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

Paul R Martin ^{Corresp., 1}, Cameron Freshwater ², Cameron K Ghalambor ³

¹ Department of Biology, Queen's University, Kingston, Ontario, Canada

² Department of Biology, University of Victoria, Victoria, British Columbia, Canada

³ Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, United States

Corresponding Author: Paul R Martin

Email address: pm45@queensu.ca

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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9 Paul R. Martin¹, Cameron Freshwater², Cameron K. Ghalambor³

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11 ¹ Department of Biology, Queen's University, Kingston, Ontario, Canada

12 ² Department of Biology, University of Victoria, Victoria, British Columbia, Canada

13 ³ Department of Biology and Graduate Degree Program in Ecology, Colorado State
14 University, Fort Collins, Colorado, USA

15

16 Corresponding Author:

17 Paul Martin¹

18 Email address: pm45@queensu.ca

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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

44 **INTRODUCTION**

45 Aggressive interactions commonly occur among closely related species (*Kruuk, 1976;*
46 *Feinsinger, 1976; Willis & Oniki, 1978; Robinson & Terborgh, 1995*). Such direct
47 interspecific interactions have been shown to play an important role in interference
48 competition for resources, including habitat, food, nest sites, and roost sites (*Chappell,*
49 *1978; Dhondt & Eyckerman, 1980; Robertson & Gaines, 1986; Alatalo & Moreno, 1987;*
50 *Wallace, Collier & Sydeman, 1992; Dhondt, 2012*). Aggressive interactions may also
51 influence indirect ecological interactions (*Martin, 1988; Martin & Martin, 2001a; Martin*
52 *& Martin, 2001b*) by reducing the fitness costs manifested through density-dependent
53 responses of predators and parasites that prey or infect closely related species (often
54 called "apparent competition"; *Holt, 1977; Holt & Kotler, 1987; Holt & Lawton, 1994*).
55 Although it has been suggested that aggressive interactions occur among closely related
56 species due to misplaced aggression (*Murray, 1976; Murray, 1981; Murray, 1988; Jones*
57 *et al., 2016*), sexual selection for aggressive displays (*Nuechterlein & Storer, 1985*), or as
58 a means of practicing for intraspecific contests (*Nuechterlein & Storer, 1985*), evidence
59 to date suggests that many aggressive interactions reflect adaptive responses to reduce
60 ecological costs for one or both species (*Robinson & Terborgh, 1995; Martin & Martin,*
61 *2001b; Leisler, 1988; Palomares & Caro, 1999; Peiman & Robinson, 2010; Blowes et al.,*
62 *2013; Losin et al., 2016*).

63 Given the ecological importance of aggressive interactions among closely related
64 species, such interactions may have broad consequences for species assemblages and trait
65 evolution (*Morse, 1974; Grether et al., 2009; Grether et al., 2013; Freshwater,*
66 *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% heavier (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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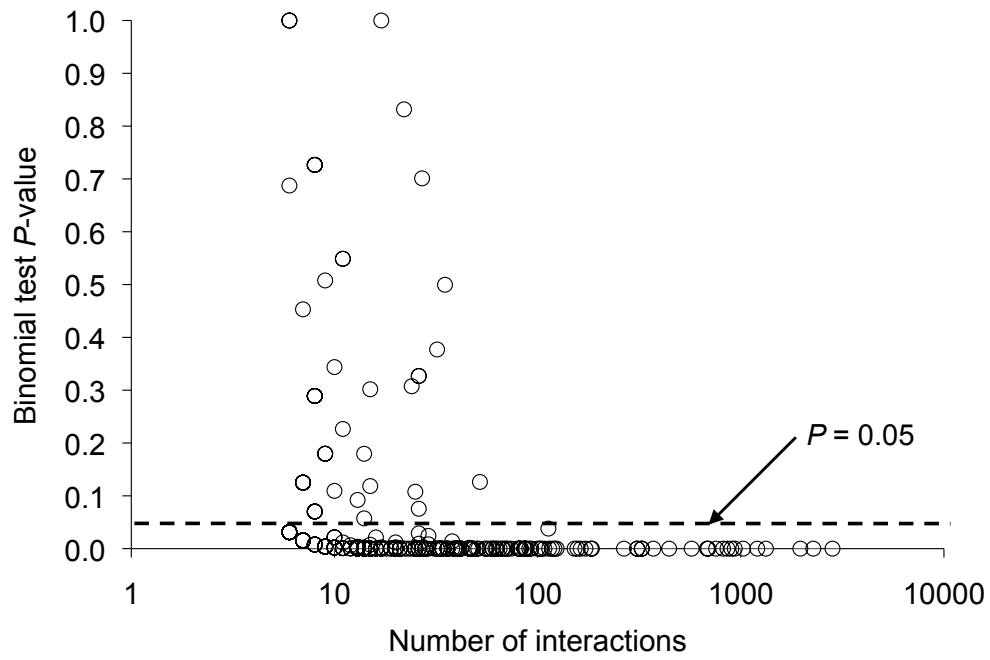
583 Figure captions

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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