

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, and 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 26,212 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. 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.

1

2

3

4

5

6 The outcomes of most aggressive interactions among closely related bird species

7 are asymmetric

8

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

10

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

20 Abstract

21 Aggressive interactions among closely related species are common, and can play an important
22 role as a selective pressure shaping species traits and assemblages. The nature of this selective
23 pressure depends on whether the outcomes of aggressive contests are asymmetric between
24 species (i.e., one species is consistently dominant), yet few studies have estimated the prevalence
25 of asymmetric versus symmetric outcomes to aggressive contests. Here we use previously
26 published data involving 26,212 interactions between 270 species pairs of birds from 26
27 taxonomic families to address the question: How often are aggressive interactions among closely
28 related bird species asymmetric? We define asymmetry using (i) the proportion of contests won
29 by one species, and (ii) statistical tests for asymmetric outcomes of aggressive contests. We
30 calculate these asymmetries using data summed across different sites for each species pair, and
31 compare results to asymmetries calculated using data separated by location. We find that 80% of
32 species pairs had aggressive outcomes where one species won 80% or more of aggressive
33 contests. We also find that the majority of aggressive interactions among closely related species
34 show statistically significant asymmetries, and above a sample size of 52 interactions, all
35 outcomes are asymmetric following binomial tests. Species pairs with dominance data from
36 multiple sites showed the same dominance relationship across locations in 93% of the species
37 pairs. Overall, our results suggest that the outcome of aggressive interactions among closely
38 related species are usually consistent and asymmetric, and should thus favor ecological and
39 evolutionary strategies specific to the position of a species within a dominance hierarchy.

41 **INTRODUCTION**

42 Aggressive interactions commonly occur among closely related species (*Kruuk, 1976;*
43 *Feinsinger, 1976; Willis & Oniki, 1978; Robinson & Terborgh, 1995*). Such direct interspecific
44 interactions have been shown to play an important role in interference competition for resources,
45 including habitat, food, nest sites, and roost sites (*Chappell, 1978; Dhondt & Eyckerman, 1980;*
46 *Robertson & Gaines, 1986; Alatalo & Moreno, 1987; Wallace, Collier & Sydean, 1992;*
47 *Dhondt, 2012*). Aggressive interactions may also reduce the costs of indirect ecological
48 interactions (*Martin, 1988; Martin & Martin, 2001a; Martin & Martin, 2001b*) that are generally
49 referred to as "apparent competition", such as density-dependent predation or parasitism
50 involving multiple prey or host species (*Holt, 1977; Holt & Kotler, 1987; Holt & Lawton, 1994*).
51 In these cases, interspecific aggression that leads to the spatial or temporal exclusion of prey or
52 host species (i.e., individuals of the subordinate species) could reduce the overall density of prey
53 or hosts, and thus reduce predation or infection rates of the dominant species (*Martin & Martin,*
54 *2001b*). Other hypotheses proposed to explain aggressive interactions among species include
55 misplaced aggression (*Murray, 1976; Murray, 1981; Murray, 1988; Jones et al., 2016*), sexual
56 selection for aggressive displays (*Nuechterlein & Storer, 1985*), and practice for intraspecific
57 contests (*Nuechterlein & Storer, 1985*); however, evidence to date suggests that many aggressive
58 interactions reflect adaptive responses to reduce ecological costs for one or both species
59 (*Robinson & Terborgh, 1995; Martin & Martin, 2001b; Leisler, 1988; Palomares & Caro, 1999;*
60 *Peiman & Robinson, 2010; Blowes et al., 2013; Losin et al., 2016*).

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

64 2014; *Martin & Ghalambor, 2014*). The nature of these consequences, however, depends on
65 whether the outcome of aggressive interactions between species are symmetric, with both species
66 regularly winning aggressive contests, or asymmetric, with one species winning the majority of
67 aggressive contests. For example, if the outcomes of aggressive interactions are asymmetric, then
68 selection may favor traits in the dominant species that enhance fighting abilities (*Young, 2003*;
69 *Owen-Ashley & Butler, 2004*; *Donadio & Buskirk, 2006*) or that signal dominance to other
70 species (*Dow, 1975*; *Flack, 1976*; *König, 1983*; *Snow & Snow, 1984*). Asymmetric interactions
71 may also favor traits in the subordinate species that reduce the likelihood of heterospecific
72 aggression, such as traits that reduce ecological overlap with dominant species (*Feinsinger,*
73 *1976*; *Willis & Oniki, 1978*; *Morse, 1974*; *König, 1983*) or that reduce aggression from dominant
74 species (e.g., the loss of signals that induce aggression from the dominant species, or the
75 evolution of signals that mimic the dominant or other dangerous species; *Gill, 1971*; *Feinsinger*
76 *& Chaplin, 1975*; *Feinsinger & Colwell, 1978*; *Rainey & Grether, 2007*; *Prum & Samuelson,*
77 *2012*; *Prum, 2014*). Conversely, if aggressive interspecific interactions are typically symmetric,
78 then selection may act similarly on the interacting species, potentially favoring individuals in
79 both species that maintain exclusive territories (*Orians & Willson, 1964*; although interspecific
80 territoriality can involve species with asymmetric relations as well). Thus, selection should shape
81 the evolution of species' traits differently if aggressive interactions are symmetric versus
82 asymmetric. Despite the importance of understanding the prevalence of asymmetric relationships
83 among interacting species, relatively little is known about how common such patterns are in
84 nature.

85 In this paper, we ask: how often are aggressive interactions among closely related species
86 asymmetric? Although the outcomes of many aggressive contests among species are asymmetric

87 (*Morse, 1974; Lawton & Hassell, 1981; Persson, 1985*), few studies have compared the
88 frequency of asymmetric versus symmetric relationships between aggressively interacting
89 species. The studies that have examined this question have found asymmetric interactions to be
90 common: 1) a study of 13 species of surgeonfish (Acanthuridae) on a barrier reef at Aldabra,
91 Indian Ocean, found evidence for asymmetric interactions among 26 of the 27 species pairs that
92 interacted aggressively (*Robertson & Gaines, 1986*), 2) a study of closely related species of birds
93 in Amazonian Peru found that 9 of the 12 focal species pairs exhibiting interspecific aggression
94 also showed statistically significant asymmetries in their response to playback of heterospecific
95 songs (*Robinson & Terborgh, 1995*), 3) a comparative study of interspecific killing among
96 carnivorous mammals found asymmetric killing (i.e., only one species was known to kill the
97 other, rather than both killing each other) in 18 of 19 species pairs that were within the same
98 taxonomic families (excluding domesticated species; *Palomares & Caro, 1999*), and 4) our own
99 comparative study of ecological traits of dominant and subordinate species of North American
100 birds found evidence that 64 of 65 congeneric species pairs had asymmetric outcomes to
101 aggressive interactions (*Freshwater, Ghalambor & Martin, 2014*).

102 Here, we compile published, quantitative data on the outcomes of aggressive interactions
103 among species within the same taxonomic families, focusing on birds where interaction data are
104 common. We estimate asymmetries in interactions among species using statistical tests for
105 asymmetries and the proportion of aggressive contests won by each species. Although statistical
106 tests provide an accepted method for identifying asymmetries in the outcomes of interactions
107 (*Crawley, 2013*), these tests may not be the optimal method for estimating their magnitude,
108 prevalence, or biological importance. For example, a lack of statistically significant dominance
109 asymmetries may simply reflect small sample sizes; in other cases, large sample sizes may result

110 in statistically significant asymmetries of small biological effect (e.g., 55:45 splits in the
111 outcomes of aggressive interactions). Thus, we also estimated the prevalence of asymmetric
112 interactions by calculating the proportion of aggressive contests won by each species, providing
113 a view of their biological importance that has not been highlighted in other studies to date (e.g.,
114 *Freshwater, Ghalambor & Martin 2014*). The outcome of aggressive contests, including which
115 species is behaviorally dominant, may also vary across different habitats or geographic locales
116 (*Altshuler, 2006; Carstensen et al., 2011*), but the frequency of such variation has not previously
117 been explored. To test how common asymmetric aggressive interactions are in birds, we
118 examined the outcome of contests across diverse groups of birds, including vultures feeding at
119 carcasses, hummingbirds feeding at nectar sources, antbirds and woodcreepers feeding on prey
120 fleeing from army ant swarms, and a broad collection of North American congeners. Where
121 possible, we also examined if the outcome of aggressive interactions between the same species
122 pairs changed between different geographic locations. Collectively, we present results from data
123 representing 270 interacting pairs of species from 26 families, and including the outcomes of
124 26,212 interactions.

125

126 **MATERIALS & METHODS**

127 **Interaction data**

128 We used published data from *Freshwater, Ghalambor & Martin (2014)* and *Martin &*
129 *Ghalambor (2014)*, supplemented with additional quantitative data, including published data for
130 interactions that had been excluded from *Martin & Ghalambor (2014)* because of a lack of
131 genetic or mass data for the interacting species. This study did not require vertebrate ethics
132 approvals because we used published data in a comparative test supplemented with a few

133 additional natural history observations. For data on North American congeners, we included only
134 the youngest phylogenetically-independent species pair for which we had quantitative data on the
135 outcomes of aggressive interactions (*Freshwater, Ghalambor & Martin 2014*). We note that
136 examining only the youngest phylogenetically-independent species pairs was important in our
137 previous work that focused on the evolution of traits associated with dominance status
138 (*Freshwater, Ghalambor & Martin 2014*), but was not part of our approach to addressing the
139 focal questions of this study. The complete datasets and sources for all of the data are included as
140 supplementary files Data S1-S3. Overall, we created two different datasets: (1) all of the data
141 combined, including data for species interactions that were gathered from multiple sites and
142 summed together for each species pair (Data S2), and (2) the same data entered for each
143 individual location separately, and where each location had at least 6 observations per species
144 pair (Data S3). We included data separated by location to address the potential effects of lumping
145 data across geographic locations on our results. Separating data by location also allowed us to
146 test for geographic variation in dominance relationships among species using the cases where the
147 same species pairs had interaction data from multiple locations. For all datasets, we included
148 only species pairs (Data S2) or locations (Data S3) that had at least 6 interactions with clear
149 outcomes (i.e., one species clearly won the interaction). We rarely had data on the number of
150 individuals involved across interactions, in part because most studies of aggressive interactions
151 did not involve marked individuals. Thus, for some of the species pairs, the number of
152 interactions includes some degree of pseudoreplication (where the same individual was involved
153 in multiple aggressive interactions), but the extent of pseudoreplication across our dataset is
154 unknown. Following the previous work, we included chases, supplants and displacements,
155 kleptoparasitism, and physical attacks as aggressive interactions (see *Freshwater, Ghalambor &*

156 *Martin 2014* for definitions of these terms). We excluded observations that involved the defense
157 of eggs or young and avoided interactions involving more than one individual of each species
158 (following *Freshwater, Ghalambor & Martin 2014; Martin & Ghalambor, 2014*). We included
159 observations related to competition for nest sites, because many birds compete aggressively with
160 other species for nesting sites (e.g., *Wallace, Collier & Sydeman, 1992*).

161

162 **Statistical tests of asymmetry**

163 We tested for asymmetries in the outcomes of aggressive contests between pairs of species using
164 binomial tests in the statistical program R (*R Core Team, 2014*). We ran binomial tests on
165 aggressive interaction data for each species pair in our analysis, and again on our dataset
166 partitioned by location within each species pair. The likelihood of detecting a significant ($P <$
167 0.05) asymmetry in the outcome of aggressive interactions among species increases with the
168 number of interactions observed (i.e., sample size; *Crawley, 2013*), so we plotted P -values as a
169 function of sample size for all species pairs.

170

171 **Proportion of interactions won**

172 We also tested for asymmetries in the outcomes of aggressive contests between pairs of species
173 by examining the proportion of interactions won by one species. We know of no cut-off for
174 designating interactions as asymmetric, so we plotted the cumulative number of species pairs
175 showing asymmetric outcomes to their interactions, varying the definition of asymmetric from
176 $>60\%$ to 100% of the interactions won by the dominant. As before, we plotted these relationships
177 for data summarized by species pairs, and again for data partitioned by location within each
178 species pair.

179

180 Variation in dominance among locations

181 For species pairs with dominance data from multiple locations (each location with greater than 6
182 interactions per species pair), we looked at the frequency with which dominance status switched
183 between species among locations, and tested for differences in the proportion of aggressive
184 contests won by each species between sites using Chi-squared tests in R (*R Core Team, 2014*).
185 We estimated the distance between different geographic locations for each species pair by
186 recording the latitude and longitude in decimal degrees for each site (from the original references,
187 or estimated based on the description of the site within the original references), and then
188 calculating the distance between these points in km using the *deg.dist* function in the R package
189 *fossil* (Vavrek 2012).

190

191 RESULTS**192 Statistical tests of asymmetry**

193 Overall, 224 of 270 species pairs (83.0%) showed statistically significant ($P < 0.05$) asymmetries
194 in the outcomes of aggressive contests. Above a sample size of 52, all aggressive interactions
195 among species were statistically significant ($P < 0.05$) (Fig. 1). Data partitioned by location
196 within species pairs revealed similar results: 235 of 288 comparisons (81.6%) showed
197 statistically significant ($P < 0.05$) asymmetries in the outcomes of aggressive contests.

198

199 Proportion of interactions won

200 For data summarized by species pair, 79.6% of species pairs had dominant species that won
201 $\geq 80\%$ of the aggressive contests (range across groups: 72.2% for vultures to 86.2% for antbirds)

202 and woodcreepers; Fig. 2). In contrast, 97.0% of species pairs had dominant species that won
203 $\geq 60\%$ of the aggressive contests (range across groups: 95.6% for hummingbirds to 100.0% for
204 vultures), while 48.1% of species pairs had dominant species that won 100% of the aggressive
205 contests (range across groups: 27.8% for vultures to 64.6% for antbirds and woodcreepers) (Fig.
206 2). Data partitioned by location within species pairs revealed similar results.

207

208 **Variation in dominance among locations**

209 Across all species pairs, 28 had aggressive interaction data from more than one location (with
210 over 6 interactions observed from each location); 21 species pairs had data for 2 locations, 7
211 species pairs had data for 3 locations. The average distance among geographic locations within
212 species pairs was 1,176 km (range 13 – 4,184 km; all distance data are available in
213 supplementary file Data S4).

214 Dominance relationships within species pairs were consistent across sites (i.e., the same
215 species won the majority of the interactions at both or all three locations) in 26 of the 28 species
216 pairs (92.9%). The 2 species pairs whose dominance relationship flipped between locations
217 included one pair of vultures (Accipitridae: Rüppell's Vulture, *Gyps rueppellii*—White-backed
218 Vulture, *Gyps africanus*, Amboseli National Park, Kenya and Serengeti National Park, Tanzania)
219 and one pair of hummingbirds (Trochilidae: Glittering-bellied Emerald, *Chlorostilbon lucidus*—
220 Ruby-topaz Hummingbird, *Chrysolampis mosquitus*, Serra do Pará, Pernambuco, Brazil and
221 Cadeia do Espinhaço, Bahia, Brazil). For 5 of the 28 species pairs (17.9%; including the 2 for
222 which dominance relationships flipped between sites), the proportions of aggressive contests
223 won by each species were significantly different among locations (i.e., Chi-squared test, $P <$

224 0.05). For the remaining 23 species pairs (82.1%), the proportion of aggressive contests won by
225 each species did not differ significantly across sites.

226 In addition to consistent dominance relationships among locations, species pairs also
227 showed the same dominance relationships in winter and summer ($N=2$ migrant species pairs;
228 *Bucephala islandica* – *clangula*; *Anas strepera* – *americana*) and in captive versus wild
229 populations ($N=3$ species pairs; *Ammodramus maritimus* – *caudacutus*; *Melospiza melodia* –
230 *georgiana*; *Spinus psaltria* – *lawrencei*), suggesting that such asymmetries are repeatable across
231 different contexts.

232

233 **DISCUSSION**

234 Whether the outcome of aggressive interactions is commonly symmetric or asymmetric has
235 important ecological and evolutionary implications. We found the outcomes of most aggressive
236 interactions among species within the same taxonomic bird family were asymmetric. Overall,
237 83% of the 270 species pairs showed statistically significant asymmetries in the outcome of
238 aggressive contests (i.e., binomial tests, $P < 0.05$; Fig. 1), with all species pairs showing
239 statistically significant asymmetries above a sample size of 52 interactions. When we
240 characterized asymmetry using the proportion of interactions won by the dominant species, we
241 found that 80% of the species pairs contained dominant species that won 80% or more of
242 aggressive contests (Fig. 2). For 28 species pairs, we had dominance data for 2 or 3 different
243 populations, allowing us to test whether dominance asymmetries among species were consistent
244 across locations. Dominance relationships were the same across locations for 93% of the species
245 pairs (i.e., the same species won the majority of aggressive contests across the different
246 locations), while the proportion of interactions won by each species was not significantly

247 different across locations for 82% of the species pairs. These results suggest that dominance
248 relationships between species are usually consistent across different sites. Below, we discuss the
249 ecological and evolutionary consequences of asymmetric interactions, the factors that underlie
250 dominance, the possible reasons to explain the few cases where dominance differed across
251 different locations, and the implications for how dominant and subordinate species respond to
252 human impacts.

253

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

255 Asymmetric outcomes to most aggressive interactions suggest that dominant species can use
256 preferred resources and reduce the access of subordinate species to those resources (*Morse,*
257 *1974*). Such patterns are not unique to birds, as experiments have demonstrated asymmetric
258 partitioning of resources in invertebrates (*Bovbjerg, 1970; Bertness, 1981a; Bertness, 1981b*) and
259 across a diverse array of vertebrates (*Chappell, 1978; Robertson & Gaines, 1986; Alatalo &*
260 *Moreno, 1987; Martin & Martin, 2001a; Hixon, 1980; Larson, 1980; Alatalo et al., 1985;*
261 *Alatalo et al., 1987; Ziv et al., 1993; Pasch, Bolker & Phelps, 2013*). In these cases, subordinates
262 are excluded from preferred resources, but are still able to use resources that cannot sustain
263 dominant species, and thus are not preferentially defended (*Morse, 1974; Martin, 2014*). The
264 result is a repeated pattern: dominant species direct aggression towards subordinate species
265 (interference competition), restricting resource use for the subordinate species.

266 The strong asymmetries in the outcomes of aggressive contests also suggest that trade-
267 offs involving aggressive ability and behavioral dominance could play an important role in the
268 partitioning of resources and coexistence of species, particularly among closely related species.
269 For example, a smaller body size requires fewer resources to grow, survive, and reproduce, but

270 comes at a cost in the form of losing aggressive contests to larger species (*Peters, 1983*; see also
271 below). Given that resources vary in time and space, large- and small-sized species could coexist
272 by partitioning habitats according to the abundance of resources, with aggressive interactions
273 among species playing a central role in habitat partitioning (*Morse, 1974; Ford, 1979; Diamond*
274 *et al., 1989; Martin, 2014*). We might expect other trade-offs involving aggressive abilities to
275 lead to similar patterns of resource partitioning and coexistence among species of birds and other
276 taxa (e.g., *Feinsinger, 1976; Willis & Oniki, 1978; Feinsinger & Colwell, 1978*).

277

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

279 Asymmetric aggressive interactions should represent an important selection pressure between
280 interacting species (*Grether et al., 2009; Pfennig & Pfennig, 2012; Grether et al., 2013*). Our
281 results suggest that we should expect such selection to favor the evolution of distinct traits and
282 strategies that depend on the position of species within a dominance hierarchy (*Morse, 1974;*
283 *Gauthreaux, 1978; Grether et al., 2013; Freshwater, Ghalambor & Martin, 2014*). For example,
284 selection may favor investment in aggression or territorial behavior in dominant species, even
285 when such traits incur some fitness costs or trade-off with other traits. Selection may also favor
286 traits, such as color patterns or displays, that signal dominance status to subordinate species in
287 order to reduce the frequency and cost of aggressive encounters among species (see *Flack, 1976;*
288 *König, 1983; Snow & Snow, 1984* for possible examples of these traits).

289 In contrast, selection might favor traits in subordinate species that reduce the costs of
290 aggressive interactions with dominants. For example, the evolution of color patterns or displays
291 in subordinate species may reduce aggression from dominant species, and thus be favored by
292 natural selection (*Gill, 1971; Sætre, Král & Bičík, 1993*). The evolution of mimicry of dominant

293 species by subordinates may also be an underappreciated outcome of asymmetric interactions
294 among species. In birds, recent evidence suggests that the mimicry of dominant species by
295 subordinates could be widespread, involving both song and color patterns (*Cody, 1973; Rainey &*
296 *Grether, 2007; Prum & Samuelson, 2012; Prum, 2014*). Similarly, selection should favor traits
297 that facilitate alternative ecological strategies that reduce the costs of aggressive contests with
298 dominant species. Such alternative strategies could include altering the timing of breeding or
299 geographic distribution to reduce temporal and spatial overlap with dominant species
300 (*Freshwater, Ghalambor & Martin, 2014*), or evolving adaptations that allow subordinate
301 species to use novel resources (e.g., physiological tolerance to conditions outside those
302 experienced in a clade). With reduced access to important resources for survival, such as food
303 and safe roosting sites, subordinate species might also be more likely to evolve distinct life
304 history strategies that invest more in annual reproductive effort at the expense of annual survival
305 (*Roff, 1992; Stearns, 1992*). Indeed, such patterns characterize dominant and subordinate species
306 within a genus: subordinate species have lower annual survival rates and lay larger eggs for a
307 given body mass (*Freshwater, Ghalambor & Martin, 2014*).

308

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

310 **species?**

311 Many factors have been identified as influencing the proportion of encounters won by dominant
312 species, including age and sex (*Stiles, 1973*), as well as proximate factors that include condition,
313 hunger level, density, and time of arrival or colonization (*Stiles, 1973; Lyon, 1976; Anderson &*
314 *Horwitz, 1979; Cole, 1983; Wallace & Temple, 1987; Robinson, 1989; Tanner & Adler, 2009*).
315 Perhaps the most important predictor of the outcome of aggressive contests, however, appears to

316 be differences in body size among the interacting species (*Morse, 1974; Peters, 1983; Robinson*
317 *& Terborgh, 1995; Donadio & Buskirk, 2006; Martin & Ghalambor, 2014*). Indeed, in the
318 results we report here, the larger species was dominant in 87% of the contests where the
319 outcomes of aggressive contests were asymmetric (defined as $\geq 80\%$ of contests won by the
320 dominant species), with the dominant species averaging 57% heavier than the subordinate (for a
321 list of reasons why larger size confers an advantage in aggressive contests, see *Martin &*
322 *Ghalambor, 2014*). This contrasts with cases where one species won between 50-69% of the
323 contests (i.e., the outcome was more symmetric), where the larger species prevailed in only 67%
324 of the species pairs and averaged only 25% heavier (data in supplemental file Data S2).

325 The importance of body size for determining the outcomes of aggressive contests,
326 however, can vary. For example, larger species win a greater proportion of aggressive
327 interactions as the difference in body size between interacting species increases, but this
328 relationship weakens with greater evolutionary distance among the interacting species (*Martin &*
329 *Ghalambor, 2014*). We hypothesize that this pattern occurs because closely related species share
330 more traits with each other (*Violle et al., 2011*), and thus differences in size alone can determine
331 the outcome of aggressive interactions (*Martin & Ghalambor, 2014*). As species become more
332 distantly related, however, they are more likely to accumulate unique traits that influence
333 behavioral dominance independent of body size. Indeed, *Martin & Ghalambor (2014)* found that
334 as species became more distantly related, the outcome of aggressive interactions became more
335 asymmetric independent of differences in body size. Few studies, however, have attempted to
336 identify the exact suite of traits that explain dominance independent of body size (*Donadio &*
337 *Buskirk, 2006; Martin & Ghalambor, 2014*).

338

339 **The rare flip: why does dominance shift for some species pairs across sites?**

340 Although the outcomes of aggressive interactions were usually asymmetric and consistent across
341 different locations, the dominant species differed across sites for two pairs of interacting species.
342 We could not determine the cause of the variation in dominance among sites in either of these
343 cases, although the two different vulture studies categorized the outcomes of aggressive
344 interactions in different ways, which could have contributed to the different patterns (*Kruuk,*
345 *1967; Anderson & Horwitz, 1979*). Studies of other examples of dominance flipping, however,
346 help to shed light on when and why such cases arise.

347 The most detailed study of shifting dominance across sites examined the relative fighting
348 performance of hummingbirds at different elevations. Rufus Hummingbirds (*Selasphorus rufus*)
349 dominate Broad-tailed Hummingbirds (*S. platycercus*) at low elevations in Colorado, USA, but
350 are subordinate at higher elevations (*Altshuler, 2006*). The dominance reversal across elevations
351 appears to result from differences in wing loading between the species and how changes in air
352 pressure alter flight performance (*Altshuler, 2006*). Specifically, at high elevations, the long-
353 winged Broad-tailed Hummingbird appears better able to achieve burst power performance, and
354 thus dominates Rufus Hummingbirds; at low elevations, burst power is unconstrained, and the
355 greater maneuverability and sustained aerodynamic performance of the shorter-winged Rufus
356 Hummingbird appears to provide a competitive advantage over Broad-tailed Hummingbirds in
357 aggressive contests (*Altshuler, 2006*).

358 Similar variation in fighting abilities may also characterize species interactions in the air
359 versus on the ground (or water), especially because a heavier weight improves fighting abilities
360 on the ground, but can compromise aerial maneuverability that can influence the outcome of
361 aggressive contests in the air (see *Peters, 1983; Bonner, 2006*). Such trade-offs in performance

362 may explain different outcomes to aggressive contests for some species pairs (that were not part
363 of our dataset in this paper); for example, Whistling Kites, *Haliastur sphenurus*, and European
364 Herring Gulls, *Larus argentatus*, are dominant to Black Kites, *Milvus migrans*, and Audouin's
365 Gulls, *Ichthyaetus audouinii*, respectively, on the ground, but are subordinate to them in the air
366 (*Marchant & Higgins, 1993: page 74; Cramp, 1983: page 784*). Such trade-offs may be more
367 widespread than is presently recognized, particularly in birds that commonly interact in both
368 aerial and terrestrial contexts (e.g., Laridae, Accipitridae, Corvidae).

369 The relative densities of subordinate species can also influence the outcomes of
370 aggressive contests, and cause variation in dominance across sites. In our study, interactions
371 between Blue-throated (*Lampornis clemenciae*) and Magnificent (*Eugenes fulgens*)
372 hummingbirds differed significantly between locations, with Blue-throateds dominant at two
373 sites, but no significant difference in the number of contests won between the species at a third
374 site. High densities of the subordinate Magnificent Hummingbird at the third site was thought to
375 have created this shift; individuals of the dominant Blue-throated Hummingbird were more likely
376 to abort and retreat from an aggressive interaction when they encountered high densities of
377 subordinates, presumably because winning one interaction would be unlikely to give them
378 sufficient access to the resource (*Lyon, 1976*). Thus, the density of subordinate species can
379 influence the outcome of individual interactions, even with a lack of coordinated fighting among
380 individuals (*Lyon, 1976; Martin & Ghalambor, 2014*). This influence of subordinate density is
381 thought to explain variation in the outcomes of aggressive interactions across sites and contexts
382 in vultures, hummingbirds, blackbirds, and perhaps other groups, where subordinate species
383 show substantial variation in their densities (*Orians, 1961; Orians & Collier, 1963; Lyon, 1976;*
384 *König, 1983; Wallace & Temple, 1987; Houston, 1988; Kirk, 1988; Buckley, 1996*).

385 Other cases of dominance flipping between sites may simply reflect changes in the
386 composition or activities of populations over time or space, particularly with respect to age, sex,
387 and territorial behavior. For example, adult male Anna's Hummingbirds (*Calypte anna*)
388 dominated adult male Costa's Hummingbirds (*C. costae*) in 23 of 25 interactions (92%); in
389 contrast, immature Anna's Hummingbirds won only 2 of 20 interactions (10%) with adult male
390 Costa's Hummingbirds (*Stiles, 1973*). The relative distributions of males and females, and adults
391 and immatures, vary because sexes and age classes show different seasonal movements and
392 distributions in many species (*King, Farner & Mewaldt, 1965; Myers, 1981*). In addition,
393 territorial behavior and associated aggression often varies over time and space (*Nelson, Badura*
394 *& Goldman, 1990*), potentially leading to variable levels of aggression across species at different
395 times or in different sites. All of these factors, from the density of air to the territorial behavior of
396 individuals can cause dominance relationships to flip between species at different sites. The
397 rarity of this dominance flipping in our dataset, however, suggests that the most important
398 determinants of dominance across species remain consistent regardless of geography, and despite
399 the many other factors that can influence the outcomes of aggressive contests.

400

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

402 Given repeated patterns of dominance and asymmetric interactions among species, we might
403 expect species to differ in their responses to anthropogenic challenges, such as climate change
404 and habitat alteration, depending on their position within a dominance hierarchy. Some
405 subordinate species appear to be better able to persist in degraded habitats (*Daily & Ehrlich,*
406 *1994*), and may have greater ecological breadth and tolerance compared to dominant species
407 (*Morse, 1974; Minot & Perrins, 1986; Blowes, Pratchett & Connolly, 2013*; but see *Freshwater,*

408 *Ghalambor & Martin, 2014*). Aggression and behavioral dominance, however, are often
409 associated with boldness that can help species cope in the face of human disturbance (*Evans,*
410 *Boudreau & Hyman, 2010; Lowry, Lill & Wong, 2013*). Thus, traits that covary with dominance
411 status could facilitate or hinder species in the face of human alteration of habitats. Regardless,
412 the importance of asymmetric interactions in determining patterns of resource use among species
413 suggests that these interactions may mediate species' responses to perturbations like habitat
414 alteration or climate change. Few models consider these kinds of species interactions in their
415 forecasts of the impacts of habitat perturbations or climate change on species abundance and
416 distributions (*Tylianakis et al., 2008; Gilman et al., 2010; Buckley, 2013*). Yet, any impacts on
417 dominant species are likely to have cascading effects on the subordinate species with which they
418 interact (*Duckworth & Badyaev, 2007; Gilman et al., 2010; Jankowski, Robinson & Levey, 2010;*
419 *Buckley, 2013; Martin & Dobbs, 2014; Freeman & Montgomery, 2015; Freeman, Class*
420 *Freeman & Hochachka, 2016*). Such asymmetric interactions could have important
421 consequences for populations, particularly in environments where the options for dispersal and
422 range shifting are limited (e.g., tropical islands and mountains; *Jankowski, Robinson & Levey,*
423 *2010; Freeman, 2016*).

424

425 **ACKNOWLEDGEMENTS**

426 We thank Fran Bonier for helpful insight and discussion, and Ben Freeman and Greg Grether for
427 comments and suggestions that significantly improved the manuscript.

428

429 **Data Availability**

430 Our data are included with this submission as supplementary files Data S1-S4.

431

432 REFERENCES

433 **Alatalo RV, Eriksson D, Gustafsson L, Larsson K. 1987.** Exploitation competition influences
434 the use of foraging sites by tits: experimental evidence. *Ecology* **68**:284-290.

435 **Alatalo RV, Gustafsson L, Linden M, Lundberg A. 1985.** Interspecific competition and niche
436 shifts in tits and the goldcrest: an experiment. *Journal of Animal Ecology* **54**:977-984.

437 **Alatalo RV, Moreno J. 1987.** Body size, interspecific interactions, and use of foraging sites in
438 tits (Paridae). *Ecology* **68**:1773-1777.

439 **Altshuler DL. 2006.** Flight performance and competitive displacement of hummingbirds across
440 elevational gradients. *American Naturalist* **167**:216-229.

441 **Anderson DJ, Horwitz RJ. 1979.** Competitive interactions among vultures and their avian
442 competitors. *Ibis* **121**:505-509.

443 **Bertness MD. 1981a.** Predation, physical stress, and the organization of a tropical rocky
444 intertidal hermit crab community. *Ecology* **62**:411-425.

445 **Bertness MD. 1981b.** Competitive dynamics of a tropical hermit crab assemblage. *Ecology*
446 **62**:751-761.

447 **Blowes SA, Pratchett MS, Connolly SR. 2013.** Heterospecific aggression and dominance in a
448 guild of coral feeding fishes: the roles of dietary ecology and phylogeny. *American*
449 *Naturalist* **182**:157-168.

450 **Bonner JT. 2006.** *Why size matters*. Princeton: Princeton University Press.

451 **Bovbjerg H. 1970.** Ecological isolation and competitive exclusion in two crayfish (*Orconectes*
452 *virillis* and *Orconectes immunis*). *Ecology* **51**:225-236.

- 453 **Buckley LB. 2013.** Get real: putting models of climate change and species interactions in
454 practice. *Annals of the New York Academy of Sciences* **1297**:126-138.
- 455 **Buckley NJ. 1996.** Food finding and the influence of information, local enhancement, and
456 communal roosting on foraging success of North American vultures. *Auk* **113**:473-488.
- 457 **Carstensen DW, Sweeny R, Ehlers B, Olesen JM. 2011.** Coexistence and habitat preference of
458 two honeyeaters and a sunbird on Lombok, Indonesia. *Biotropica* **43**:351-356.
- 459 **Chappell MA. 1978.** Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*).
460 *Ecology* **59**:565–579.
- 461 **Cody ML. 1973.** Character convergence. *Annual Review of Ecology and Systematics* **4**:189-211.
- 462 **Cole BJ. 1983.** Assembly of mangrove ant communities: patterns of geographical distribution.
463 *Journal of Animal Ecology* **52**:339–347.
- 464 **Cramp S. (ed) 1983.** *The birds of the Western Palearctic. Vol. III. Waders to gulls.* Oxford:
465 Oxford University Press.
- 466 **Crawley MJ. 2013.** *The R book, second edition.* Chichester: John Wiley & Sons.
- 467 **Daily GC, Ehrlich PR. 1994.** Influence of social status on individual foraging and community
468 structure in a bird guild. *Oecologia* **100**:153–165.
- 469 **Dhondt AA. 2012.** Interspecific competition in birds. Oxford: Oxford University Press.
- 470 **Dhondt AA, Eyckerman R. 1980.** Competition between the great tit and the blue tit outside the
471 breeding season in field experiments. *Ecology* **61**:1291-1296.
- 472 **Diamond J, Pimm SL, Gilpin ME, LeCroy M. 1989.** Rapid evolution of character
473 displacement in Myzomelid honeyeaters. *American Naturalist* **134**:675-708.
- 474 **Donadio E, Buskirk SW. 2006.** Diet, morphology, and interspecific killing in Carnivora.
475 *American Naturalist* **67**:524–536.

- 476 **Dow DD. 1975.** Displays of the honeyeater *Manorina melanocephala*. *Zeitschrift für*
477 *Tierpsychologie* **38**:70-96.
- 478 **Duckworth RA, Badyaev AV. 2007.** Coupling of dispersal and aggression facilitates the rapid
479 range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of*
480 *the USA* **104**:15017–15022.
- 481 **Evans J, Boudreau K, Hyman J. 2010.** Behavioural syndromes in urban and rural populations
482 of song sparrows. *Ethology* **116**:588-595.
- 483 **Feinsinger P. 1976.** Organization of a tropical guild of nectarivorous birds. *Ecological*
484 *Monographs* **46**:257–291.
- 485 **Feinsinger P, Chaplin SB. 1975.** On the relationship between wing disc loading and foraging
486 strategy in hummingbirds. *American Naturalist* **109**:217–224.
- 487 **Feinsinger P, Colwell RK. 1978.** Community organization among neotropical nectar-feeding
488 birds. *American Zoologist* **18**:779–795.
- 489 **Flack JAD. 1976.** The use of frontal spot and crown feathers in inter- and intraspecific display
490 by the South Island Robin *Petroica australis australis*. *Notornis* **23**:90-105.
- 491 **Ford HA. 1979.** Interspecific competition in Australian honeyeaters – depletion of common
492 resources. *Australian Journal of Ecology* **4**:145-164.
- 493 **Freeman BG. 2016.** Strong asymmetric interspecific aggression between two sympatric New
494 Guinean robins. *Ibis* **158**:75-81.
- 495 **Freeman BG, Class Freeman AM, Hochachka WM. 2016.** Asymmetric interspecific
496 aggression in New Guinean songbirds that replace one another along an elevational
497 gradient. *Ibis* **158**:726-737.

- 498 **Freeman BG, Montgomery, G. 2015.** Interspecific aggression by the Swainson's Thrush
499 (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush
500 (*Catharus bicknelli*) in the Adirondack Mountains. *Condor* **118**:169-178.
- 501 **Freshwater C, Ghalambor CK, Martin PR. 2014.** Repeated patterns of trait divergence
502 between closely related dominant and subordinate bird species. *Ecology* **95**:2334-2345.
- 503 **Gauthreaux SA Jr. 1978.** The ecological significance of behavioral dominance. In: Bateson
504 PPG, Klopfer PH, eds. *Perspectives in ethology*. New York: Plenum Press, 17-54.
- 505 **Gill FB. 1971.** Ecology and evolution of the sympatric Mascarene white-eyes, *Zosterops*
506 *borbonica* and *Zosterops olivacea*. *Auk* **88**:35-60.
- 507 **Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010.** A framework for
508 community interactions under climate change. *Trends in Ecology and Evolution* **25**:325-
509 331.
- 510 **Grether GF, Anderson CN, Drury JP, Kirschel ANG, Losin N, Okamoto K, Peiman KS.**
511 **2013.** The evolutionary consequences of interspecific aggression. *Annals of the New York*
512 *Academy of Sciences* **1289**:48–68.
- 513 **Grether GF, Losin N, Anderson CN, Okamoto K. 2009.** The role of interspecific interference
514 competition in character displacement and the evolution of competitor recognition.
515 *Biological Reviews* **84**:617–635.
- 516 **Hixon MA. 1980.** Competitive interactions between California reef fishes of the genus
517 *Embiotica*. *Ecology* **61**:918-931.
- 518 **Holt RD. 1977.** Predation, apparent competition, and the structure of prey communities.
519 *Theoretical Population Biology* **12**:197–229.
- 520 **Holt RD, Kotler BP. 1987.** Short-term apparent competition. *American Naturalist* **130**:412–430.

- 521 **Holt RD, Lawton JH. 1994.** The ecological consequences of shared natural enemies. *Annual*
522 *Review of Ecology and Systematics* **25**:495–520.
- 523 **Houston DC. 1988.** Competition for food in Neotropical vultures in forest. *Ibis* **130**:402-417.
- 524 **Jankowski JE, Robinson SK, Levey DJ. 2010.** Squeezed at the top: interspecific aggression
525 may constrain elevational ranges in tropical birds. *Ecology* **91**:1877–1884.
- 526 **Jones JA, Tisdale AC, Tucker JL, Bakermans MH, Larkin JL, Smalling CG, Siefferman L.**
527 **2016.** A case of mistaken identity: understanding the stimulus of agonism between two
528 wood warblers. *Animal Behaviour* **114**:81-91.
- 529 **King JR, Farner DS, Mewaldt LR. 1965.** Seasonal sex and age ratios in populations of the
530 White-crowned Sparrows of the race *gambelii*. *Condor* **67**:489-504.
- 531 **Kirk DA. 1988.** *Ecological separation of small Cathartid vultures in South America*. PhD thesis.
532 Glasgow: University of Glasgow.
- 533 **König C. 1983.** Interspecific and intraspecific competition for food among Old World vultures.
534 In: Wilbur SR, Jackson JA, eds. *Vulture biology and management*. Berkeley: University of
535 California Press, 153–171.
- 536 **Kruuk H. 1967.** Competition for food between vultures in east Africa. *Ardea* **55**:171-193.
- 537 **Larson RJ. 1980.** Competition, habitat selection, and the bathymetric segregation of two
538 rockfish (*Sebastes*). *Ecological Monographs* **50**:221-239.
- 539 **Lawton JH, Hassell MP. 1981.** Asymmetrical competition in insects. *Nature* **289**:793-795.
- 540 **Leisler B. 1988.** Interspecific interactions among European marsh-nesting passerines. In: Ouellet
541 H, ed. *Acta XIX Congressus Internationalis Ornithologici, Vol. 2*. Ottawa: Ottawa
542 University Press, 2635-2644.

- 543 **Losin N, Drury JP, Peiman KS, Storch C, Grether GF. 2016.** The ecological and evolutionary
544 stability of interspecific territoriality. *Ecology Letters* **19**:260-267.
- 545 **Lowry H, Lill A, Wong B. 2013.** Behavioural responses of wildlife to urban environments.
546 *Biological Reviews* **88**:537-549.
- 547 **Lyon DL. 1976.** A montane hummingbird territorial system in Oaxaca, Mexico. *Wilson Bulletin*
548 **88**:280–299.
- 549 **Marchant S, Higgins PJ. (eds) 1993.** *Handbook of Australian, New Zealand and Antarctic*
550 *Birds. Volume 2: Raptors to lapwings.* Melbourne: Oxford University Press.
- 551 **Martin PR. 2014.** Trade-offs and biological diversity: integrative answers to ecological
552 questions. In: Martin LB, Ghalambor CK, Woods HA, eds. *Integrative organismal biology.*
553 New York: John Wiley & Sons, 291-308.
- 554 **Martin PR, Dobbs RC. 2014.** Asymmetric response to heterospecific songs in two sympatric
555 wrens (Troglodytidae) in Argentina: House Wren (*Troglodytes aedon*) and Mountain Wren
556 (*T. solstitialis*). *Ornitología Neotropical* **25**:407-419.
- 557 **Martin PR, Ghalambor CK. 2014.** When David beats Goliath: The advantage of large size in
558 interspecific aggressive contests declines over evolutionary time. *PLoS ONE* **9**: e108741.
- 559 **Martin PR, Martin TE. 2001a.** Ecological and fitness consequences of species coexistence: a
560 removal experiment with wood warblers. *Ecology* **82**:189-206.
- 561 **Martin PR, Martin TE. 2001b.** Behavioral interactions between coexisting species: song
562 playback experiments with wood warblers. *Ecology* **82**:207-218.
- 563 **Martin TE. 1988.** On the advantage of being different: nest predation and the coexistence of
564 bird species. *Proceedings of the National Academy of Sciences of the USA* **85**:2196–2199.

- 565 **Minot EO, Perrins CM. 1986.** Interspecific interference competition — nest sites for blue and
566 great tits. *Journal of Animal Ecology* **55**:331-350.
- 567 **Morse DH. 1974.** Niche breadth and social dominance. *American Naturalist* **108**:818–830.
- 568 **Murray BG. 1976.** Critique of interspecific territoriality and character convergence. *Condor*
569 **78**:518-525.
- 570 **Murray BG. 1981.** The origins of adaptive interspecific territorialism. *Biological Reviews of the*
571 *Cambridge Philosophical Society* **56**:1-22.
- 572 **Murray BG. 1988.** Interspecific territoriality in *Acrocephalus*: a critical review. *Ornis*
573 *Scandinavica* **19**:309-313.
- 574 **Myers JP. 1981.** A test of three hypotheses for latitudinal segregation of the sexes in wintering
575 birds. *Canadian Journal of Zoology* **59**:1527-1534.
- 576 **Nelson RJ, Badura LL, Goldman BD. 1990.** Mechanisms of seasonal cycles of behavior.
577 *Annual Review of Psychology* **41**:81-108.
- 578 **Nuechterlein GL, Storer RW. 1985.** Aggressive behavior and interspecific killing by Flying
579 Steamer-Ducks in Argentina. *Condor* **87**:87-91.
- 580 **Orians GH. 1961.** The ecology of blackbird (*Agelaius*) social systems. *Ecological Monographs*
581 **31**:285–312.
- 582 **Orians GH, Collier G. 1963.** Competition and blackbird social systems. *Evolution* **17**:449–459.
- 583 **Orians GH, Willson MF. 1964.** Interspecific territories of birds. *Ecology* **45**:736-745.
- 584 **Owen-Ashley NT, Butler LK. 2004.** Androgens, interspecific competition and species
585 replacement in hybridizing warblers? *Proceedings of the Royal Society, Series B*
586 **271**:S498–S500.

- 587 **Palomares F, Caro TM. 1999.** Interspecific killing among mammalian carnivores. *American*
588 *Naturalist* **153**:492-508.
- 589 **Pasch B, Bolker BM, Phelps SM. 2013.** Interspecific dominance via vocal interactions mediates
590 altitudinal zonation in Neotropical singing mice. *American Naturalist* **182**:E161-E173.
- 591 **Peiman KS, Robinson BW. 2010.** Ecology and evolution of resource-related heterospecific
592 aggression. *Quarterly Review of Biology* **85**:133–158.
- 593 **Persson L. 1985.** Asymmetrical competition: are larger animals competitively superior?
594 *American Naturalist* **126**:261-266.
- 595 **Peters RH. 1983.** *The ecological implications of body size.* Cambridge: Cambridge University
596 Press.
- 597 **Pfennig DW, Pfennig, KS. 2012.** *Evolution's wedge: competition and the origins of diversity.*
598 Berkeley: University of California Press.
- 599 **Prum RO. 2014.** Interspecific social dominance mimicry in birds. *Zoological Journal of the*
600 *Linnean Society* **172**:910-941.
- 601 **Prum RO, Samuelson L. 2012.** The Hairy-Downy Game: a model of interspecific social
602 dominance mimicry. *Journal of Theoretical Biology* **313**:42-60.
- 603 **R Core Team. 2014.** *R: A language and environment for statistical computing.* Vienna: R
604 Foundation for Statistical Computing. <http://www.R-project.org/>.
- 605 **Rainey MM, Grether GF. 2007.** Competitive mimicry: synthesis of a neglected class of
606 mimetic relationships. *Ecology* **88**:2440–2448.
- 607 **Robertson DR, Gaines SD. 1986.** Interference competition structures habitat use in a local
608 assemblage of coral reef surgeonfishes. *Ecology* **67**:1372-1383.

- 609 **Robinson D. 1989.** Interspecific aggression and territorial behavior between Scarlet Robin
610 *Petroica multicolor* and Flame Robin *P. phoenicea*. *Emu* **89**:93-101.
- 611 **Robinson SK, Terborgh J. 1995.** Interspecific aggression and habitat selection by Amazonian
612 birds. *Journal of Animal Ecology* **64**:1–11.
- 613 **Roff DA. 1992.** *Evolution of life histories: theory and analysis*. New York: Springer.
- 614 **Sætre G-P, Král M, Bičík V. 1993.** Experimental evidence for interspecific female mimicry in
615 sympatric *Ficedula* flycatchers. *Evolution* **47**:939–945.
- 616 **Snow BK, Snow DW. 1984.** Long-term defence of fruit by Mistle Thrushes *Turdus viscivorus*.
617 *Ibis* **126**:39-49.
- 618 **Stearns SC. 1992.** *The evolution of life histories*. Oxford: Oxford University Press.
- 619 **Stiles FG. 1973.** Food supply and the annual cycle of the Anna Hummingbird. *University of*
620 *California Publications in Zoology* **97**:1–109.
- 621 **Tanner CJ, Adler FR. 2009.** To fight or not to fight: context-dependent interspecific aggression
622 in competing ants. *Animal Behaviour* **77**:297–305.
- 623 **Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008.** Global change and species
624 interactions in terrestrial ecosystems. *Ecology Letters* **11**:1351–1363.
- 625 **Vavrek MJ. 2012.** *fossil*: Palaeoecological and palaeogeographical analysis tools. R package
626 version 0.3.7.
- 627 **Violle C, Nemergut DR, Pu Z, Jiang L. 2011.** Phylogenetic limiting similarity and competitive
628 exclusion. *Ecology Letters* **14**:782–787.
- 629 **Wallace GE, Collier B, Sydeman WJ. 1992.** Interspecific nest-site competition among cavity-
630 nesting alcids on southeast Farallon Island, California. *Colonial Waterbirds* **15**:241-244.

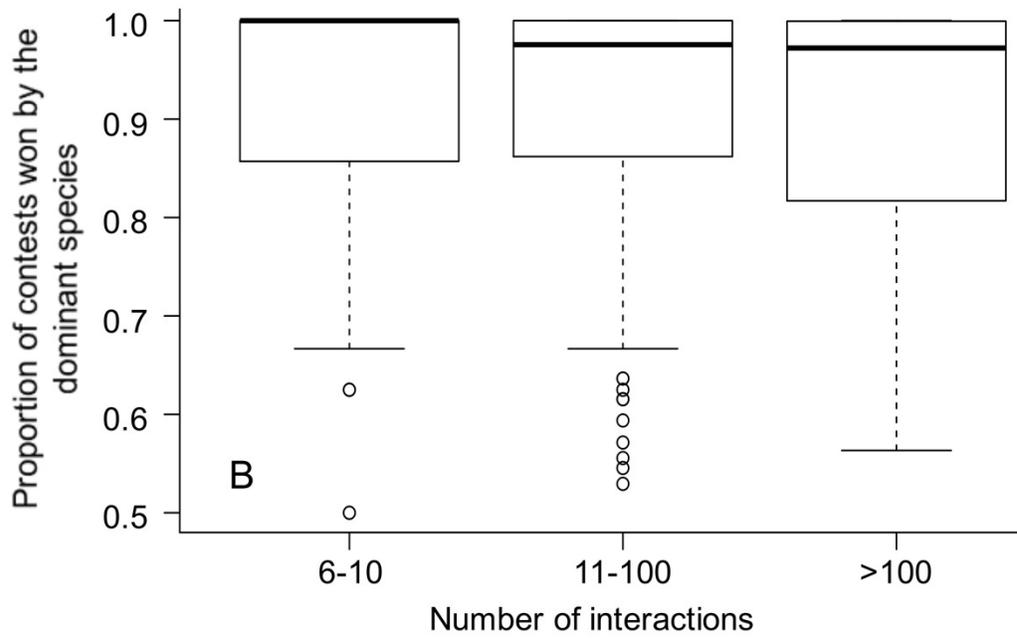
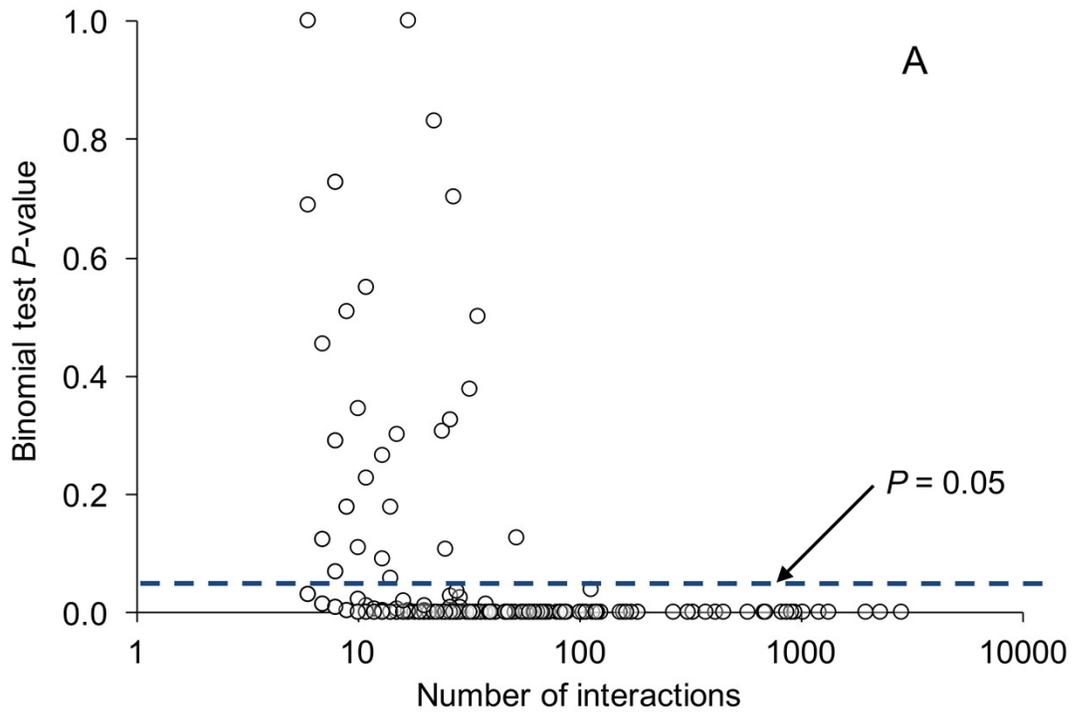
- 631 **Wallace MP, Temple SA. 1987.** Competitive interactions within and between species in a guild
632 of avian scavengers. *Auk* **104**:290-295.
- 633 **Willis EO, Oniki Y. 1978.** Birds and army ants. *Annual Review of Ecology and Systematics*
634 **9**:243–263.
- 635 **Young KA. 2003.** Evolution of fighting behavior under asymmetric competition: an
636 experimental test with juvenile salmonids. *Behavioral Ecology* **14**:127–134.
- 637 **Ziv Y, Abramsky Z, Kotler BP, Subach A. 1993.** Interference competition and temporal and
638 habitat partitioning in two gerbil species. *Oikos* **66**:237-46.
- 639

641 Figure captions

642 **Figure 1: Relationship between the number of aggressive interactions observed between**
643 **each species pair and (A) binomial test P -values testing for asymmetries in the outcomes of**
644 **aggressive interactions, and (B) the proportion of aggressive contests won by the dominant**
645 **species.**

646 In panel (A), the dashed line illustrates the common P -value cutoff for statistical significance at
647 0.05. All species pairs with greater than 52 interactions showed statistically significant
648 asymmetries; overall, 83% of species pairs showed statistically significant asymmetries. In panel
649 (B), box plots show the median as a center line, the interquartile range as a box, values within
650 1.5*interquartile range as whiskers, and all data that lie outside the whiskers as circles. Overall,
651 84 species pairs had sample sizes between 6-10 interactions, 151 species pairs had 11-100
652 interactions, and 35 species pairs had >100 interactions.

653



654 **Figure 2: The proportion of species pairs showing asymmetric outcomes to their aggressive**
655 **interactions.**

656 Asymmetry was measured by the proportion of interactions won by the dominant species, and
657 was defined on a scale from >60% of the interactions won by the dominant species to 100% of
658 the interactions won by the dominant species (x-axis). The thick black line represents the entire
659 dataset; the blue lines represent different groups within the dataset. Plots are line plots
660 connecting points at 0.01 x-value increments. The sample sizes for the different groups are:
661 vultures ($N = 18$ comparisons, 5,820 interactions), hummingbirds ($N = 135$ comparisons, 6,685
662 interactions), woodcreepers and antbirds ($N = 65$ comparisons, 9,263 interactions), North
663 American congeners ($N = 52$ comparisons, 4,444 interactions).

664

665

