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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 favor ecological and evolutionary strategies specific to the position of a species within a 41 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
- 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
- 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
- evolution (*Morse, 1974*; *Grether et al., 2009*; *Grether et al., 2013*; *Freshwater,*
- 66 *Ghalambor & Martin, 2014; Martin & Ghalambor, 2014*). The nature of these

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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

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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

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

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

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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

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

163

164 Statistical tests of asymmetry

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

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

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

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

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

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.

182 Variation in dominance among locations

- 183 For species pairs with dominance data from multiple locations (each location with greater
- than 6 interactions per species pair), we looked at the frequency with which dominance
- 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)
- asymmetries in the outcomes of aggressive contests. Above a sample size of 52, all
- 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%
- for antbirds and woodcreepers; Fig. 2). In contrast, 97.0% of species pairs had dominant
- species that won >60% of the aggressive contests (range across groups: 95.6% for
- hummingbirds to 100.0% for vultures), while 48.1% of species pairs had dominant

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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,
- Bahia, Brazil). For 6 of the 30 species pairs (20.0%; including the 2 for which dominance
- relationships flipped between sites), the proportions of aggressive contests won by each
- species were significantly different among locations (i.e., Chi-squared test, P < 0.05). For
- the remaining 24 species pairs (80.0%), the proportion of aggressive contests won by
- each species did not differ significantly across sites.
- 234

235 **DISCUSSION**

Whether the outcome of aggressive interactions is commonly symmetric or asymmetric has important ecological and evolutionary implications. We found the outcomes of most aggressive interactions within the same taxonomic bird family were asymmetric. Overall, 83% of the 270 species pairs showed statistically significant asymmetries in the outcome of aggressive contests (i.e., binomial tests, P < 0.05; Fig. 1), with all species pairs

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

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

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

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

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

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

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- 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
- 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

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

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

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

266 direct aggression towards subordinate species (interference competition) restricting

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

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

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

270 *2001a*).

The strong asymmetries in the outcomes of aggressive contests also suggest that 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
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285 286 287	Asymmetric aggressive interactions should represent an important selection pressure between interacting species (<i>Grether et al., 2009</i> ; <i>Pfennig & Pfennig, 2012</i> ; <i>Grether et al.,</i> <i>2013</i>). Our results suggest that we should expect such selection to favor the evolution of
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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 (Codv, 1973; Rainev & 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; Lvon, 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

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,

- 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
- dispersal and range shifting are limited (e.g., tropical islands and mountains; Jankowski,
- 372 *Robinson & Levey, 2010; Freeman, 2016).*
- 373

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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
- **Figure 1** Binomial test *P*-values testing for asymmetries in the outcomes of aggressive
- interactions for each species pair in our study, as a function of the number of interactions
- 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
- 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
- within the dataset. Plots are line plots connecting points at 0.01 x-value increments.

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(Proportion of interactions won by the dominant species)