships flipped between sites), the proportions of aggressive contests won by each

231   species were significantly different among locations (i.e., Chi-squared test, $P < 0.05$). For

232   the remaining 24 species pairs (80.0%), the proportion of aggressive contests won by

233   each species did not differ significantly across sites.

234

235   **DISCUSSION**

236   Whether the outcome of aggressive interactions is commonly symmetric or asymmetric

237   has important ecological and evolutionary implications. We found the outcomes of most

238   aggressive interactions within the same taxonomic bird family were asymmetric. Overall,

239   83% of the 270 species pairs showed statistically significant asymmetries in the outcome

240   of aggressive contests (i.e., binomial tests, $P < 0.05$; Fig. 1), with all species pairs

241   showing statistically significant asymmetries above a sample size of 52 interactions.

242   When we estimated asymmetry using the proportion of interactions won by the dominant

243   species, we found that 80% of the species pairs contained dominant species that won 80%

244   or more of aggressive contests (Fig. 2). For 30 species pairs, we had dominance data for 2

245   or 3 different populations, allowing us to test whether dominance asymmetries among

246   species were consistent across locations. Dominance relationships were the same across

247   locations for 93% of the species pairs (i.e., the same species was dominant across all

248   locations), while the proportion of interactions won by each species was not significantly

249   different across locations for 80% of the species pairs. These results suggest that

250   dominance relationships between species are usually consistent across different sites.

251   Below, we discuss the ecological and evolutionary consequences of asymmetric

252   interactions, the factors that underlie dominance, and the implications for how dominant

253   and subordinate species respond to human impacts.

254

255   **Asymmetric interactions and their consequences for ecology**

256   Asymmetric outcomes to most aggressive interactions suggest that dominant species can

257   use preferred resources and reduce the access of subordinate species to those resources

258   (*Morse, 1974*). Such patterns are not unique to birds, as experiments have demonstrated

259   asymmetric partitioning of resources in invertebrates (*Bovbjerg, 1970*; *Bertness, 1981a*;

260   *Bertness, 1981b*) and across a diverse array of vertebrates (*Chappell, 1978*; *Robertson &*

261   *Gaines, 1986*; *Alatalo & Moreno, 1987*; *Martin & Martin, 2001a*; *Hixon, 1980*; *Larson,*

262   *1980*; *Alatalo et al., 1985*; *Alatalo et al., 1987*; *Ziv et al., 1993*; *Pasch, Bolker & Phelps,*

263   *2013*). In these cases, subordinates are excluded from preferred resources, but are still

264   able to use resources that cannot sustain dominant species, and thus are not preferentially

265   defended (*Morse, 1974*; *Martin, 2014*). The result is a repeated pattern: dominant species

266   direct aggression towards subordinate species (interference competition) restricting

267   resource use for the subordinate species, with indirect interactions potentially influencing

268   both dominant and subordinate species (i.e., interactions through shared predators,

269   parasites, or prey, including apparent or exploitative competition) (*Martin & Martin,*

270   *2001a*).

271   The strong asymmetries in the outcomes of aggressive contests also suggest that

272   trade-offs involving aggressive ability and behavioral dominance could play an important

273   role in the partitioning of resources and coexistence of species, particularly among

274   closely related species. For example, a smaller body size allows species to grow, survive,

275   and reproduce with fewer resources, but comes at a cost in the form of losing aggressive

276   contests to larger species (*Peters, 1983*; see also below). Given that resources vary in

277   time and space, large- and small-sized species could coexist by partitioning habitats

278   according to the abundance of resources, with aggressive interactions among species

279   playing a central role in habitat partitioning (*Morse, 1974*; *Ford, 1979*; *Diamond et al.,*

280   *1989*; *Martin, 2014*). We might expect other trade-offs involving aggressive abilities to

281   lead to similar patterns of resource partitioning and coexistence among species of birds

282   and other taxa (e.g., *Feinsinger, 1976*; *Willis & Oniki, 1978*; *Feinsinger & Colwell, 1978*).

283

284   **Asymmetric interactions and their consequences for evolution**

285   Asymmetric aggressive interactions should represent an important selection pressure

286   between interacting species (*Grether et al., 2009*; *Pfennig & Pfennig, 2012*; *Grether et al.,*

287   *2013*). Our results suggest that we should expect such selection to favor the evolution of

288   distinct traits and strategies that depend on the position of species within a dominance

289   hierarchy (*Morse, 1974*; *Gauthreaux, 1978*; *Grether et al., 2013*; *Freshwater, Ghalambor*

290   *& Martin, 2014*). For example, selection may favor investment in aggression or territorial

291   behavior in dominant species, even when such traits incur some fitness costs or trade-off

292   with other traits. Selection may also favor traits, such as color patterns or displays, that

293   signal dominance status to subordinate species in order to reduce the frequency and cost

294   of aggressive encounters among species (see *Flack, 1976*; *König, 1983*; *Snow & Snow,*

295   *1984* for possible examples of these traits).

296   In contrast, selection might favor traits in subordinate species that reduce the costs

297   of aggressive interactions with dominants. For example, the evolution of color patterns or

298   displays in subordinate species may reduce aggression from dominant species, and thus

299   be favored by natural selection (*Gill, 1971*; *Sætre, Král & Bičík, 1993*). The evolution of

300   mimicry of dominant species by subordinates may also be an underappreciated outcome

301   of asymmetric interactions among species. In birds, recent evidence suggests that the

302   mimicry of dominant species by subordinates could be widespread, involving both song

303   and color patterns (*Cody, 1973*; *Rainey & Grether, 2007*; *Prum & Samuelson, 2012*;

304   *Prum, 2014*). Similarly, selection should favor traits that facilitate alternative ecological

305   strategies that reduce the costs of aggressive contests with dominant species. Such

306   alternative strategies could include altering the timing of breeding or geographic

307   distribution to reduce temporal and spatial overlap with dominant species (*Freshwater,*

308   *Ghalambor & Martin, 2014*), or evolving adaptations that allow subordinate species to

309   use novel resources (e.g., physiological tolerance to conditions outside those experienced

310   in a clade). With reduced access to important resources for survival, such as food and safe

311   roosting sites, subordinate species might also be more likely to evolve distinct life history

312   strategies that invest more in annual reproductive effort at the expense of annual survival

313   (*Roff, 1992*; *Stearns, 1992*). Indeed, such patterns characterize dominant and subordinate

314   species within a genus: subordinate species have lower annual survival rates and lay

315   larger eggs for a given body mass (*Freshwater, Ghalambor & Martin, 2014*).

316

317   **What causes variation in the asymmetric outcomes of aggressive encounters among**

318   **species?**

319   Many factors have been identified as influencing the proportion of encounters won by

320   dominant species, including age and sex (*Stiles, 1973*) and the context in which the

321   encounter occurs (*Altshuler, 2006*), as well as proximate factors that include condition,

322   hunger level, density, and time of arrival or colonization (*Stiles, 1973*; *Lyon, 1976*;

323   *Anderson & Horwitz, 1979*; *Cole, 1983*; *Wallace & Temple, 1987*; *Robinson, 1989*;

324   *Tanner & Adler, 2009*). Perhaps the most important predictor of the outcome of

325   aggressive contests, however, appears to be differences in body size among the

326   interacting species (*Morse, 1974*; *Peters, 1983*; *Robinson & Terborgh, 1995*; *Donadio &*

327   *Buskirk, 2006*; *Martin & Ghalambor, 2014*). Indeed, in the results we report here, the

328   larger species was dominant in 88% of the contests where the outcomes of aggressive

329   contests were asymmetric (defined as over 80% contests won by the dominant species),

330   with the dominant species averaging 57% heavier than the subordinate (for a list of

331   reasons why larger size confers an advantage in aggressive contests, see *Martin &*

332   *Ghalambor, 2014*). This contrasts with cases where one species won between 50-69% of

333   the contests (i.e., the outcome was more symmetric), where the larger species prevailed in

334   only 63% of the species pairs and averaged only 24% heaver (data in Dryad).

335   The importance of body size for determining the outcomes of aggressive contests,

336   however, can vary. For example, larger species win a greater proportion of aggressive

337   interactions as the difference in body size between interacting species increases, but this

338   relationship weakens with greater evolutionary distance among the interacting species

339   (*Martin & Ghalambor, 2014*). We hypothesize this pattern occurs because closely related

340   species share more traits with each other (*Violle et al., 2011*), and thus differences in size

341   alone can determine the outcome of aggressive interactions (*Martin & Ghalambor, 2014*).

342   As species become more distantly related, however, they are more likely to accumulate

343   unique traits that influence behavioral dominance independent of body size. Indeed,

344   *Martin & Ghalambor (2014)* found that as species became more distantly related, the

345   outcome of aggressive interactions became more asymmetric independent of differences

346   in body size. Few studies, however, have attempted to identify the exact suite of traits

347   that explain dominance independent of body size (*Donadio & Buskirk, 2006*; *Martin &*

348   *Ghalambor, 2014*).

349

350   **Asymmetric interactions and their consequences for human impacts**

351   Given broad asymmetries, we should also expect species to differ in their responses to

352   anthropogenic challenges, such as climate change and habitat alteration, depending on

353   their position within a dominance hierarchy. Some subordinate species appear to be better

354   able to persist in degraded habitats (*Daily & Ehrlich, 1994*), and may have greater

355   ecological breadth and tolerance compared to dominant species (*Morse, 1974*; *Minot &*

356   *Perrins, 1986*; *Blowes, Pratchett & Connolly, 2013*; but see *Freshwater, Ghalambor &*

357   *Martin, 2014*). Aggression and behavioral dominance, however, are often associated with

358   boldness that can help species cope in the face of human disturbance (*Evans, Boudreau &*

359   *Hyman, 2010*; *Lowry, Lill & Wong, 2013*). Thus, traits that covary with dominance status

360   could facilitate or hinder species in the face of human alteration of habitats. Regardless,

361   the importance of asymmetric interactions in determining patterns of resource use among

362   species suggests that these interactions may mediate species' responses to perturbations

363   like habitat alteration or climate change. Few models consider these kinds of species

364   interactions in their forecasts of the impacts of habitat perturbations or climate change on

365   species abundance and distributions (*Tylianakis et al., 2008*; *Gilman et al., 2010*; *Buckley,*

366   *2013*). Yet, any impacts on dominant species are likely to have cascading effects on the

367   subordinate species with which they interact (*Duckworth & Badyaev, 2007*; *Gilman et al.,*

368   *2010*; *Jankowski, Robinson & Levey, 2010*; *Buckley, 2013*; *Martin & Dobbs, 2014*;

369   *Freeman & Montgomery, 2015*). Such asymmetric interactions could have important

370   consequences for populations, particularly in environments where the options for

371   dispersal and range shifting are limited (e.g., tropical islands and mountains; *Jankowski,*

372   *Robinson & Levey, 2010*; *Freeman, 2016*).

373

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376

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381   **Data Availability**

382   Our data are included with this submission as supplementary files Data S1-S3.

383

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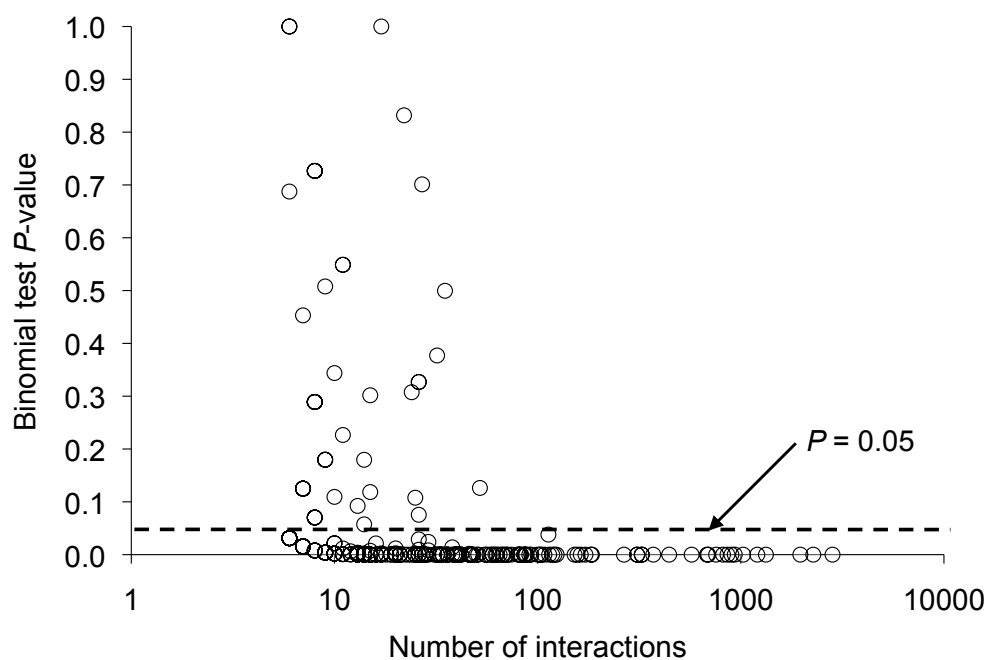547   R Foundation for Statistical Computing. http://www.R-project.org/.

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583   Figure captions

584   **Figure 1** Binomial test *P*-values testing for asymmetries in the outcomes of aggressive

585   interactions for each species pair in our study, as a function of the number of interactions

586   observed between each pair. The dashed line illustrates the common *P*-value cutoff for

587   statistical significance at 0.05. All species pairs with greater than 52 interactions showed

588   statistically significant asymmetries; overall, 83% of species pairs showed statistically

589   significant asymmetries.

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593   **Figure 2** The proportion of species pairs showing asymmetric outcomes to their

594   aggressive interactions. Asymmetry was measured by the proportion of interactions won

595   by the dominant species, and was defined on a scale from >60% of the interactions won

596   by the dominant species to 100% of the interactions won by the dominant species (x-axis).

597   The thick black line represents the entire dataset; the gray lines represent different groups

598   within the dataset. Plots are line plots connecting points at 0.01 x-value increments.

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