The effect of sociality on competitive interactions among birds

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ABSTRACT

Sociality can provide many benefits, including increased foraging success, reproductive opportunities, and defence against predation. How does sociality influence the dominance hierarchies of ecological competitors? Here, we address this question using a large dataset of competitive interactions among birds foraging at backyard feeders across North America, representing a network of over 88,000 interactions among 196 bird species. We quantify sociality as the number of conspecifics observed together, and show that this measure of group size varies across bird species. More social species are less likely to dominate similarly sized opponents, suggesting that the evolution of social clustering is associated with reduced competitive ability overall. At the same time, we find that more social species also gain a greater competitive advantage from the presence of their conspecifics. We show that within-species competition occurs more often than expected in a null model, with the most social species exhibiting the greatest proportion of conflict originating from conspecifics. Overall, these results demonstrate that sociality influences the outcome of competition in ecological networks. Species that evolve greater sociality exhibit decreased competitive ability as individuals, but increased competitive ability in groups.

INTRODUCTION

Animal sociality can provide many ecological and evolutionary advantages, including increased foraging success [1,2], more frequent mating opportunities [3,4], and improved survival through dilution and confusion effects on predators [5,6]. However, sociality may also incur costs under certain circumstance, such as conflict among conspecific group members that share a similar niche [7,8]. The causes and consequences of animal sociality have historically been of interest in evolutionary biology, with several different hypotheses for benefits that may explain the evolution of social grouping. One hypothesized benefit of sociality is that social coalitions may provide an advantage during conflict with competitors [9,10]. While both inter- and intraspecific dominance is often enhanced by body size [11,12] and age/experience [13], there may also be opportunities for subordinate individuals to gain an advantage over dominant competitors through social coalitions [9,14]. During foraging, animals face competition from both conspecifics and heterospecifics, but the influence of social grouping on the structure of these competitive systems has not yet been described. Our aim in this study is to evaluate how sociality influences competition in communities where interactions occur both within and between species.

One system which could measure such effects is the competition among seed-eating birds at backyard bird feeders. In many temperate systems, survival in winter depends on acquiring adequate food resources [15,16]. Moreover, the use of artificial food sources (e.g., bird feeders) during winter foraging has been identified as having important evolutionary consequences in birds [17,18], including high rates of competitive interactions among and within species foraging at feeder locations [19,20]. In the context of sociality, group foraging can provide more opportunities for resource acquisition than foraging independently due to the shared vigilant

effort [21,22] (but see [23]), social information gathering [24,25], and improved rates of
60 competition success over solitary foragers [26]. Individuals may be particularly likely to adopt social foraging strategies in the winter when resources are scarce.

62 Here, we investigate how sociality influences competition using interactions among birds that visit backyard feeders. Our general predictions are that more social species gain a benefit in
64 interspecific conflict, at a cost of increased rates of intraspecific conflict. We tested these predictions using data from Project FeederWatch (PFW), a surveying program with a network of
66 tens of thousands of observers across North America who monitor the presence and interactions of hundreds of bird species throughout winter (Figure 1). This project has yielded a rich dataset
68 indicating who competes with whom, and how often (Figure 1D). Previous research using PFW behavioural observations has revealed that species body mass is the primary predictor of
70 competitive dominance within communities of winter resident birds across the North American continent [12]. Owing to the large number of interactions observed and variation in competitive
72 outcomes (Figure 1D), the PFW program provides an ideal system to test how variation in sociality influences competitive interactions after accounting for the effects of body size.

74 We quantify variation in social behaviour in the PFW database using conspecific group size (i.e., the number of individuals of a given bird species observed at a given a location at the
76 same time; Figure 1A-C) [27]. It is important to note that sociality also has other dimensions beyond the simple tempo-spatial aggregation studied here, such as the stability of group
78 membership, the types of relationships between group members, and other emergent properties of group organization [28,29]. Nevertheless, conspecific groupings – individuals found in the
80 same place at the same time – represent the most fundamental dimension of sociality that we expect to influence competitive outcomes across species.

As a first step in this study, we determine whether winter sociality differs across bird species by quantifying the repeatability of group size (Figure 1A). We also estimate the phylogenetic signal of average group size, which describes the extent to which this trait is more similar among closely related species (Figure 1B). Second, we evaluate whether average group size (as a species trait) is associated with species differences in competitive dominance against similarly sized opponents (Figure 1D). We expect that larger social group size has coevolved with greater interspecific dominance. Third, for each species studied, we test whether the presence of conspecifics affects the outcome of interspecific dominance interactions (hereafter, we refer to this as a "conspecific effect"). After estimating the conspecific effect for each species, we test whether more social species exhibit a more positive conspecific effect. Finally, to evaluate the hypothesized costs of social grouping, we consider the frequency of conflict with conspecifics (Figure 1D), and compare the observed rates of within-group conflict to those expected in a null model. If large group sizes lead to increased within-group conflict, we expect more social species to experience a greater proportion of conflict originating from conspecifics.

MATERIALS AND METHODS

(a) Data sources

We used a dataset collected by Project FeederWatch (PFW), a population monitoring program with over 9 million observations of bird species observed at winter feeding locations in North America during the months of November through April, 2015-2020. Participants were invited to monitor their chosen feeding location during weekly two-day observation periods throughout the winter. Participants recorded which species they observed and the maximum number of co-occurring individuals that they observed simultaneously at the feeding location for each species.

Additionally, as a measure of observation effort, each participant indicated whether they performed morning and/or afternoon monitoring sessions during each day (up to a maximum value of four monitoring sessions per two-day observation period). For the purpose of the present study, we sampled species with at least 100 displacement interactions in PFW as the focal species for our further comparative analyses (n = 68 species). All data analyses were performed in R (version 4.0.3) [30].

(b) Quantifying species differences in sociality

As our measure of sociality, we used group size, defined as the maximum number of individuals of a given species observed simultaneously during a given monitoring session (Figure 1A). To assess whether focal species differ in their average winter sociality, we analyzed the repeatability of this metric using the "rptR" package [31]. Hence, repeatability is defined as the proportion of total variation in group size that is attributed to differences among species. A high value of repeatability in this analysis indicates that most of the variation in group size is due to differences among species, whereas a low value (near 0) indicates that species differences in this trait are not detected. Because the size of the dataset was so large (n = 8,575,748 observations of the 68 focal species), we used a bootstrapping approach to estimate repeatability. For each bootstrap iteration, we randomly selected a subset of data with 1,000 observed group sizes for each of the 68 focal species (randomly chosen from the full dataset available for each species). We used this subset to compute conditional repeatability, adjusted by observation effort, using the Poisson distribution and log link as appropriate for these count data. This procedure was repeated 100 times to derive a distribution of repeatability estimates for species differences in average group size.

Upon finding that average group size differs among species, we estimated each focal species' average group size as our measure of sociality for further comparative analyses of species traits. To do this, we fit a regression model for each focal species where the response variable was the observed group size (log-transformed; n = 3,200 – 551,026 observations, depending on the species), with a fixed effect of observation effort. From the fitted models, we defined each species' sociality as its predicted average group size on a log scale given an effort of one monitoring session (Figure 1B). We also estimated Pagel's lambda for species average group size [32]. This value ranges between 0 and 1, where values closer to 1 indicate that closely related species have similar trait values, and values near 0 indicate that trait variation is independent of phylogenetic relatedness.

As an additional check on our metric of group size, we collected information on the natural history each focal species during winter from species accounts in the Birds of the World online resource [33]. We used these descriptive accounts to classify each focal species into one of three categories: often flocking (clear descriptions of winter flocking and/or group behaviour), sometimes flocking (indicators of occasional winter flocking and/or participation as a satellite member), and rarely flocking (described as independent in winter).

(c) Quantifying species dominance traits

We studied dominance interactions by using a dataset of displacement events collected by participants during a subset of the PFW observation periods. Dominance events were defined as instances when one species displaced another at a feeding location. Participants recorded 88,988 displacement interactions among 196 bird species, with most of these observations (71%) collected in winters of 2017-18 and 2018-19. Note that although we filtered non-focal species

from our comparative analyses, we retained the interactions they had with focal species when characterizing focal species traits.

For each focal species, we quantified two species dominance traits: a species' average competitive dominance and its 'conspecific effect'. Competitive dominance was defined as the probability that a focal species would be the displacer in a dominance interaction against a same-sized (body mass) heterospecific opponent. To estimate competitive dominance, we fit a binomial mixed-effects model for each focal species where the response variable was the outcome of their displacement interactions (i.e., whether the focal species was the displacer, or was displaced). These models were fit using the "lme4" package [34] and included two fixed effects: the focal species' observed group size during that monitoring session (Figure S1), and the relative body mass of the opponent species . Relative body mass was defined as the difference in log-transformed species body masses (opponent species body mass – focal species body mass). To account for repeated measures at the same spatial location, the models also included region as a random effect, defined by latitude and longitude coordinates rounded to the nearest degree. The average sample size for these models was 1,606 displacement interactions per focal species (ranging 83 – 10,583).

We used these same models to calculate the conspecific effect for each species, defined as the average effect (positive or negative) of nearby conspecifics on the outcome of between-species competition. As illustrated in Figure 2B, C: the conspecific effect was calculated as the expected increase in the probability of the focal species being the displacer over a heterospecific opponent, given a focal species group size of three, as compared to a focal species group size of one. Note that we chose a group size of three because such smaller group sizes are far more commonly observed. The resulting metric, the conspecific effect, can take values from –1 to 1,

with negative values indicating that a species' dominance decreases in the presence of conspecifics, and positive values indicating that a species' dominance increases in the presence of conspecifics. A conspecific effect value of 0 would indicate that the presence of conspecifics does not affect a species' dominance. We consider analyses of this trait to be conservative because the PFW observers reported only one group size per species per monitoring session (the maximum group size they observed). As a result, our estimates for the conspecific effect hinge on the assumption that species group sizes are relatively stable at a given feeder within a short span of time (e.g., [35–37]). Alternatively, if species group sizes are highly variable over the span of a few hours, it would reduce our ability to detect conspecific effects.

(d) Dominance traits in relation to sociality

To test whether species dominance traits are related to species differences in sociality, we used two regression models. The first model related a species' competitive dominance to group size, and the second model related a species' conspecific effect to group size (n = 68 focal species). In both models, the main predictor of interest was species average group size, and body mass was included as an additional predictor. Models were fit using the "brms" package [38] with a Gaussian error distribution. We ran these models both with and without accounting for the phylogenetic relationships among focal species in the random effects structure. If the phylogenetically adjusted model estimated a weaker effect size for a given predictor than the simpler model, it would indicate that the relationship is driven by differences among broader lineages. We ran models for 10,000 iterations using two chains and verified that Rhat values were all between 1.00 and 1.01, indicating model convergence.

(e) Within-species conflict

Competitive interactions with conspecifics are among the most common (Figure 1D). To test whether within-species conflict occurs more often than expected, we compared the observed frequencies of within-species displacement interactions in PFW with expected values based on a null model that was spatially constrained by region. The null model was computed as follows: within each region (defined by latitude and longitude rounded to the nearest degree), we first determined the proportion of total interactors for each species. Then, we calculated the expected number of conspecific interactions for each species, under the assumption that interaction rates are determined by the composition of interactors in that region. We took the square of a given species' regional proportion as the expected probability of a conspecific interaction for that species and region. We then multiplied this probability by the number of interactions in the region to obtain an expected count. Finally, we took the sum of these expected conspecific interaction counts across all regions for a given focal species. When analyzing the expected and observed within-species interactions, we log-transformed both variables to normalize residuals.

To test whether a species' social behaviour predicts within-species conflict, we fit a regression model where the response variable was the proportion of competitive displacement interactions that were conspecific (one value per focal species). The predictors in this analysis included three species traits: average group size, the conspecific effect, and body mass. This model was fit using the Bayesian brms package as described above, and we examined the model with and without accounting for the phylogenetic relationships among focal species.

RESULTS

(a) Species differ in the degree of sociality

220 There is substantial variation both among and within species in average group size, as indicated the repeatability for this trait ($R_{\text{link-scale}}$ = 0.36, 95% CI = [0.29, 0.44]; Figure 1A, n = 68 focal
222 species). Species average group size also has a strong phylogenetic signal (lambda = 0.99, $p < 0.001$), indicating that closely related species share a very similar degree of sociality (Figure 1B).
224 Species average group size also corresponds to broad descriptions from natural history accounts (Figure 1C). Notably, our metric captures group size variation both within and among species.
226

(b) Estimates of the conspecific effect

228 The conspecific effect varied widely across species, with most estimates centred on 0 (average conspecific effect of -0.10, 95% CI = [-0.37, 0.17]; Figure S1). We detected a significant positive
230 conspecific effect in only one species, the pine siskin (*Carduelis pinus*), indicating that pine siskins gain a large increase in competitive dominance when more group members are present
232 (0.12, 95% CI = [0.08, 0.17]; Figure 2A, B). We detected significant negative conspecific effects in 14 species, including the pine warbler (*Dendroica pinus*; -0.27 [-0.44, -0.10]), the white-
234 winged dove (*Zenaida asiatica*; -0.16 [-0.32, -0.05]; Figure 2A, C), and the eastern bluebird (*Sialia sialis*; -0.13 [-0.21, -0.04]). These species are less dominant when more conspecific group
236 members are present.

238 *(c) Social species are poor competitors, but gain a competitive advantage in groups*

Contrary to our initial expectation, we found that more social species were less likely to
240 dominate other similarly-sized opponent species (Figure 3A, Table S2). The conclusions of this analysis were consistent when accounting for phylogeny (Table S2). More social species also

had more positive conspecific effects (Figure 3B, Table S3). This effect remained strong when accounting for phylogenetic nonindependence (Table S3).

(d) Social species have elevated within-group conflict

In 62 of the 68 focal species, displacement interactions with conspecifics occurred more often than expected in the null model (Figure 4A). As expected, more social species receive a greater proportion of conflict originating from conspecifics (Figure 4B, S2, Table S4). This association was weaker when accounting for phylogenetic relationships, indicating that it is primarily driven by differences among lineages within our sample (Table S4).

DISCUSSION

Here, we examine the effect of social clustering on competition among birds across the North American continent. We find that species vary in their average group size, and that sociality during winter foraging has been highly conserved in avian evolution. Contrary to our initial prediction, we find that more social species are also weaker competitors when interacting with similarly sized heterospecific opponents. This result suggests that there may be an evolutionary trade-off whereby the evolution of greater sociality is correlated with reduced individual competitive ability against other opponent species. Our results also show that more social species gain a greater dominance advantage in the presence of their conspecifics, whereas solitary species are less dominant in the presence of conspecifics. Collectively, these results suggest that more social species have reduced competitive ability as individuals, but enhanced competitive ability in groups.

These results indicate that selection for pro-social behaviours may be associated with a reduction in traits such as aggression that would provide an advantage to an individual in heterospecific competition [39]. As species evolve to become more social, they may also acquire behavioral plasticity in aggression, boldness, or vigilance behaviour that may facilitate greater dominance over heterospecific opponents when in the presence of one or more conspecifics [40,41]. It is also possible that opponents respond differently to social species depending on their group size (e.g., because larger groups generate a more intimidating visual and/or acoustic signal). To test these hypotheses, experiments are needed to measure behavioural outcomes under controlled conditions where the social environment can also be carefully manipulated.

Our results examining within-species conflict support the hypothesis that the evolution of sociality leads to greater conflict within-groups. In the presence of many conspecifics, individuals may interact more often, especially if they are collecting similar resources [7,8]. Members of a group may experience increased rates of aggressive interactions at times of food scarcity [42,43]. One way to reduce competition pressures between conspecifics may be through the participation in a mixed-species flock. Mixed-species flocks have been found to provide members with greater advantages than conspecific coalitions, including increased foraging rates and reduce vigilance effort [1]. While some evidence suggests that members of mixed-species flocks are more similar than expected [44], they undoubtedly vary more in their ecological needs than same-species flocks and therefore may demonstrate a reduced level of within-group conflict than a conspecific coalition [45–47]. A key question for future research is whether mixed-species flocking reduces the frequency of within-group conflict.

It is important to note that while we define sociality as the aggregation of individuals in space and time, there are other dimensions of sociality that are also expected to play a role in

influencing competition. For example, members of a temporary flock with short-term social bonds may experience a weaker influence of conspecifics than of members in a structured dominance hierarchy with long-term, persistent bonds [12,48–50]. This raises interesting questions that can only be addressed by tracking individuals within groups, such as: How does the strength of social bonds and the organization of a group influence a species' competitive ability? Do such effects on competition change with temporal variation in species social organization? Within a species, how does the strength of a coalitionary relationship affect the dominance of one group over others?

Previous studies have examined the benefits of coalitionary behaviour on within-species conflict [9,14,51]. Our results here demonstrate how sociality can also influence the dynamics of ecological competition, and how a species' tendency to form social groups is associated with the evolution of reduced competitive ability as individuals. These findings provided valuable insight into the fundamental effects of grouping behaviour on competitive interactions during foraging. Further questions remain as to the effects of specific social bonds and the emergent properties of groups on competitive interactions.

FIGURE LEGENDS

Figure 1. North American bird species differ in winter sociality and competitive dominance. A) Example of daily average group sizes (± SE) for seven bird species during winter 2017-18, with average group size indicated by colour of the line. B) Phylogeny of 68 focal bird species with average group size shown by the size and colour of the outer bars. Note that the colour gradient throughout this figure follows the legend in (A). C) Species average group size in relation to descriptions from natural history accounts. Horizontal lines indicate medians. D) Network illustrating dominance interactions among a subset of the most common species. Each row represents a species, and the grey connections show frequencies of competitive interactions. Horizontal connections represent competitive interactions with conspecifics. Species nodes are ordered vertically (top to bottom) from the most to least dominant, and coloured by average group size. Labels represent species common names (see Table S1 for details).

Figure 2. Predictors of competitive dominance against other species. A) Partial residual plot showing the predicted probability of competitive dominance as a function of group size for two species models, the pine siskin (green circles) and white-winged dove (orange triangles). B-C) These fitted models were used to calculate the conspecific effect by determining the change in the probability of being the displacer when comparing a group size of three with a solitary condition. D) Caterpillar plot showing estimates of the conspecific effect for each focal species (± 95% confidence intervals). Species shown in grey have a confidence interval that includes zero, those shown in red have a significant negative conspecific effect, and the species shown in blue has a significant positive conspecific effect.

Figure 3. Social species are poor competitors as individuals, but gain a competitive advantage in groups. Partial residual plots show the analysis of two species traits: (A) competitive dominance, and (B) the conspecific effect, in relation to average group size (n = 68 focal species). Partial residuals on the y-axis account for other predictors in the analysis. The lines show the fitted model.

Figure 4. Conflict with conspecifics occurs more often than expected, especially in more social lineages. (A) Observed and expected counts of conspecific displacement interactions (n = 68 focal species). The red dotted line indicates a 1:1 line where the observed frequency matches the expected value in the null model; the black line is the line of best fit for the observed and expected values. (B) Partial residual plot showing the analysis of conspecific conflict. The line indicates the fitted model.

DATA ACCESSIBILITY

All data and R scripts are available at: https://figshare.com/s/1cd6708a27a541029409
The repository will be made public when the final version of the study is published.

AUTHOR CONTRIBUTIONS

IB and RD designed the study with input from ETM. ETM developed the behaviour interactions methodology in Project FeederWatch. IB and RD analyzed the data and wrote the manuscript. All authors edited the manuscript.

COMPETING INTERESTS

We have no competing interests.

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Figure 1

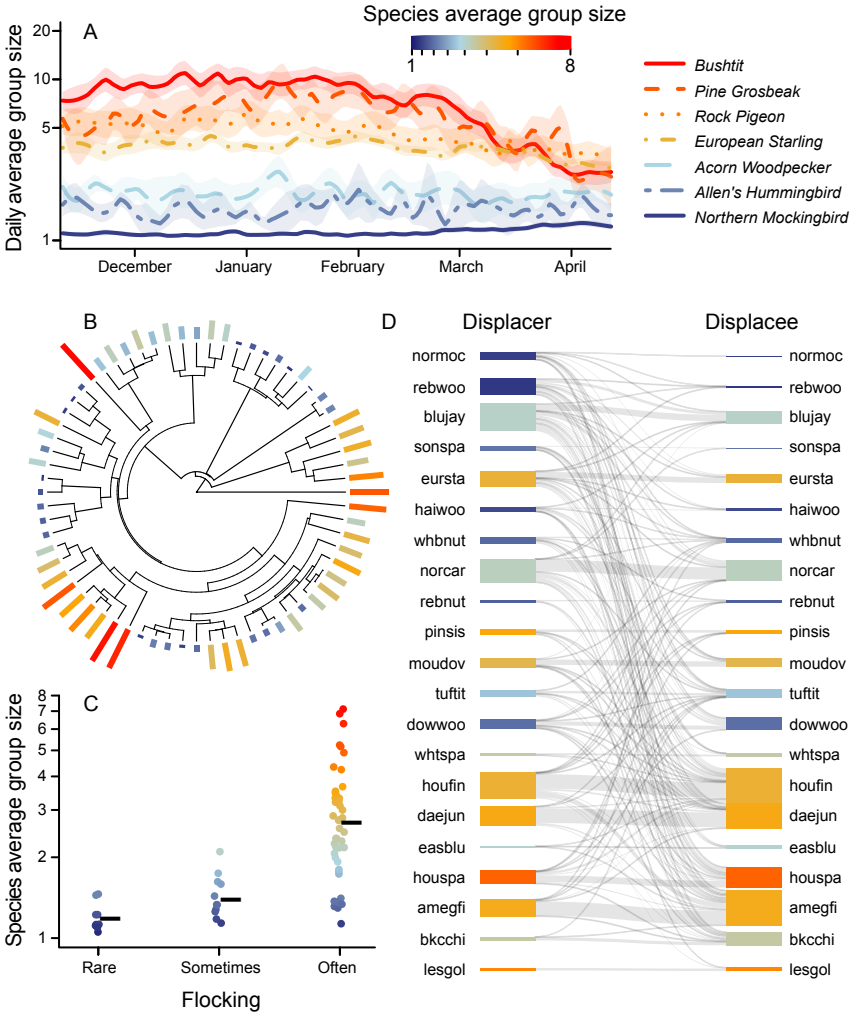

A
Species average group size
1
8
Daily average group size
20
10
5
1
December
January
February
March
April
Bushtit
Pine Grosbeak
Rock Pigeon
European Starling
Acorn Woodpecker
Allen's Hummingbird
Northern Mockingbird
B
C
Species average group size
8
7
6
5
4
3
2
1
Rare
Sometimes
Often
Flocking
D
Displacer
Displacee
normoc
rebwoo
blujay
sonspa
eursta
haiwoo
whbnut
norcar
rebnut
pinsis
moudov
tuftit
dowwoo
whtspa
houfin
daejun
easblu
houspa
amegfi
bkcchi
lesgol

Figure 2

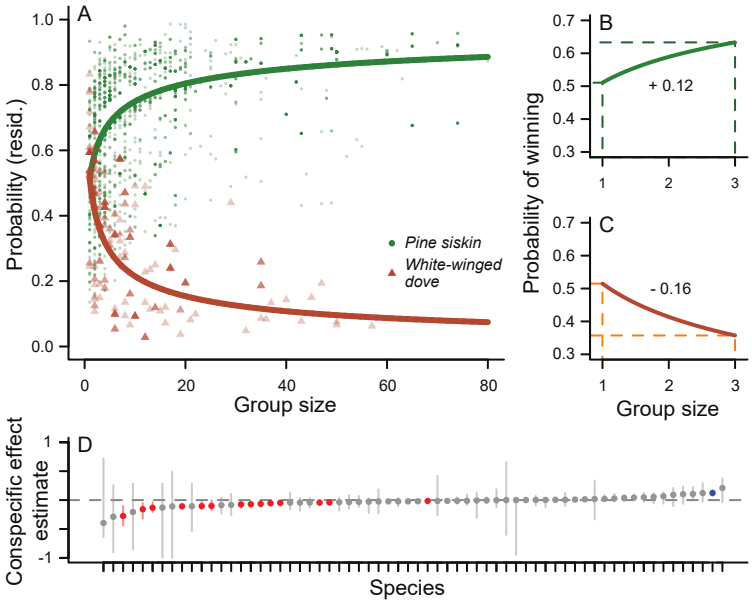

A
Probability (resid.)
Group size
Pine siskin
White-winged dove
B
+ 0.12
C
- 0.16
Probability of winning
Group size
D
Conspecific effect estimate
Species

Figure 3

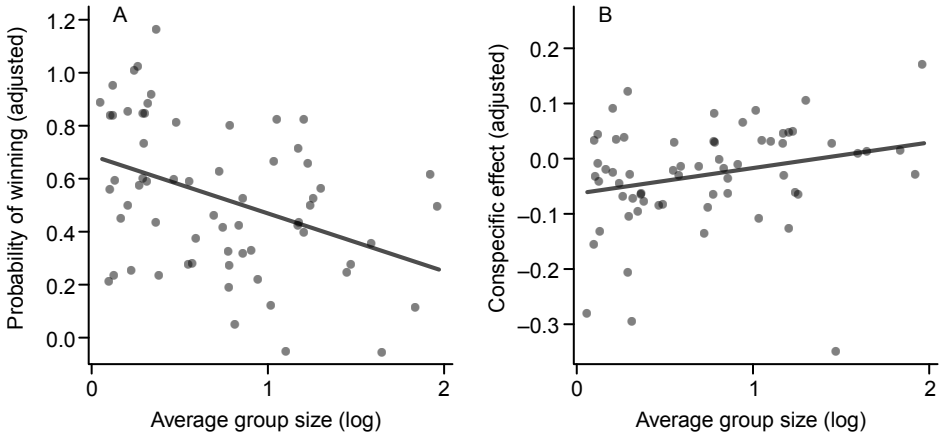
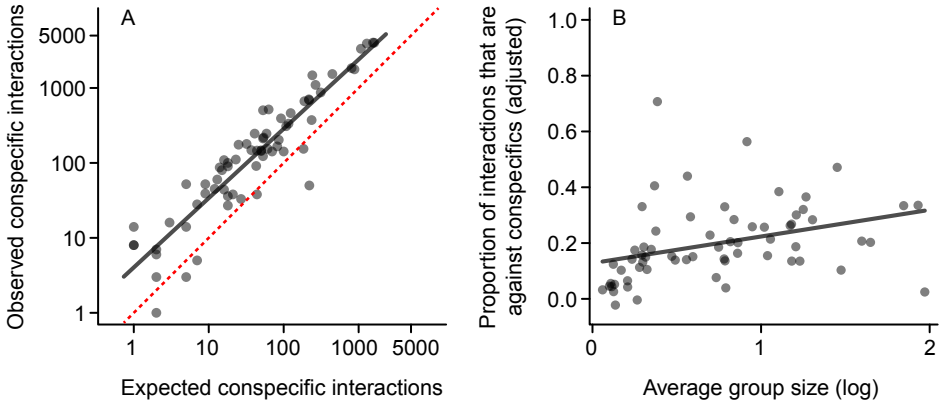

A
Probability of winning (adjusted)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
Average group size (log)
B
Conspecific effect (adjusted)
0.2
0.1
0.0
−0.1
−0.2
−0.3
0
1
2
Average group size (log)

Figure 4


A
Observed conspecific interactions
5000
1000
100
10
1
1
10
100
1000
5000
Expected conspecific interactions
B
Proportion of interactions that are against conspecifics (adjusted)
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
Average group size (log)