

Pecking order: establishing a hierarchy of dominance among common feeder birds in western Montana

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ABSTRACT

Dominance among bird species has been shown to be closely-linked to body size, with larger bird species tending to be dominant over smaller bird species. Within Moiese Valley in Montana, however, most of the local bird species are comparable in size, providing a unique opportunity to understand what drives success in competitive interactions between these species. Feeders at four sites were under video surveillance to record aggressive displays or displacements. Such competitive interactions were scored and used to rank bird species into a single hierarchy of feeder dominance. The three primary species (black-headed grosbeaks, house finches, and house sparrows) exhibited a relationship in which house sparrows were dominant to the other two and grosbeaks were dominant to finches, upsetting Miller's findings that size predicts aggression. This is explained in that competitive success in grosbeaks was linked to sex – male grosbeaks consistently won but females did not. These findings present novel information on both interspecific and intraspecific competition and how bird species may adapt their foraging behavior in response to the presence of other species, increasing human presence and potentially, loss of habitat and other natural food resources in the wake of climate change.

Keywords: feeder dominance, interspecific and intraspecific competition

INTRODUCTION

Urban ecology is a severely understudied but increasingly important field, especially in the wake of growing human populations and the problems often associated with it, including, but not limited to, increasing urbanization, loss of biodiversity, pollution, and climate change. More than just the destruction of pristine wilderness however, there is a global crisis in the loss of farmland due to increasing urbanization (Satterthwaite et al. 2010; Gottlieb 2015). In both of these scenarios concerning the loss of land, contact with humans becomes more common, if not inevitable, for most organisms. Natural selection will doubtlessly favor the survival of those organisms most capable of adjusting to living with, and in some cases, relying on humans for food (Brittingham and Temple 1992).

Aside from classically “urban birds” such as pigeons and crows that have long adapted to human presence, there is much to be studied about avian species on the brink of two landscapes – one with humans and one without (Bonier et al. 2007). In many systems, this interaction point serves as a food source in the form of recreational bird feeding by landowners. While probably not intentionally, humans thus also set up an arena for competition over the food resource (Galbraith et al. 2017). In turn this may serve as an avenue for natural selection on a smaller scale, as birds aggressively compete for access to food, exhibiting commonly observed but understudied behaviors like displacement (Hotchkiss et al. 2005; Adelman et al. 2015). These aggressive displays can lead to dominance hierarchies between different bird species and can be categorized into interspecific and intraspecific competition (Jankowski 2012). Although intraspecific competition amongst members of the same species is common and to be expected, interspecific competition between multiple species may be more relevant from entire-ecosystem

perspectives. As climate change and urbanization of land continue to threaten most, if not all, of the earth's biomes, parsing out both interspecific and intraspecific competition and adaptability to human-sources of food can become critical to predicting which species will persist, as well as projecting their populations and ranges. Among these competition studies however, a clear discrepancy can be seen – there are few studies concerning the bird species of the American grasslands (Cody 1968; Cody 1974).

Miller et al. (2017) recently created a hierarchy of bird dominance using instances of aggression and feeder displacement for common bird species across the continental United States based off of the citizen science *Project FeederWatch* run by the Cornell Lab of Ornithology. Miller's data suggest that there is often a positive correlation with feeder dominance and body size – in short, the bigger the bird species, the more likely it is to win at a bird feeder.

However, due to the similarity in body size between different bird species in some systems, a dominance hierarchy may not be so easily defined in all cases. Thus, it may be necessary to further elucidate what additional characteristics determine dominance in such systems. Moiese Valley in Montana is one such location, home to a diverse collection of bird species, but of which many could be simply referred to as “little brown birds.” Basing our hypothesis on the well-studied ideal free distribution, we predict that resource partitioning may occur such that different bird species will arrive at different times so as to minimize competition (Cody 1968; Dewitt Fretwell and Lucas 1969). An alternative hypothesis may be that within similarly-sized species groups, an intransitivity may exist which creates a relationship akin to a “rock-paper-scissors” competitive balance (e.g. species $A > B$, $B > C$, $C > A$) that could prevent any one species from entirely dominating resources (May and Leonard 1975).

METHODS

Study sites

Data was collected from four study sites located on properties within Moiese Valley in Montana. All sites were either private residences or areas with frequent exposure to humans and were selected to ensure that visitations to the feeder would occur. Sites were located at least 200 m apart to avoid pseudoreplication of the same birds (Brittingham and Temple 1992).

Coordinates for each sampling site are provided in the Appendix. tab

Feeding station setup

The study lasted for eight days at the end of July 2018. Each site had one house-shaped wooden feeder (Pennington Classic Cedar Dinette bird feeder, 21x11x8 cm) that hung from a 1.5 m feeder crook, such that the bottom of the feeder was suspended approximately 0.9 m from the ground. Feeders were filled with black oil sunflower seeds as an accessible and appealing food resource for a wide number of bird species due to their high fat content, small size, and thin, easy-to-crack shells. Mixed seeds were avoided to prevent resource partitioning and increase direct competition, as well as to avoid invasive species introduction.

Positioned 1.5 m directly across from the feeder was a trail camera (Bushnell, Overland Park, KS) mounted on a 1.2 m metal utility stake that was set to record all motion and sound at the bird feeder on video continuously, for the duration of the study. This procedure was modified from Hotchkiss et al. 2005.

Video analysis

The video footage was examined for the following information: bird species, number of individuals of a single species at any one time, and any interspecific or intraspecific interactions

observed such as displacement, attempted displacement, fighting, or other displays of aggression. Where possible, sex and age were determined to test for differences in competitive behavior between the genders and age group (adult or juvenile) of a single species.

Statistical analysis

All statistical analyses were run in RStudio (3.3.2), using either base functions or the package *networkTricks* (<https://github.com/eliotmiller/networkTricks>, accessed 26 June 2018). Each competitive interaction between two birds was scored binarily as either a win from a successful displacement or defense (1) or a loss from an unsuccessful displacement or defense (0). Species' scores were subjected to a chi-square test to confirm differences between competitive ability and then ranked in a dominance hierarchy using the modified Bradley-Terry scores from Miller et al. (2017). Finally, the hierarchy for these western Montana sites were then compared to the rankings generated by Miller et al. (2017).

RESULTS & DISCUSSION

Overall view of competition

The study found 415 instances of competition, 218 of which were interspecific and 197 were intraspecific. A total of nine bird species were observed at the feeders: American goldfinches (*Spinus tristis*), black-headed grosbeaks (*Pheucticus melanocephalus*), Cassin's finches (*Haemorhous cassinii*), cedar waxwings (*Bombycilla cedrorum*), Eastern kingbirds (*Tyrannus tyrannus*), house finches (*Haemorhous mexicanus*), house sparrows (*Passer domesticus*), house wrens (*Troglodytes aedon*), and pine siskins (*Spinus pinus*).

Of these nine species, only the following species actually fed and competed at the feeder: black-headed grosbeaks, Cassin's finches, house finches, house sparrows, house wrens, and pine siskins. Among these six species, black-headed grosbeaks, house finches, and house sparrows dominated more than 98% of the observed competitive interactions. Their interactions are summarized in Table 1.

Interspecific competition

Chi-square tests found statistically-significant differences across all three bird species' competitive ability, more so than would be anticipated by chance alone (Table 2).

For interactions between black-headed grosbeaks and house finches,

$$N = 47, X^2 = 29.13, df = 1, p\text{-value} < 0.00001.$$

For interactions between black-headed grosbeaks and house sparrows,

$$N = 49, X^2 = 2.47, df = 1, p\text{-value} = 0.1161.$$

For interactions between house finches against house sparrows,

$$N = 30, X^2 = 30, df = 1, p\text{-value} < 0.00001.$$

These results suggest that success at a bird feeder is not ever randomly distributed for house finches, but is the consequence of other factors. In the case of grosbeaks and sparrows, their interactions are statistically as predictable as a coin-toss, hence the p-value of 0.1161 which allows for limited interpretation.

The generated network suggested the following hierarchy from most dominant to least: house sparrow, black-headed grosbeak, house finch, pine siskin, and Cassin's finch (Figure 1).

Of these five species, the most notable relationships are that the house sparrow is dominant to both other species and that the black-headed grosbeak is dominant to the house finch. When a competitive network is generated solely for the interactions between black-headed grosbeaks, house finches, and house sparrows, it reaffirms the relationships mentioned earlier (Figure 2, panels A - B).

Given that house finches are the smallest of the three bird species observed, it would be expected that they should be subordinate to the larger black-headed grosbeak and the slightly-larger house sparrow. However, the finding that house sparrows dominate grosbeaks not only contradicts the expected findings based off of Miller's prediction but also field observations – black-headed grosbeaks are larger and heavier than house sparrows and have been witnessed to frequently displace them.

Intersexual differences in interspecific competition

Due to field observations of differential behavior exhibited by male and female grosbeaks when confronted over the feeder resource, the entire data set was assessed for differences between how male and female members of a species behave and compete with other species (Table 3). Depending on the sex grosbeaks may win either 50% (females) or 80% (males) of the times they encounter another species at a feeder.

Thus, chi-square tests were conducted, illustrating that all three species vary in competitive abilities by sex. Both male and female grosbeaks were dominant over house finches (M: $N = 14$, $X^2 = 14$, $df = 1$, p-value = 0.000183; F: $N = 33$, $X^2 = 16.03$, $df = 1$, p-value < 0.00001) but female grosbeaks were subordinate to house finches ($N = 33$, $X^2 = 6.82$, $df = 1$, p-value = 0.009024). Male grosbeaks and house sparrows had no detectable pattern of

competition ($N = 16$, $X^2 = 1$, $df = 1$, $p\text{-value} = 0.317$). Upon recognizing this discrepancy in competitive abilities between male and female grosbeaks, two new, separate competition networks were generated that showed that male grosbeaks dominate over both house finches and sparrows whereas female grosbeaks are subordinate to house sparrows but dominant over house finches (Figure 2, panels B and C). Additionally, the same chi-square tests found that male and female house finches were always subordinate to both black-headed grosbeaks (M: $N = 8$, $X^2 = 8$, $df = 1$, $p\text{-value} = 0.004678$; F: $N = 39$, $X^2 = 21.56$, $df = 1$, $p\text{-value} < 0.00001$) and house sparrows (M: $N = 22$, $X^2 = 4.545$, $df = 1$, $p\text{-value} = 0.033$; F: $N = 98$, $X^2 = 25.51$, $df = 1$, $p\text{-value} < 0.00001$). Neither male nor female house sparrows showed any competitive relationship with the black-headed grosbeaks (M: $N = 20$, $X^2 = 1.8$, $df = 1$, $p\text{-value} = 0.179$; F: $N = 29$, $X^2 = 0.862$, $df = 1$, $p\text{-value} = 0.3532$) but both sexes were dominant to the house finches (M: $N = 36$, $X^2 = 4$, $df = 1$, $p\text{-value} = 0.0455$; F: $N = 74$, $X^2 = 19.51$, $df = 1$, $p\text{-value} < 0.00001$).

Intraspecific competition

Given these differences between sexes when competing against other species, the next obvious question is: how do the sexes of a single species fare against each other? Additional chi-square tests were done to check the proportion of wins by one sex over the other.

Black-headed grosbeaks exhibited a statistically-significant difference between intraspecific competition between genders, with males being dominant to females ($N = 17$, $X^2 = 4.76$, $df = 1$, $p\text{-value} = 0.0291$). Neither house finches nor house sparrows exhibited significant differences between sex within a single species ($N = 42$, $X^2 = 0.2571$, $p\text{-value} = 0.6121$; $N = 26$, $X^2 = 0$, $p\text{-value} = 1$).

Interspecific and intersexual discrepancies in competitive ability

Of the grosbeaks, finches, and sparrows studied, all three species were sexually dimorphic in terms of plumage and coloration but not notably so in size (Ortega and Hill 2011). In-field observations suggested that grosbeak females were slightly smaller and shorter than their male conspecifics but this may be due to natural variation within a single flock or family group. No such observations were noted for the finches and sparrows, which seemed to be relatively the same size, regardless of sex. Thus, size alone cannot be predictive of why female house finches outcompete male finches or why male black-headed grosbeaks and male house sparrows outcompete their female counterparts.

It is important to note that of all 415 competitive interactions, females participated in over two-thirds of them, indicating a clear imbalance in how sexes of a single species competed and foraged for food at these bird feeders. From this observation, three potential theories, or some combination thereof, may explain the discrepancy in both visitation frequency and intraspecific competition success rates.

The first potential explanation may be due to the breeding and family structure of these avian species. The imbalance in the sex ratio may be due to a polygamous mating system where one male defends a territory to provide for multiple females. However, this theory is refutable for the given system because all three primary species form monogamous pairs, occasionally for life (Kroodsma 1974; Kaufmann 1996; Veiga 1992). Following breeding, the males of two of the three species – the grosbeaks and the house finches – provide parental care for the offspring, thus creating relatively stable family groups (Weston Jr. 1947; Evenden 1957). Nevertheless, it is possible that because the juveniles of all three species are indistinguishable from the females of

the species up until through their first full year after hatching, entire family groups, including young, were visiting the feeder, artificially inflating the counts of female over male specimens.

Another consideration is that, due to increased levels of testosterone in male birds leading to increased aggression and higher social dominance, male birds feed preferentially at better times and have fewer conflicts as other subordinate species will avoid them (Pravosudov et al. 1999). This is particularly true during breeding season when males' testosterone levels are notably higher than at any other point in the year (Wingfield et al. 1987). With such a social structure in place, females would have to feed, and therefore, compete more frequently to compensate for the limit on resource access imposed by overly-aggressive males.

The third and final consideration is that each sex may vary in its metabolic need. Because basal metabolic rate (BMR) is related to mass, smaller organisms will have higher BMRs than larger ones (Glazier 2008). Within avians, passerine birds like those observed in this study tend to have higher BMRs than non-passerine birds (Trevelyan et al. 1990; McNab 2001). Presumably, in species where females are smaller than males, the females may have higher BMRs that require them to forage more frequently in order to maintain a healthy body weight.

As previously discussed, there is no notable size difference between any of the three species in this system. However, a number of studies have documented that BMR varies between sex in different bird species, both passerine and non-passerine, both sexually dimorphic in size and not (Mitchell et al. 1927; Maloney and Dawson 1993; Hegemann et al. 2012; Elarabany 2015). The findings of these studies present challenges in interpreting the current study, however, depending on the species and its evolutionary history, the sex with the higher BMR and metabolic needs can vary (Trevelyan et al. 1990). As of this time, no such research into the

potentially variant BMRs of either black-headed grosbeaks, house finches, or house sparrows has been conducted so it remains to be speculated whether or not any of the noted species exhibit intersexual metabolic differences and whether this might explain the frequency of feeder visits by females.

Although intersexual differences in BMR cannot be confirmed, all avians irrespective of species or sex, will expend greater amounts of energy during breeding season (Bennett and Harvey 1987). Even with greater resource availability in summer, black oil sunflower seeds are a coveted, high-energy food source for black-headed grosbeaks, house finches, and house sparrows alike (Ortega and Hill 2010; Hotchkiss et al. 2005; Perkins et al. 2007). The quality of the sunflower seed resource may help explain the frequency of visits, particularly by breeding and nesting females in the summer.

These three hypotheses, or some combination thereof, may at least partially account for the small portion of unexpected variance between frequency and displacement rates across species observed at the feeding stations. With the exception of the socially-timid and easily-displaced female grosbeaks, the rest of the hierarchy was well-aligned by Miller's hypothesis of size dictating interspecific relationships, suggesting that while size is generally a fair predictor of dominance, other aspects of an organism's evolutionary history are also important to consider in predicting its competitive ability.

While neither efficiency nor duration of foraging were measured for this experiment but both of these measures could have offered additional insight into the species' overall fitness and thus, aid in predicting the species's competitive ability. Another potential avenue for research is to conduct the same study with the addition of identifying individuals visiting the feeding

stations such that visitation frequency, foraging efficiency, and competitive ability could have been directly tied to an individual specimen's fitness. This would have made a more compelling argument on how the differential ability to successfully forage at a novel food source and displace competitors is critical for the survival of individuals and their species on the threshold of less-impacted to more-impacted environments.

It is these differences in competitive abilities both across and within species that suggest ample opportunity for selection to act as resources become more limited due to loss of land and climate change. The findings presented here offer critical insight into how species that do not typically interact with humans in urbanized areas can quickly adapt to a novel food source in an increasingly human-impacted landscape. This is perhaps best seen in the presence of the normally-insectivorous black-headed grosbeak at the feeders and their willingness to take advantage of a novel food source. It may be expected that a rise in omnivory will occur as more and more species become opportunistic and accustomed to feeding in close proximity to humans.

As more woodlands, grasslands, and farmlands are converted into suburban and then urban areas, those avian species with an elastic diet and a willingness to not just tolerate, but cooperate with humans, will survive and thrive.

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TABLES AND FIGURES

All tables and figures appear in the order by which they were referenced in the text.

TABLE 1

Competitive interactions between common feeder species. The table shows the total summation of all the competitive interactions (both intraspecific and interspecific) between black-headed grosbeaks, house finches, and house sparrows. The leftmost column indicates the winning species and the topmost row indicates the losing species. A chi-square test found that the outcomes of these interactions is not due to random chance but rather, differing competitive ability across the three species ($X^2 = 50.17$, $df = 4$, $p\text{-value} < 0.005$).

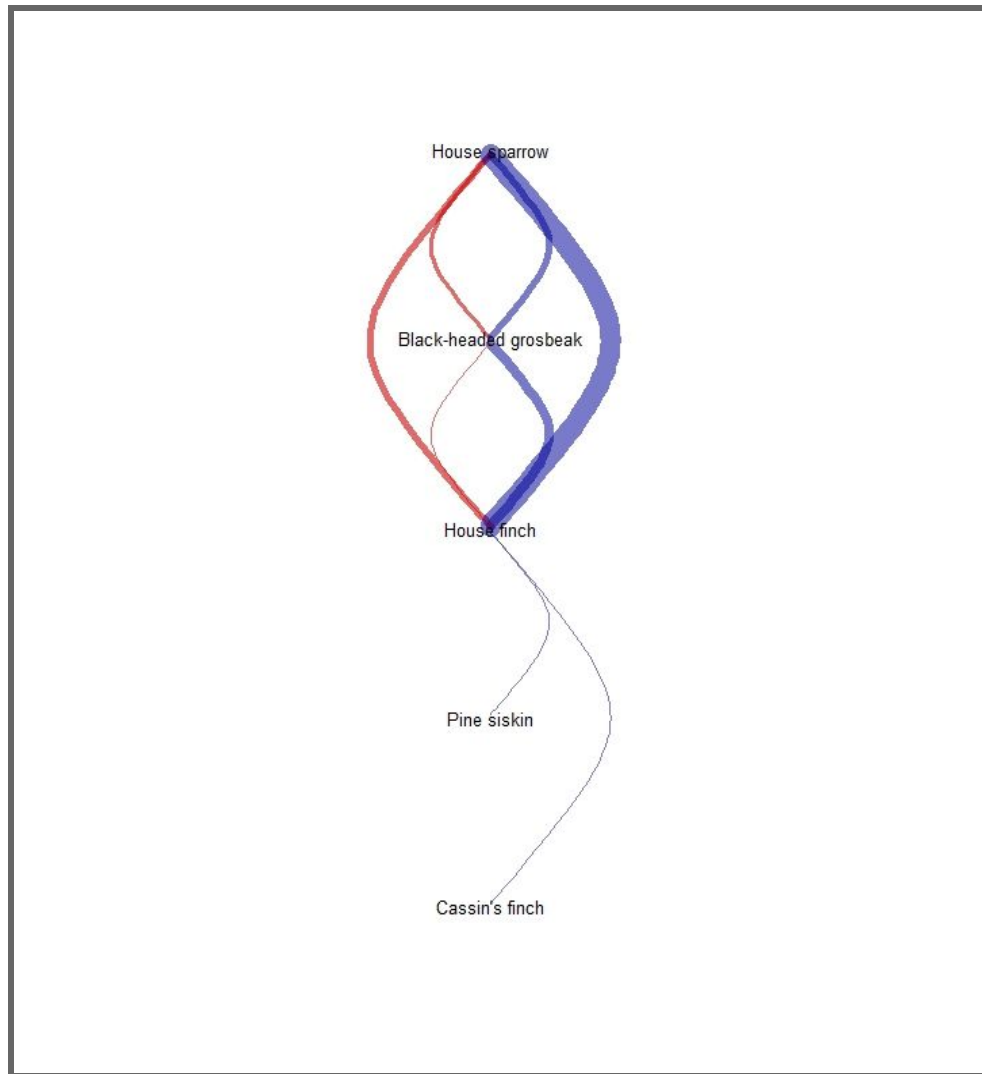
	Black-headed grosbeak	House finch	House sparrow	TOTAL
Black-headed grosbeak	32	42	18	92
House finch	5	98	30	133
House sparrow	30	90	65	185
TOTAL	67	230	113	410

TABLE 2

Chi-square analysis on interspecific competition. The following table shows the results of the chi-square analysis comparing how different species competed against each other at the feeding stations. The p-value for two of the three tests was found to be statistically significant ($\alpha = 0.05$, significance denoted by an asterisk *), suggesting that displacement at the bird feeders for house finches in all cases was not due to random chance but rather, was a result of other factors such as size and aggression. For black-headed grosbeaks and house sparrows, however, no competitive difference was detected (p-value = 0.1161).

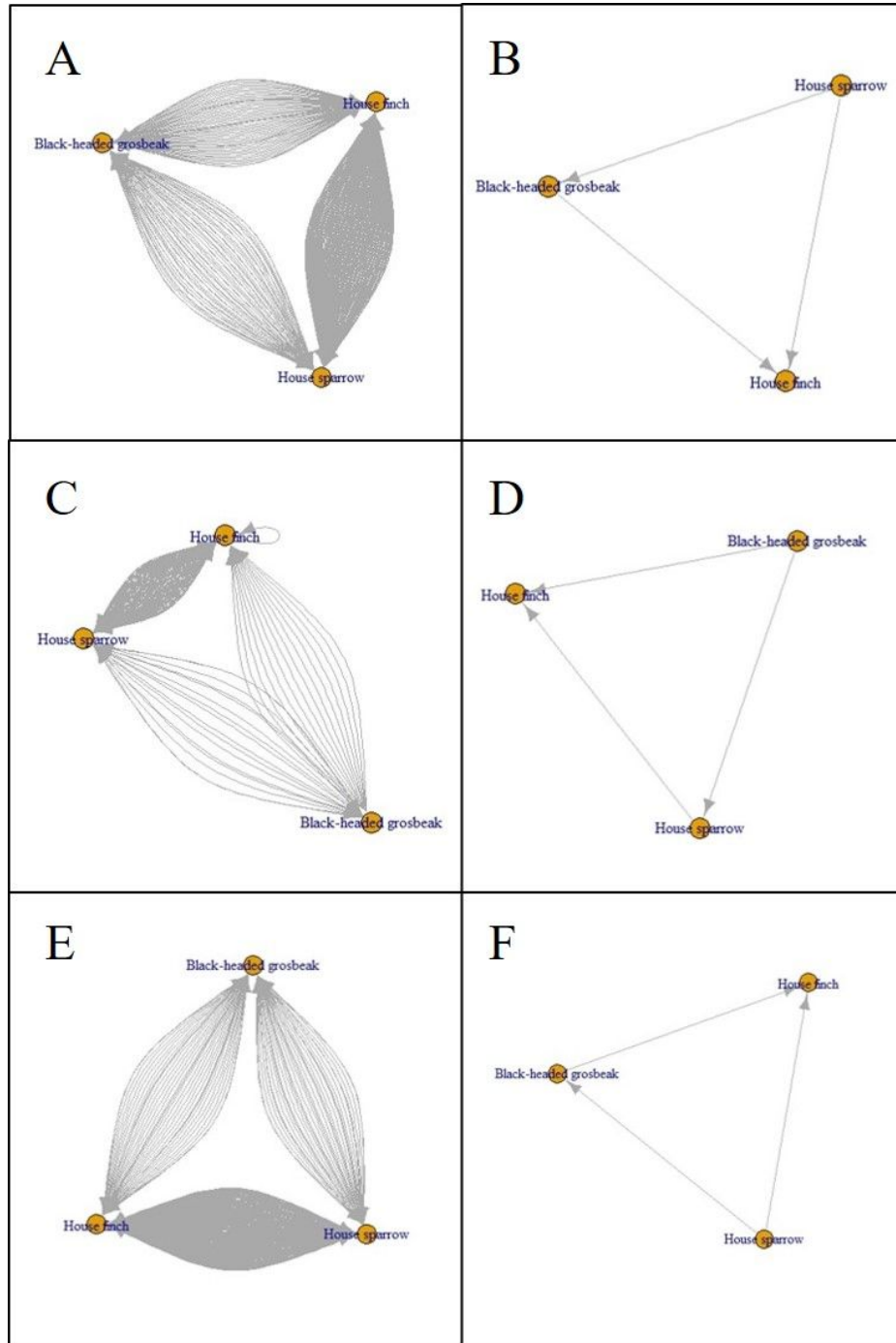
	Black-headed grosbeak	House finch ²	House sparrow
Black-headed grosbeak		< 0.00001 *	0.1161
House finch	< 0.00001 *		< 0.00001 *
House sparrow	0.1161	< 0.00001 *	

FIGURE 1



Dominance hierarchy for five feeder species. The figure shows the hierarchy from most to least dominant: house sparrow, black-headed grosbeak, house finch, pine siskin, and Cassin's finch. Line thickness visually demonstrates the intensity of dominance over another species (i.e. the more weighted line, the greater the number of interactions between the two species). Blue lines indicate interactions predicted by the hierarchy ranks (higher-ranked bird defeats a lower-ranked bird) whereas red lines indicate interactions not predicted (lower-ranked bird defeats a higher-ranked bird).

FIGURE 2



Interaction networks between black-headed grosbeaks, house finches, and house sparrows, both complete and separated by sex. The following diagram shows both the complex (left column) and simple networks (right columns) for each of the three studied species. Panels A and B show the network relationships where all grosbeak interactions are included, Panels C and D show only male grosbeaks, and Panels E and F show only female grosbeaks. All arrows point away from the dominant species and toward the subordinate species. The more arrows on a complex model, the more recorded interactions showing a particular relationship.

TABLE 3

Chi-square analysis on intersexual differences in interspecific competition. The following table shows the results of the chi-square analysis comparing how different sexes within the same species compete against other species (e.g. how male grosbeaks fare against house sparrows versus how female grosbeaks fare against house sparrows) at the feeding stations. The p-value for nine of the twelve tests was found to be statistically significant ($\alpha = 0.05$, significance denoted by an asterisk *). The only exceptions to significance were due to the lack of a nonrandom relationship between male black-headed grosbeaks and all house sparrows and female house sparrows and all black-headed grosbeaks. Overall, the data suggests that competitive abilities vary by sex across all three species with at least one other species.

MALES	Black-headed grosbeak	House finch	House sparrow
Black-headed grosbeak		0.000183 *	0.317
House finch	0.00468 *		0.033 *
House sparrow	0.179	0.0455 *	
FEMALES			
Black-headed grosbeak		< 0.00001 *	0.009024 *
House finch	< 0.00001 *		< 0.00001 *
House sparrow	0.3532	< 0.00001 *	

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APPENDIX

Study site descriptions. The following table gives the coordinates and site description for the four study sites utilized in this study. All four locations were personal residences with some amount of tree cover and confirmed bird presence. Feeding stations consisting of a bird feeder and trail camera were left up continuously for the duration of the study (between 4 to 8 days) at each respective location.

Site ID	Latitude	Longitude	Description
A	47.3689	-114.2518	Personal residence located along the north-western boundary of the National Bison Range in Charlo, MT; Backyard had a cluster of willow trees, maintained lawn grass, no fence
B	47.3672	-114.2515	Personal residence located along the north-western boundary of the National Bison Range in Charlo, MT; Backyard had oak and spruce trees, maintained lawn grass, chain-link fence
C	47.4297	-114.3110	Personal residence located in farmland adjacent to National Bison Range in Moiese Valley; Backyard had elm and cottonwood trees with some mixed low-lying plants including prickly lettuce, dandelion, etc., and lawn grass
D	47.3169	-114.3245	Personal residence located adjacent to farmland on outskirts of the town of Dixon, MT; Backyard had extensive variety of trees, shrubs, and flowers, as well as multiple gardens and lawn grass