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

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Abstract

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 26,656 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.
INTRODUCTION

Aggressive interactions commonly occur among closely related species (Kruuk, 1976; Feinsinger, 1976; Willis & Oniki, 1978; Robinson & Terborgh, 1995). Such direct interspecific interactions have been shown to play an important role in interference competition for resources, including habitat, food, nest sites, and roost sites (Chappell, 1978; Dhondt & Eyckerman, 1980; Robertson & Gaines, 1986; Alatalo & Moreno, 1987; Wallace, Collier & Sydeman, 1992; Dhondt, 2012). Aggressive interactions may also influence indirect ecological interactions (Martin, 1988; Martin & Martin, 2001a; Martin & Martin, 2001b) by reducing the fitness costs manifested through density-dependent responses of predators and parasites that prey or infect closely related species (often called "apparent competition"; Holt, 1977; Holt & Kotler, 1987; Holt & Lawton, 1994).

Although it has been suggested that aggressive interactions occur among closely related species due to misplaced aggression (Murray, 1976; Murray, 1981; Murray, 1988; Jones et al., 2016), sexual selection for aggressive displays (Nuechterlein & Storer, 1985), or as a means of practicing for intraspecific contests (Nuechterlein & Storer, 1985), evidence to date suggests that many aggressive interactions reflect adaptive responses to reduce ecological costs for one or both species (Robinson & Terborgh, 1995; Martin & Martin, 2001b; Leisler, 1988; Palomares & Caro, 1999; Peiman & Robinson, 2010; Blowes et al., 2013; Losin et al., 2016).

Given the ecological importance of aggressive interactions among closely related species, such interactions may have broad consequences for species assemblages and trait evolution (Morse, 1974; Grether et al., 2009; Grether et al., 2013; Freshwater, Ghalambor & Martin, 2014; Martin & Ghalambor, 2014). The nature of these
consequences, however, depends on whether the outcome of aggressive interactions between species are symmetric, with both species regularly winning aggressive contests, or asymmetric, with one species winning the majority of aggressive contests. For example, if the outcomes of aggressive interactions are asymmetric, then selection may favor traits in the dominant species that enhance fighting abilities (Young, 2003; Owen-Ashley & Butler, 2004; Donadio & Buskirk, 2006) or that signal dominance to other species (Dow, 1975; Flack, 1976; König, 1983; Snow & Snow, 1984). Asymmetric interactions may also favor traits in the subordinate species that reduce the likelihood of heterospecific aggression, such as traits that reduce ecological overlap with dominant species (Feinsinger, 1976; Willis & Oniki, 1978; Morse, 1974; König, 1983) or that reduce aggression from dominant species (e.g., the loss of signals that induce aggression from the dominant species, or the evolution of signals that mimic the dominant or other dangerous species; Gill, 1971; Feinsinger & Chaplin, 1975; Feinsinger & Colwell, 1978; Rainey & Grether, 2007; Prum & Samuelson, 2012; Prum, 2014). Conversely, if aggressive interspecific interactions are typically symmetric, then selection may act similarly on the interacting species, potentially favoring traits such as interspecific territoriality (Orians & Willson, 1964). Thus, selection should shape the evolution of species’ traits differently if aggressive interactions are symmetric versus asymmetric. Despite the importance of understanding the prevalence of asymmetric relationships among interacting species, relatively little is known about how common such patterns are in nature.

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

Here, we compile published, quantitative data on the outcomes of aggressive interactions among species within the same taxonomic families, focusing on birds where interaction data are common. We estimate asymmetries in interactions among species 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
optimal method for estimating their magnitude, prevalence, or biological importance. For example, a lack of statistically significant dominance asymmetries may simply reflect small sample sizes; in other cases, large sample sizes may result in statistically significant asymmetries of small biological effect (e.g., 55:45 splits in the outcomes of aggressive interactions). Thus, we also estimated the prevalence of asymmetric interactions by calculating the proportion of aggressive contests won by each species, providing a view of their biological importance that has not been highlighted in other studies to date (e.g., Freshwater, Ghalambor & Martin 2014). The outcome of aggressive contests, including which species is behaviorally dominant, may also vary across different habitats or geographic locales (Altshuler, 2006; Carstensen et al., 2011), but the frequency of such variation has not previously been explored. To test how common asymmetric aggressive interactions are in birds, we examined the outcome of contests across diverse groups of birds, including vultures feeding at carcasses, hummingbirds feeding at nectar sources, antbirds and woodcreepers feeding on prey fleeing from army ant swarms, and a broad collection of North American congeners. Where possible, we also examined if the outcome of aggressive interactions between the same species pairs changed between different geographic locations. Collectively, we present results from data representing 270 interacting pairs of species from 26 families, and including the outcomes of 26,656 interactions.

MATERIALS & METHODS

Interaction data
We used published data from Freshwater, Ghalambor & Martin (2014) and Martin & Ghalambor (2014), supplemented with additional quantitative data, including published data for interactions that had been excluded from Martin & Ghalambor (2014) because of a lack of genetic or mass data for the interacting species. This study did not require vertebrate ethics approvals because we used published data in a comparative test supplemented with a few additional natural history observations. For data on North American congeners, we included only the youngest phylogenetically-independent species pair for which we had quantitative data on the outcomes of aggressive interactions (following Freshwater, Ghalambor & Martin 2014). The complete datasets and sources for all of the data are included with this submission as supplementary files Data S1-S3. Overall, we created two different datasets: (1) all of the data combined, including data for species interactions that were gathered from multiple sites and summed together for each species pair (Data S2), and (2) the same data entered for each individual location separately, and where each location had at least 6 observations per species pair (Data S3). We included data separated by location to address the potential effects of lumping data across geographic locations on our results. Separating data by location also allowed us to test for geographic variation in dominance relationships among species using the cases where the same species pairs had interaction data from multiple locations. For all datasets, we included only species pairs (Data S2) or locations (Data S3) that had at least 6 interactions with clear outcomes (i.e., one species clearly won the interaction). Following the previous work, we included chases, supplants and displacements, kleptoparasitism, and physical attacks as aggressive interactions (see Freshwater, Ghalambor & Martin 2014 for definitions of these terms). We excluded observations that
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.,

Statistical tests of asymmetry

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

Proportion of interactions won

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
cut-off for designating interactions as asymmetric, so we plotted the cumulative number
of species pairs showing asymmetric outcomes to their interactions, varying the definition
of asymmetric from >60% to 100% of the interactions won by the dominant. As before,
we plotted these relationships for data summarized by species pairs, and again for data
partitioned by location within each species pair.
Variation in dominance among locations

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 proportion of aggressive contests won by each species between sites using Chi-squared tests in R (R Core Team, 2014).

RESULTS

Statistical tests of asymmetry

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). Data partitioned by location within species pairs revealed similar results: 235 of 287 comparisons (81.9%) showed statistically significant ($P < 0.05$) asymmetries in the outcomes of aggressive contests.

Proportion of interactions won

For data summarized by species pair, 79.6% of species pairs had dominant species that 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
species that won 100% of the aggressive contests (range across groups: 27.8% for vultures to 65.2% for antbirds and woodcreepers) (Fig. 2). Data partitioned by location within species pairs revealed similar results: 79.8% of species pairs had dominant species that won >80% of the aggressive contests (range across groups: 72.0% for vultures to 89.1% for antbirds and woodcreepers), 96.2% of species pairs had dominant species that won >60% of the aggressive contests (range across groups: 88.0% for vultures to 98.4% for antbirds and woodcreepers), and 50.5% of species pairs had dominant species that won 100% of the aggressive contests (range across groups: 32.0% for vultures to 70.3% for antbirds and woodcreepers).

Variation in dominance among locations

Across all species pairs, 30 had aggressive interaction data from more than one location (with over 6 interactions observed from each location); 23 species pairs had data for 2 locations, 7 species pairs had data for 3 locations. Of the 30 species pairs with data from different geographic locations, 12 species pairs had data from different countries, 13 species pairs had data from different states or provinces within the same countries, and 5 species pairs had data from different geographic locales within the same state or province.

Dominance relationships within species pairs were consistent across sites (i.e., the same species won the majority of the interactions at both or all three locations) in 28 of the 30 species pairs (93.3%). The 2 species pairs whose dominance relationship flipped between locations included one pair of vultures (Accipitridae: Rüppell’s Vulture, Gyps rueppellii—White-backed Vulture, Gyps africanus, Amboseli National Park, Kenya and Serengeti National Park, Tanzania) and one pair of hummingbirds (Trochilidae:
Glittering-bellied Emerald, *Chlorostilbon lucidus*— Ruby-topaz Hummingbird,

*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.

**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.

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 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 locations), while the proportion of interactions won by each species was not significantly different across locations for 80% of the species pairs. These results suggest that
dominance relationships between species are usually consistent across different sites.

Below, we discuss the ecological and evolutionary consequences of asymmetric interactions, the factors that underlie dominance, and the implications for how dominant and subordinate species respond to human impacts.

Asymmetric interactions and their consequences for ecology

Asymmetric outcomes to most aggressive interactions suggest that dominant species can use preferred resources and reduce the access of subordinate species to those resources (Morse, 1974). Such patterns are not unique to birds, as experiments have demonstrated asymmetric partitioning of resources in invertebrates (Bovbjerg, 1970; Bertness, 1981a; Bertness, 1981b) and across a diverse array of vertebrates (Chappell, 1978; Robertson & Gaines, 1986; Alatalo & Moreno, 1987; Martin & Martin, 2001a; Hixon, 1980; Larson, 1980; Alatalo et al., 1985; Alatalo et al., 1987; Ziv et al., 1993; Pasch, Bolker & Phelps, 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 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, parasites, or prey, including apparent or exploitative competition) (Martin & Martin, 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
role in the partitioning of resources and coexistence of species, particularly among closely related species. For example, a smaller body size allows species to grow, survive, and reproduce with fewer resources, but comes at a cost in the form of losing aggressive contests to larger species (Peters, 1983; see also below). Given that resources vary in time and space, large- and small-sized species could coexist by partitioning habitats according to the abundance of resources, with aggressive interactions among species playing a central role in habitat partitioning (Morse, 1974; Ford, 1979; Diamond et al., 1989; Martin, 2014). We might expect other trade-offs involving aggressive abilities to lead to similar patterns of resource partitioning and coexistence among species of birds and other taxa (e.g., Feinsinger, 1976; Willis & Oniki, 1978; Feinsinger & Colwell, 1978).

**Asymmetric interactions and their consequences for evolution**

Asymmetric aggressive interactions should represent an important selection pressure between interacting species (Grether et al., 2009; Pfennig & Pfennig, 2012; Grether et al., 2013). Our results suggest that we should expect such selection to favor the evolution of distinct traits and strategies that depend on the position of species within a dominance hierarchy (Morse, 1974; Gauthreaux, 1978; Grether et al., 2013; Freshwater, Ghalambor & Martin, 2014). For example, selection may favor investment in aggression or territorial behavior in dominant species, even when such traits incur some fitness costs or trade-off with other traits. Selection may also favor traits, such as color patterns or displays, that signal dominance status to subordinate species in order to reduce the frequency and cost of aggressive encounters among species (see Flack, 1976; König, 1983; Snow & Snow, 1984 for possible examples of these traits).
In contrast, selection might favor traits in subordinate species that reduce the costs of aggressive interactions with dominants. For example, the evolution of color patterns or displays in subordinate species may reduce aggression from dominant species, and thus be favored by natural selection (Gill, 1971; Sætre, Král & Bičík, 1993). The evolution of mimicry of dominant species by subordinates may also be an underappreciated outcome of asymmetric interactions among species. In birds, recent evidence suggests that the mimicry of dominant species by subordinates could be widespread, involving both song and color patterns (Cody, 1973; Rainey & Grether, 2007; Prum & Samuelson, 2012; Prum, 2014). Similarly, selection should favor traits that facilitate alternative ecological strategies that reduce the costs of aggressive contests with dominant species. Such alternative strategies could include altering the timing of breeding or geographic distribution to reduce temporal and spatial overlap with dominant species (Freshwater, Ghalambor & Martin, 2014), or evolving adaptations that allow subordinate species to use novel resources (e.g., physiological tolerance to conditions outside those experienced in a clade). With reduced access to important resources for survival, such as food and safe roosting sites, subordinate species might also be more likely to evolve distinct life history strategies that invest more in annual reproductive effort at the expense of annual survival (Roff, 1992; Stearns, 1992). Indeed, such patterns characterize dominant and subordinate species within a genus: subordinate species have lower annual survival rates and lay larger eggs for a given body mass (Freshwater, Ghalambor & Martin, 2014).

What causes variation in the asymmetric outcomes of aggressive encounters among species?
Many factors have been identified as influencing the proportion of encounters won by dominant species, including age and sex (Stiles, 1973) and the context in which the encounter occurs (Altshuler, 2006), as well as proximate factors that include condition, hunger level, density, and time of arrival or colonization (Stiles, 1973; Lyon, 1976; Anderson & Horwitz, 1979; Cole, 1983; Wallace & Temple, 1987; Robinson, 1989; Tanner & Adler, 2009). Perhaps the most important predictor of the outcome of aggressive contests, however, appears to be differences in body size among the interacting species (Morse, 1974; Peters, 1983; Robinson & Terborgh, 1995; Donadio & Buskirk, 2006; Martin & Ghalambor, 2014). Indeed, in the results we report here, the larger species was dominant in 88% of the contests where the outcomes of aggressive contests were asymmetric (defined as over 80% contests won by the dominant species), with the dominant species averaging 57% heavier than the subordinate (for a list of reasons why larger size confers an advantage in aggressive contests, see Martin & Ghalambor, 2014). This contrasts with cases where one species won between 50-69% of the contests (i.e., the outcome was more symmetric), where the larger species prevailed in only 63% of the species pairs and averaged only 24% heavier (data in Dryad).

The importance of body size for determining the outcomes of aggressive contests, however, can vary. For example, larger species win a greater proportion of aggressive interactions as the difference in body size between interacting species increases, but this relationship weakens with greater evolutionary distance among the interacting species (Martin & Ghalambor, 2014). We hypothesize this pattern occurs because closely related 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).
As species become more distantly related, however, they are more likely to accumulate unique traits that influence behavioral dominance independent of body size. Indeed, Martin & Ghalambor (2014) found that as species became more distantly related, the outcome of aggressive interactions became more asymmetric independent of differences in body size. Few studies, however, have attempted to identify the exact suite of traits that explain dominance independent of body size (Donadio & Buskirk, 2006; Martin & Ghalambor, 2014).

Asymmetric interactions and their consequences for human impacts

Given broad asymmetries, we should also expect species to differ in their responses to anthropogenic challenges, such as climate change and habitat alteration, depending on their position within a dominance hierarchy. Some subordinate species appear to be better able to persist in degraded habitats (Daily & Ehrlich, 1994), and may have greater ecological breadth and tolerance compared to dominant species (Morse, 1974; Minot & Perrins, 1986; Blowes, Pratchett & Connolly, 2013; but see Freshwater, Ghalambor & Martin, 2014). Aggression and behavioral dominance, however, are often associated with boldness that can help species cope in the face of human disturbance (Evans, Boudreau & Hyman, 2010; Lowry, Lill & Wong, 2013). Thus, traits that covary with dominance status 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 species suggests that these interactions may mediate species' responses to perturbations like habitat alteration or climate change. Few models consider these kinds of species interactions in their forecasts of the impacts of habitat perturbations or climate change on
species abundance and distributions (Tylianakis et al., 2008; Gilman et al., 2010; Buckley, 2013). Yet, any impacts on dominant species are likely to have cascading effects on the subordinate species with which they interact (Duckworth & Badyaev, 2007; Gilman et al., 2010; Jankowski, Robinson & Levey, 2010; Buckley, 2013; Martin & Dobbs, 2014; Freeman & Montgomery, 2015). Such asymmetric interactions could have important consequences for populations, particularly in environments where the options for dispersal and range shifting are limited (e.g., tropical islands and mountains; Jankowski, Robinson & Levey, 2010; Freeman, 2016).

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Data Availability

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

REFERENCES


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 statistical significance at 0.05. All species pairs with greater than 52 interactions showed statistically significant asymmetries; overall, 83% of species pairs showed statistically significant asymmetries.
Binomial test P-value

Number of interactions

P = 0.05
Figure 2 The proportion of species pairs showing asymmetric outcomes to their aggressive interactions. Asymmetry was measured by the proportion of interactions won by the dominant species, and was defined on a scale from >60% of the interactions won by the dominant species to 100% of the interactions won by the dominant species (x-axis). 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.
The graph illustrates the proportion of species pairs with asymmetric outcomes for different categories of species. The x-axis represents the cutoff for defining asymmetric outcomes, which is the proportion of interactions won by the dominant species. The y-axis shows the proportion of species pairs with asymmetric outcomes. Different line styles and colors represent various groups: Woodcreepers & antbirds, Hummingbirds, North American congeners, and Vultures. The graph shows a trend where the proportion of asymmetric outcomes increases as the cutoff for defining asymmetric outcomes increases.