Effects of Bird Feeder Density on the Behavior and Ecology of a Feeder-Dependent Songbird: Patterns and Implications for Disease Transmission

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ACADEMIC ABSTRACT

Anthropogenic resource provisioning of wildlife has increasingly been hypothesized to alter pathogen spread. Although bird feeding is the most widespread form of intentional wildlife provisioning, we know relatively little about how the degree of anthropogenic feeding at a site impacts wild birds in ways relevant to disease transmission. We manipulated the density of bird feeders (low versus high) available at otherwise similar sites and tracked the local abundance, body condition (scaled-mass index), feeding behavior, and movement across the landscape in wild house finches (*Haemorhous mexicanus*), a feeder-dependent species subject to outbreaks of a contagious pathogen commonly spread at feeders. The local abundance of house finches was significantly higher at sites with high feeder density but, surprisingly, finches at high-density feeder sites had poorer body condition than those at low-density sites. Behaviorally, birds at high-density feeder sites had longer average feeding bouts and spent more time per day on feeders than birds at low-density feeder sites. Further, birds first recorded at low-density feeder sites were more likely to move to a neighboring high-density feeder site than vice versa. Overall, because local abundance and time spent on feeders have been linked with the risk of disease outbreaks in this species, effects of bird feeder density on both traits may, in turn, influence disease dynamics in house finches. Our results suggest that heterogeneity in the density of bird feeders can have diverse effects on wild birds, with potential consequences for disease transmission.

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PUBLIC ABSTRACT

Feeding wildlife has increasingly been thought to change the spread of disease. Although bird feeding is the most widespread form of intentional wildlife feeding, we know relatively little about how much human feeding impacts wild birds in ways that affect disease transmission. We changed the density of bird feeders (low versus high) available at otherwise similar areas and tracked the local abundance, body condition, feeding behavior, and movement across the landscape in wild house finches (*Haemorhous mexicanus*), a feeder-dependent species subject to outbreaks of a infectious disease commonly spread at feeders. The local abundance of house finches was significantly higher at sites with high feeder density but, surprisingly, finches at high-density feeder sites had poorer body condition than those at low-density sites. Behaviorally, birds at high-density feeder sites had longer average bouts on feeders and spent more time per day on feeders than birds at low-density feeder sites. Further, birds first recorded at low-density feeder sites were more likely to move to a neighboring high-density feeder site than vice versa. Overall, because local abundance and time spent on feeders have been linked with the risk of disease outbreaks in this species, effects of bird feeder density on both traits may, in turn, increase disease spread in house finches. Our results suggest that variation in the density of bird feeders can have diverse effects on wild birds, with potential consequences for disease transmission.

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1. INTRODUCTION

Anthropogenic food provisioning is an increasingly important phenomenon to consider in understanding the behavior and ecology of wildlife in a rapidly urbanizing world. Whether anthropogenic provisioning is intentional or unintentional, it can have far-reaching and diverse consequences for wildlife. For example, anthropogenic resource subsidies can alter individual nutrition (Jessop et al. 2012) and space use (Newsome et al. 2013), cause migratory populations to become sedentary (Altizer et al. 2011), and in some cases, decouple predator-prey relationships by providing alternative food sources for predators (Rodewald et al. 2011). Thus, anthropogenic food provisioning can have critical implications for wildlife across biological scales of organization.

A growing body of work is revealing that anthropogenic food provisioning can alter the risk of infectious diseases for wildlife. For example, elk (*Cervus elaphus*) feeding on managed food sources have higher exposure to *Brucella abortis* (Cross et al. 2007a) and white-tailed deer (*Odocoileus virginianus*) with access to more feeding sites have higher prevalence of *Mycobacterium bovis* (Miller et al. 2003). Similarly, banded mongooses with access to unintentional anthropogenic food resources (i.e., garbage) show higher rates of aggression and injury, which facilitates the invasion of a lethal pathogen, *M. mungi*, into open wounds (Flint et al. 2016). Conversely, studies of other systems have found that provisioning can also dampen the degree of disease spread. Long-tailed macaques (*Macaca fascicularus*) that are fed by tourists have increased nutrition and lower pathogen exposure (Lane et al. 2011). Additionally, red foxes (*Vulpes vulpes*) feeding on anthropogenic food sources are less likely to consume prey infected

with parasites (Hegglin et al. 2007). Thus, anthropogenic food provisioning has been associated with both augmented and dampened risk of disease in wildlife.

There are several mechanisms that can underlie changes in the transmission of pathogens in the presence of supplemental food. First, anthropogenic resource subsidies can lead to aggregation of potential hosts and/or smaller home ranges (Boutin 1990), thus leading to greater potential for direct or indirect contact with conspecifics, and in some cases, heterospecifics. For directly-transmitted pathogens, aggregation of hosts around supplemental food is predicted to augment exposure rates and transmission. For example, an experimental study of wild raccoons (*Procyon lotor*) showed that supplemental food resulted in greater contacts between raccoons and an increased prevalence of several parasites that are transmitted both directly and indirectly (Wright and Gompper 2005). Thus, behavioral effects associated with supplemental feeding are generally thought to increase exposure and disease risk for both directly and indirectly-transmitted pathogens. On the other hand, behavioral changes associated with supplemental feeding may dampen disease spread if they cause individuals to reduce movements across the landscape, decreasing the rate of contact among social groups (Cross et al. 2007b).

The second mechanism by which food supplementation can mediate disease dynamics is by altering the physiology and immune function of individuals by changing a host's nutritional state (Nelson 2002). Food supplementation can alter the nutritional state of a host either positively or negatively. If a high quality food source is available, an individual's body condition, and thus, their immune defenses can be improved (Becker et al. 2015, Strandin et al. 2018). For example, an observational study of lace monitors (*Varanus varius*) showed that supplemented individuals were in better body condition and had lower intensities of blood parasites (Jessop et al. 2012). Alternatively, a poor quality anthropogenic food source can have

the opposite effect if the diet reduces immune function (Van Heugten et al. 1996, Maggini et al. 2007). Individuals feeding on anthropogenic food can also be exposed to harmful compounds, such as lead, which can also negatively impact immune function (Strandin et al. 2018). Additionally, food supplementation can increase the amount of time a pathogen could be spread by allowing infected hosts to survive for longer than they otherwise would have (Jansson et al. 1981, Råberg et al. 2009, Vale et al. 2013).

Finally, food supplementation can alter disease dynamics through demographic changes such as increased birth rates or immigration of susceptible hosts (Becker et al. 2015). Studies have shown that access to supplemental food can lead to earlier laying dates, higher brood sizes, or increased health of chicks in different bird species (Robb et al. 2008). If a host is able to reproduce at a higher rate in response to anthropogenic food sources, more immunologically naïve members will be introduced into the population (Becker et al. 2015), which will increase the reproductive rate of a pathogen, R_0 (Lloyd-Smith et al. 2005). Food supplementation can also increase the density of hosts in a given area, leading to higher rates of infection by pathogens like bovine tuberculosis in white-tailed deer and brucellosis in elk (Miller et al. 2003, Cross et al. 2007a). This can lead to sudden and steep declines in a population, as was reported in greenfinches in Great Britain following an outbreak of *Trichomonas gallinae* (Lawson et al. 2018).

Overall, all three of the above mechanisms have proven to be important either in isolation or in conjunction in various host-pathogen systems (Becker et al. 2015). A meta-analysis of supplemental feeding studies to date revealed that there is significant evidence for both behavioral and immunological mechanisms across systems (Becker et al. 2015). Further, theoretical work shows that the presence of immunological mechanisms (i.e., decreased

susceptibility in the presence of supplemental food) can counter the effects of increased contact rates in some cases, thus making it critical to understand how supplemental feeding alters both behavior and physiology to predict outcomes for the spread of emergent diseases.

Changes in behavior are one of the most commonly predicted outcomes of supplemental feeding, yet there have been surprisingly few studies that have examined behavioral changes in response to supplemental feeding. Anthropogenic feeding of wild birds is arguably the most common type of intentional supplemental feeding of wildlife (Jones 2011), with a suite of documented effects on bird survival, reproduction, and species ranges (Robb et al. 2008). However, no studies to date have examined how the degree of anthropogenic feeding of wild birds influences their feeding behavior in ways relevant for disease transmission. A useful method for tracking the behavior of wild birds at feeders is radio-frequency identification (RFID). Radio transmitters attached to perches on feeders can read passive integrated transponder (PIT) tags that are attached to color bands on the legs of wild birds. The tags store a unique identification number which is added to timestamps that are continuously recorded by the radio transmitter to give a real time accounting of the number of visits to the feeder by an individual bird, as well as how long each visit was (Bridge and Bonter 2011). To date, this technology has been used in several experiments related to bird feeders, including studies looking at the risk of disease acquisition at feeders (Adelman et al. 2015), and examining the effects of bird feeders on species interactions (Galbraith et al. 2017).

A common example of pathogens spreading at backyard bird feeders is the highly infectious bacterium, *Mycoplasma gallisepticum* (Mg), in house finches (*Haemorhous mexicanus*). Since the mid-1990s, house finches have been subject to seasonal outbreaks of Mg, resulting in mycoplasmal conjunctivitis (Altizer et al. 2004b). Originally a pathogen of poultry,

Mg quickly spread among Eastern United States populations of house finches after its initial appearance (Fischer et al. 1997). House finches are highly dependent on bird feeders during the autumn and winter, when the largest outbreaks of Mg occur (Altizer et al. 2004b). In house finches, Mg causes inflammation of the conjunctival tissue, resulting in swelling, redness, and watery discharge. Mycoplasmal conjunctivitis is associated with lower over-winter survival (Faustino et al. 2004) and led to sharp population declines after its introduction in house finches (Hochachka and Dhondt 2000).

Mg is in the class Mollicutes and lacks a cell wall, making it less viable outside of hosts than other bacteria (Dhondt et al. 2005). Despite its low viability outside of a host, Mg can survive on environmental surfaces for 12-24 hours, making bird feeders an important vector, or fomite, for the spread of Mg among house finches (Dhondt et al. 2005). In fact, recent work has found that finches who spend the most time on feeders are also the most likely to acquire Mg (Adelman et al. 2015). Furthermore, house finches that display the highest levels of pathology are the most likely to deposit Mg onto bird feeders (Adelman et al. 2013a). Given that past work has shown that diseased house finches spend the most time on feeders (Hotchkiss et al. 2005), it is important to understand how house finch behavior is altered in ways that may make them remain for longer or shorter amounts of time on bird feeders. Further, bird feeders also have the potential to alter local abundance (and thus contact rates) of house finches, individual physiology, and the movement of house finches across the landscape. Thus, this system is ideal for understanding how supplemental food provided at bird feeders impacts the local abundance, behavior, and physiology of house finches in ways that affect an emergent disease.

2. Effects of Bird Feeder Density on the Behavior and Ecology of a Feeder-Dependent Songbird: Patterns and Implications for Disease Transmission

Introduction

The diverse impacts of anthropogenic food subsidies on wildlife populations and ecosystems are just beginning to be fully appreciated (Oro et al. 2013). Although many anthropogenic food subsidies are an unintentional result of agricultural practices or garbage, intentional human feeding of wildlife is a globally popular activity (Cox and Gaston 2018). Whether intentional or not, anthropogenic food supplementation can result in a suite of effects on wildlife populations, including increases in population sizes (e.g., Fuller et al. 2012, Jessop et al. 2012), behavioral changes (e.g., Flint et al. 2016), and changes in body condition (e.g., Jessop et al. 2012). Because food supplementation has the potential to alter traits relevant to both host exposure to pathogens (e.g., host population size, contact rates, space use) and the susceptibility of hosts once exposed (e.g., stress, host condition), there is a growing interest in understanding how anthropogenic food supplementation impacts wildlife disease dynamics (Becker et al. 2015, Altizer et al. 2018).

The use of bird feeders is arguably the most common form of intentional human supplementation of wildlife worldwide (Cox and Gaston 2018). In the United States alone, an estimated 52 million households have at least one backyard bird feeder (U.S. Department of the Interior et al. 2011). However, we still know relatively little about the effects of this large-scale anthropogenic provisioning on wild bird populations (Reynolds et al. 2017). There are multiple mechanisms by which bird feeding could influence wild bird populations in ways relevant for

disease transmission (Becker et al. 2015). First, feeders may facilitate higher local host abundance via increased over-winter survival (e.g., Jansson et al. 1981) and/or behavioral aggregation, both of which would augment host-to-host transmission. Second, feeders may reduce the foraging ranges of hosts (e.g., Boutin 1990), which could increase local transmission, but decrease transmission across the landscape. Third, feeders might augment host condition, and thus, increase the ability of hosts to resist parasites or pathogens once exposed.

To date, two experimental studies have manipulated bird feeder presence and examined impacts on disease dynamics in wild bird populations (Wilcoxen et al. 2015, Galbraith et al. 2017). Wilcoxen et al. (2015) found that birds captured at forested sites with an experimental bird feeder were largely in better physiological condition, but these individuals had a higher prevalence of a variety of pathogens. Similarly, Galbraith et al. (2017) observed that a variety of avian species captured at suburban sites with bird feeders over the course of 18 months had higher prevalence of several endo- and ectoparasites than birds caught at non-feeding suburban sites, but again, birds at feeder sites tended to have better body condition. Although these studies show that the presence of bird feeders can detectably alter bird condition and parasite prevalence, neither examined the potential behavioral mechanisms involved. Furthermore, no studies to date have examined how variation in feeder density at a given site influences bird condition and behavior. There is likely to be considerable heterogeneity in both the presence and density of backyard bird feeders across the landscape. For example, participants in the Cornell Lab of Ornithology's Project FeederWatch program report substantial variation in the number of backyard feeders they provision in their yards (In 2017: range of 1-61 feeders per yard; D. Bonter personal communication). This heterogeneity in feeder density is likely to have important

consequences for backyard birds that rely heavily on anthropogenic food, such as North American populations of house finches (*Haemorhous mexicanus*).

House finches are a common backyard songbird that are largely dependent on bird feeders throughout their introduced range in eastern North America (Badyaev et al. 2012). In fact, house finch densities in the introduced range are positively associated with human population density, a likely proxy for bird feeding intensity (Fischer and Miller 2015). Bird feeders also are known to play an important role in the spread of *Mycoplasma gallisepticum* (Mg), a common infectious bacterial pathogen of house finches. This pathogen, which causes debilitating conjunctivitis, emerged in eastern populations of house finches in the 1990s (Ley et al. 1996), and continues to cause annual epidemics in this species. Feeders serve as points of aggregation within and among flocks, and act as environmental fomites for indirect transmission of Mg (Dhondt et al. 2005, Adelman et al. 2015). Feeders may also act as a "crutch" by allowing infected birds to survive (Fischer and Miller 2015). Outbreaks of Mg primarily occur outside of the breeding season, when house finches are gregarious and form loose foraging flocks of 5-8 individuals that largely forage at backyard bird feeders in the introduced range (Altizer et al. 2004b). House finches are thus an ideal system to address how bird feeder density at a site influences local abundance, behavior, and condition in ways relevant to disease transmission.

There is growing evidence that bird feeders facilitate the spread of Mg among house finches. A recent study found that the average time per day that individuals spent on bird feeders was the strongest predictor of the risk of mycoplasmal conjunctivitis in wild house finches (Adelman et al. 2015). Further, in experimental epidemics in captive house finch flocks, rates of transmission of Mg were higher in flocks with a high density of bird feeders than in flocks of equal size with a lower feeder density (Moyers et al. 2018). Interestingly, flocks with a high

feeder density also had lower levels of direct aggressive interactions, suggesting that direct, aggressive contacts did not underlie the elevated rate of transmission at higher feeder densities (Moyers et al. 2018). Together, these studies suggest that variation in feeding behavior has implications for disease dynamics in house finches, but the exact behavioral mechanisms driving these patterns remain unclear.

In the present study, we examined how variation in bird feeder density alters house finch abundance, behavior, body condition, and the concentration of Mg-specific antibodies. We experimentally manipulated feeder density at eight otherwise similar suburban sites within a four km area and tracked feeding behavior with radio-frequency identification (RFID) on all accessible feeder ports. We predicted that sites with a higher density of bird feeders would have a higher local abundance of house finches, which we measured via capture rate. We predicted that birds caught at sites with a higher density of feeders would also have better body condition due to increased food access. Behaviorally, we predicted that birds at sites with a higher feeder density would spend more time per day on bird feeders due to more available perches, and that their bouts on feeders would be longer on average. We also predicted that a higher density of feeders would favor feeding site preference, and thus individuals would be more likely to move to a neighboring block of sites when those sites contained a higher rather than lower feeder density. Finally, we predicted that house finches caught at high-density feeder sites would be more likely to harbor Mg-specific antibodies, indicating higher exposure to Mg at high-density feeder sites.

Methods

Experimental Design

To determine how the number of bird feeders at a site influences house finch ecology and behavior, we manipulated the density of bird feeders at otherwise similar sites on or near the Virginia Tech campus in Blacksburg, VA during the fall and winter (Oct-Jan) of two consecutive years. All sites (n=8 in Year 1, n=6 in Year 2) initially had one bird feeder to equalize early attraction to sites, and then after four weeks, half of the sites were manipulated to have a higher feeder density (3 feeders / site) while half remained at a lower feeder density (1 feeder / site) (Fig 2).

In both years, sites that were closest to each other (0.4-0.7 km apart) were paired for experimental design purposes (Fig 1). Each pair of sites, which we term a block, was located 1.1-1.9 km from the next closest block, with the maximum distance between blocks being 4.2 km. The blocks spanned a northwest-southeast axis that we divided into two geographic areas (NW / SE) in Year 1 only (Fig 1*a*; see below). Blocks were A, B, C, and D going from northwest to southeast (Fig. 1). There was considerable individual movement among sites and blocks (Figs 3, 4), which is consistent with prior work showing that house finches can move up to 3 km per day while foraging (Dhondt et al. 2006). Because block D (sites D1 and D2 in Fig 1*a*) had very low visitation by house finches in Year 1 (see Results), this block was not used in Year 2 (Fig 1*b*) and was removed from all statistical analyses.

In year 1, both sites within a block received the same experimental treatment (high-feeder density or low-feeder density; Fig 2). Treatments were randomly assigned to a block within each

geographic area (NW or SE) to ensure that our treatment effects were not confounded by differences in geography. Hence, we had one block of high-density feeder sites and one block of low-density feeder sites in both the NW and SE areas (Fig. 1). Because only six sites were used in Year 2, treatments were assigned within blocks to account for geographic differences. One site within each block was randomly assigned as a low-density feeder site and one as a high-density feeder site. Thus, between years, half of the sites switched to a different feeder treatment, while half remained the same. This allowed us to better control for potential site-specific variation in the subset of statistical analyses that spanned both years.

We examined effects of feeder density on the local abundance, condition, and behavior of house finches via two primary methods: first, we trapped at all sites twice weekly (see Timeline), ensuring that weekly trapping effort was equal across high and low-density feeder sites. Second, we continuously tracked feeding behaviors of all banded birds using radio-frequency identification (RFID) antennae on all feeders (see below). The timing of the experiment was selected so that we would observe effects of feeder density during fall and winter when Mg epidemics are most likely in free-living house finches (Altizer et al. 2004b). Even though observed cases of disease in this study were limited (see *Results*), we can use these results to understand the possible implications that changes in house finch behavior and physiology in response to feeder density may have on Mg transmission.

Experimental Timeline

The experiment was conducted over two fall and winter seasons (Oct-Jan 2016-17 and 2017-18) in Blacksburg, VA. Tube-style feeders were put up at all sites and kept filled with black-oil sunflower seed one month prior to the start of trapping to establish regular visitation.

Every feeder had two available feeder ports, each equipped with its own RFID antennae. After one month of baseline trapping (Fig 2) and RFID data collection, feeder density was increased at half of the sites assigned to high-density feeder treatments (Fig 2). High-density feeder sites were given three feeders, each spaced 3 m apart in a straight line parallel to the nearest tree line. Thus, high-density feeder sites had a total of 6 available feeder ports equipped with RFID antennae, while low-density feeder sites had 2 available feeder ports equipped with RFID antennae. All feeders were kept full throughout the study, such that the food rarely fell below the level of the available feeding ports.

In both years, trapping was done at each site twice weekly for 3-4 hours beginning at sunrise. On any given day, trapping was done at equal numbers of high and low-feeder density sites, to ensure that capture effort was equivalent among treatments. Most trapping was done using baited cage traps, but mist nets were also used. When using baited cage traps, only one trap was set up per site regardless of feeder density treatment. While trapping at high-density feeder sites, the two extra feeders were covered up until trapping concluded. Thus, birds at all sites had access to only one feeder per site on trapping days to standardize for potential variation in detectability.

When caught, all unbanded house finches were given a numbered aluminum USFWS band and a small (2 x 8 mm) passive integrated transponder (PIT) tag (0.1 g; ~0.5% of body mass) attached to colored leg bands. Similar-sized PIT tags did not affect the condition or survival of free-living great tits (*Parus major*) which are comparable in size to house finches (Nicolaus et al. 2008). Upon all initial and subsequent captures, house finches had their mass and tarsus length measured. Using 26-gauge needles, blood samples (approximately 100 µl) were taken from the brachial vein and collected in heparin-coated capillary tubes. Blood was drawn

from all individuals who had not been captured previously or had not had their blood sampled within the prior 14 days if the bird was a recapture. Capillary tubes were stored on ice until the plasma could be separated via centrifugation, typically within 2-4 hours after sampling. Plasma was then separated out and stored in a -20C freezer until we ran enzyme-linked immunosorbent assays (ELISA) to test for the presence and concentration of Mg-specific antibodies (as per Hawley et al. 2011). Finally, all house finches had their eye pathology scored on a scale from 0 (no pathology) to 3 (most severe pathology) in each eye to determine conjunctivitis severity, as described in Sydenstricker et al (2006).

Statistical Analyses

All analyses were done using R (R Core Team, 2013) and the lme4 package. We had very low house finch activity at sites D1 and D2 in Year 1, with only one bird captured at either site post-manipulation. Although this low activity could have been a true effect of treatment (both were low-density feeder sites), these were new study sites that had not used in past studies (Adelman et al. 2015). Thus, we could not distinguish whether these sites had low activity due to feeder density treatment or some other characteristic that made them unattractive to house finches. To be conservative, we eliminated sites D1 and D2 from our Year 1 analyses. Our final data set for analysis thus included six sites per year, with an unbalanced design in Year 1 after the elimination of sites D1 and D2 (two low-density feeder sites, and four high-density feeder sites in Year 1; three low-density feeder sites, three high-density feeder sites in Year 2).

We calculated body condition for all birds using scaled body mass index. To account for variation in structural size, we regressed body mass at capture onto tarsus length and took the residuals of the relationship as our metric of scaled body mass. Scaled body mass for all birds

captured post-manipulation was then modeled using a linear mixed effects model. Fixed effects were the feeder density treatment an individual was caught at, year of capture, the pairwise interaction between year and treatment, and time of day of capture (which is known to influence body mass). Sex was also included as a fixed effect, both alone and in pairwise interaction with treatment. Capture site and individual ID were included as random effects.

We quantified capture rate (a proxy for local abundance) as the number of house finches caught at each site on days that we actively trapped at those sites and caught at least one bird at any site. To determine the effect of feeder density on local abundance, we ran a linear mixed effects model on capture rate with feeder density treatment, year of capture, and the pairwise interaction between year and treatment as fixed effects and capture site as a random effect.

Feeder bouts were extracted from the RFID data and were used to quantify foraging behaviors and movement between sites. For RFID analyses, we only included individuals who were detected via RFID for > 1 unique day and for a minimum total of 10 unique feeder bouts. A bout was defined as any time a house finch was recorded on the same feeding port continuously for a minimum of 3 seconds. To account for missed RFID reads, multiple bouts by the same individual at the same port were only defined as such if there was a 4-second or longer gap between detections of that individual. Because of the potential effects of Mg on house finch foraging behavior (Hotchkiss et al. 2005, Hawley et al. 2007), we eliminated from this analysis a single individual who met our RFID standards but was captured while showing clinical signs of mycoplasmal conjunctivitis. Because we had extremely low RFID reads in Year 2, and no reads at our low-density feeder sites in that year, all RFID analyses were limited to Year 1 of the study.

The main foraging behaviors of interest that we extracted from our RFID data were the average time spent on feeders per day and average bout length. All analyses of feeding behaviors were done using generalized linear mixed effects models with a negative binomial distribution. Fixed effects were feeder density treatment, sex, and the pairwise interaction between treatment and sex, to account for potential sex differences in behavior. Individual ID was included as a random effect in all models to account for the fact that some individuals made feeding visits to both high and low-density feeder sites, and thus those individuals were represented twice in our dataset. We also included site as another random effect to control for site-level differences.

We also used the RFID data to examine whether house finches were more likely to move between blocks if that movement resulted in an increased density of feeders available. We accounted for our unbalanced design in Year 1 and the spatial arrangement of sites by considering that birds initially observed in block B had the option of two among-block movements: either to the north or to the south (Fig 1*a*), whereas birds initially observed in blocks A or C could only move in one direction. Thus, birds in block B were replicated in our data set, with each potential movement considered as independent (though individual ID was included as a random effect). We then analyzed the probability of an individual moving to a neighboring block using a GLMM with first feeder density treatment visited as the fixed effect and individual as a random effect. Because our response variable was 0 or 1, our model used a binomial distribution.

For analyses of disease risk, we analyzed Mg-specific antibodies using both the continuously distributed absorbance values, and seropositivity, where our response variable was 0 or 1. We controlled for inter-assay variation by calculating all output values as the ratio of the sample absorbance to that of the positive control using the following equation: (sample mean –

negative control) / (positive control – negative control). Seropositivity (0/1) was determined using a cut-off established by Hawley et al. (2011). We then ran linear mixed effects models with a binomial distribution for seropositivity and a normal distribution for concentration of circulating Mg-specific antibodies, with feeder density treatment as the fixed effect and individual as a random effect.

Results

Sample size

Over the course of two years, we caught and PIT-tagged 327 unique house finches (Year 1: n = 233, Year 2: n = 94). Among those captures, 41 birds were caught more than once, and 17 birds had visible signs of mycoplasmal conjunctivitis at capture. However, the vast majority (15/17) of birds with observed mycoplasmal conjunctivitis were captured during the pre-manipulation period. For the RFID analyses (foraging behavior and movement), 79 birds in Year 1 met our standard for inclusion, which was a minimum of 10 unique recorded feeding bouts over at least two days of the study. Among those birds, we had > 11,000 recorded feeding bouts.

Capture rates

Feeder density had a significant effect on daily capture rates (n = 69 days; treatment HD estimate: 1.30 ± SE: 0.86, treatment LD estimate: 0.79 ± SE: 1.50, $F_{1,69} = 5.59$, p = 0.018, Fig. 5). On average, high-density feeder sites (HD) had approximately twice as many captures per day relative to low-density feeder sites (LD). There was no effect of year on daily capture rates, either alone ($F_{1,69} = 0.03$, p = 0.87) or in interaction with feeder density treatment (year * feeder density treatment: $F_{1,69} = 1.87$, p = 0.17).

Body condition

Feeder density had a significant effect on individual body condition (n = 128; treatment HD estimate: -2.29 ± SE: 1.04, treatment LD estimate: 1.47 ± SE: 0.96, $F_{1,128} = 4.96$, p = 0.028, Fig. 6). On average, the scaled mass index of birds caught at high-density feeder sites was three times lower than that of birds caught at low-density feeder sites. Year ($F_{1,128} = 1.91$, p = 0.16), and sex ($F_{1,128} = 1.18$, p = 0.54) did not predict body condition, either alone or in interaction with feeder density treatment or year (both p > 0.05). Time of day at capture approached significance in predicting body condition ($F_{1,128} = 3.95$, p = 0.07).

Foraging behaviors

Feeder density was a significant predictor of average feeder bout length, with feeder bouts at high-density feeder sites being on average three times longer than at low-density feeder sites (n= 79; treatment HD estimate: 2.34 ± SE: 0.094, treatment LD estimate: -0.74 ± SE: 0.17, $F_{1,79} = 38.02$, p < 0.001, Fig. 7). Sex was also significant in determining feeder bout length, with males having shorter feeder bouts (sex M estimate: -0.21 ± SE: 0.14, $F_{1,79} = 3.90$, p = 0.048, Fig. 7). However, there was no significant interaction between sex and feeder density treatment on feeder bout length ($F_{1,79} = 2.21$, p =0.13).

We also saw strong effects of feeder density on the average time per day spent on feeders, with birds at high-density feeder sites spending almost five times as much time on feeders per day than birds at low-density feeder sites (n = 79; treatment HD estimate: 4.69 ± SE: 0.15, treatment LD estimate: -0.48 ± SE: 0.28, $F_{1,79} = 14.73$, p < .001, Fig. 8). Sex was not significant as a main effect ($F_{1,79} = 1.21$, p = 0.26), but there was a significant interaction between sex and feeder density treatment (feeder density treatment * sex: $F_{1,79} = 5.80$, p = 0.018,

Fig. 8), such that male house finches spend significantly less time per day on feeders than females at low-density feeder sites, whereas sex differences were not apparent at high-density feeder sites.

Movement between treatments

House finches first observed at the low-density feeder block were significantly more likely to later visit a neighboring block with the high-density feeder treatment than house finches first observed at a high-density feeder block were to visit the neighboring low-density feeder block (n = 98; treatment HD estimate: -2.69 ± SE: 0.73, treatment LD estimate: 1.90 ± SE: 0.70, $F_{1,98} = 8.72$, p = 0.0064, Fig. 9). House finches that first visited a low-density feeder block were almost four times more likely to visit a neighboring block at some point during the experiment than house finches who first visited a high-density feeder block.

Mg-Specific Antibody Concentration

Disease prevalence was low overall, with only 5.2% of house finches captured post-manipulation showing visible signs of disease and only 22% of tested house finches coming up as seropositive. Potentially, as a result of this low prevalence, we did not observe an effect of feeder density on whether an individual house finch was seropositive for Mg (n=106; $F_{1,106} = 0.59$, p = 0.22). Similarly, feeder density did not predict the concentration of circulating Mg-specific antibodies (n=106; $F_{1,106} = 0.01$, p = 0.91) in house finches.

Discussion

This study is one of the first to examine how the degree of supplementary feeding affects the behavior and physiology of a wild bird species that is largely dependent on supplemental food during the non-breeding season. We found that feeder density was associated with changes in many aspects of house finch ecology, physiology, and foraging behavior during the non-breeding season. Given the importance of local abundance (Altizer et al. 2004b) and foraging at feeders for the acquisition of a contagious bacterial pathogen in this species (Adelman et al. 2015), our results suggest that the degree of supplemental feeding in backyards has the potential to influence disease dynamics in house finches.

We examined effects of feeder density on several types of foraging behaviors in house finches during the non-breeding season. Consistent with our predictions, we found that house finches at high-density feeder sites had significantly longer average bout lengths and spent more time per day on feeders than those at low-density feeder sites. This suggests that competition for limited feeding ports constrains bout lengths and total time on the feeder for house finches at low-density feeder sites. Consistent with this idea, past research in a captive setting showed that house finch flocks with a low-density of feeders exhibited more aggressive displacements to compete over limited feeding opportunities than flocks of the same size with a high-density of feeders (Moyers et al. 2018). One caveat of our study is that the RFID units only record the presence of house finches at a port, but do not record the time spent eating while individuals are present at the port. Future work should determine whether house finches at high-density feeder sites, by spending more total time on feeder perches, are also obtaining significantly more food than house finches at low-density feeder sites. Nevertheless, given that time spent on feeders per day was the strongest predictor of an individual's risk in acquiring mycoplasmal conjunctivitis

(Adelman et al. 2015), our results suggest that individuals foraging at high-density feeder sites may be at higher risk of disease.

We also detected some sex differences in foraging behaviors that may influence individual responses to variation in feeder density in house finches. Female house finches had significantly longer bout lengths than males, and females spent significantly more time per day on feeders than males, but only at low-density feeder sites. Given that some studies have found that female house finches are socially dominant to males (Brown and Brown 1988, Shedd 1990, Belthoff and Gauthreaux Jr. 1991), future studies should explore the role of sex-specific dominance in driving some of the observed differences we detected between the sexes.

Feeder density had a significant effect on local house finch foraging movements as well. Prior studies have shown both that anthropogenic resource supplementation can reduce migratory behavior and thus limit landscape-level movements of animals (reviewed in Satterfield et al. 2018), and that supplemental feeding can shift or reduce local movements, and thus home ranges (e.g., Boutin 1990, Corcoran et al. 2013, Schuttler et al. 2015). Because house finches have fairly large home ranges in the non-breeding season (Dhondt et al. 2005), we examined whether the feeder density treatment in the block where finches were initially detected by RFID influenced the likelihood of moving to a neighboring block harboring the opposite feeder density. As predicted, house finches that first visited a high-density feeder block were much less likely to visit a neighboring block than birds that initially visited a low-density feeder block. Thus, house finches appear to move from low-density to high-density blocks more readily than the opposite, indicating a preference for high-density sites when given the choice across the landscape. Because house finches spend more time on feeders per day at high-density sites, and high-density feeder sites are more attractive to birds foraging nearby, sites with a high-density of

feeders could be at higher risk for individuals acquiring Mg. Thus, sites with a high-feeder density could act as a major source of disease by facilitating behaviors in house finches that could lead to higher risk of acquiring Mg. Conversely, high-density feeder sites could act as a potential disease sink, because house finches that visit high-density sites tend to remain at those sites, potentially reducing the ability of infectious individuals to spread the disease across the landscape.

We also examined the potential effects of feeder density on house finch body condition. In contrast to our predictions, although house finches at high-density feeder sites had longer foraging bouts and spent more time on feeders per day, they had poorer body condition than finches at low-density feeder sites. There are a few possible mechanisms that could explain this discrepancy. Due to trade-offs between food availability and other risks, birds with stable food access may have a reduced body mass because of an increase in non-foraging behaviors such as predator vigilance (Lima 1986). Experiments in European starlings (*Sturnus vulgaris*) on the adaptive mass-regulation hypothesis, which states that birds can regulate body mass in response to changes in foraging conditions, have shown that food-deprived starlings have increased body mass because they store more fat (Witter et al. 1995). The reduced movement away from high-density feeder sites relative to low-density feeder sites is consistent with the idea that house finches may perceive these sites as more reliable food sources, and thus could retain a reduced mass, leading to lower scaled-mass index scores. Alternatively, the detected relationship between body condition and feeder density treatment may not be due to causative effects of treatment, but instead could arise if house finches with poor body condition are actively seeking out high-density feeder sites. If lower body condition in house finches is associated with higher susceptibility to disease, this could result in more susceptible individuals being attracted to sites

with high feeder density, where they are then more likely to stay and engage in feeding behaviors associated with a high risk of disease. Past work has found associations between the severity of mycoplasmal conjunctivitis and body condition (Altizer et al. 2004a). However, it remains unknown whether poor body condition is a cause or consequence of disease in this species, and thus future work should examine whether poor body condition results in higher susceptibility to Mg infection.

We used capture rate as a proxy for local site abundance and found significantly higher capture rates at high-density feeder sites. Thus, there appear to be more house finches, on average, present around high-density feeder sites than low-density feeder sites. However, the higher number of individuals at high-density feeder sites did not appear to proportionately increase competition for food, as foraging bouts and total time on the feeder were still significantly longer at high-density feeder sites relative to low-density feeder sites. Our study design assigned distinct feeder density treatments to half of the sites across years, and thus one-half of our sites changed treatments from Year 1 to Year 2. Nonetheless, feeder density was a significant predictor of capture rate in both years, indicating that feeder density treatment, rather than site-specific variation, drove the detected patterns in local abundance. Given the importance of host density for the spread of contagious pathogens like Mg (Altizer et al. 2004b, Hochachka and Dhondt 2006), the increased local abundance of house finches at high density sites likely has important implications for the spread of Mg.

Although the changes in behavior and local abundance that we observed with the high-density feeder treatment would be predicted to increase disease transmission, we are unable to draw definitive conclusions about Mg transmission due to low overall prevalence of Mg during the study. We observed few instances of visible pathology (5.2%), and low rates of seropositivity

(22%) during the treatment period in both years. Given the low prevalence of Mg during our study, it is perhaps not surprising that we did not detect significant effects of feeder density on seroprevalence or the concentration of Mg-specific antibodies. Recent work manipulating the presence or absence of bird feeders at forested sites documented that birds captured at sites with feeders had higher rates of seropositivity to Mg (Vana et al. 2018). However, the sample in this study included a suite of feeder-visiting species, and thus was not limited to house finches. Future work in areas with higher disease prevalence should examine whether sites with a high-density of feeders are associated with higher rates of Mg clinical signs or seroprevalence in free-living house finches.

In conclusion, this study is one of the few to directly examine how the degree of supplementary feeding in the wild affects songbird behavior and physiology. This study highlights the importance of considering not only whether supplementary food is available to a population, but how that food is provided as well. Overall, our results suggest that the degree of supplemental feeding can have key effects on foraging behavior, local movements, local abundance, and condition for a songbird species that is heavily reliant on anthropogenic food. Because all these effects have the potential to influence disease dynamics in this species, variation in the degree of supplemental feeding across the landscape is likely to have implications for disease maintenance and spread in house finches. Given the enormous popularity of wild bird feeding (Jones 2011), it is critical that future work explore these effects in other wild bird species, as well as their potential implications for wild bird fitness.

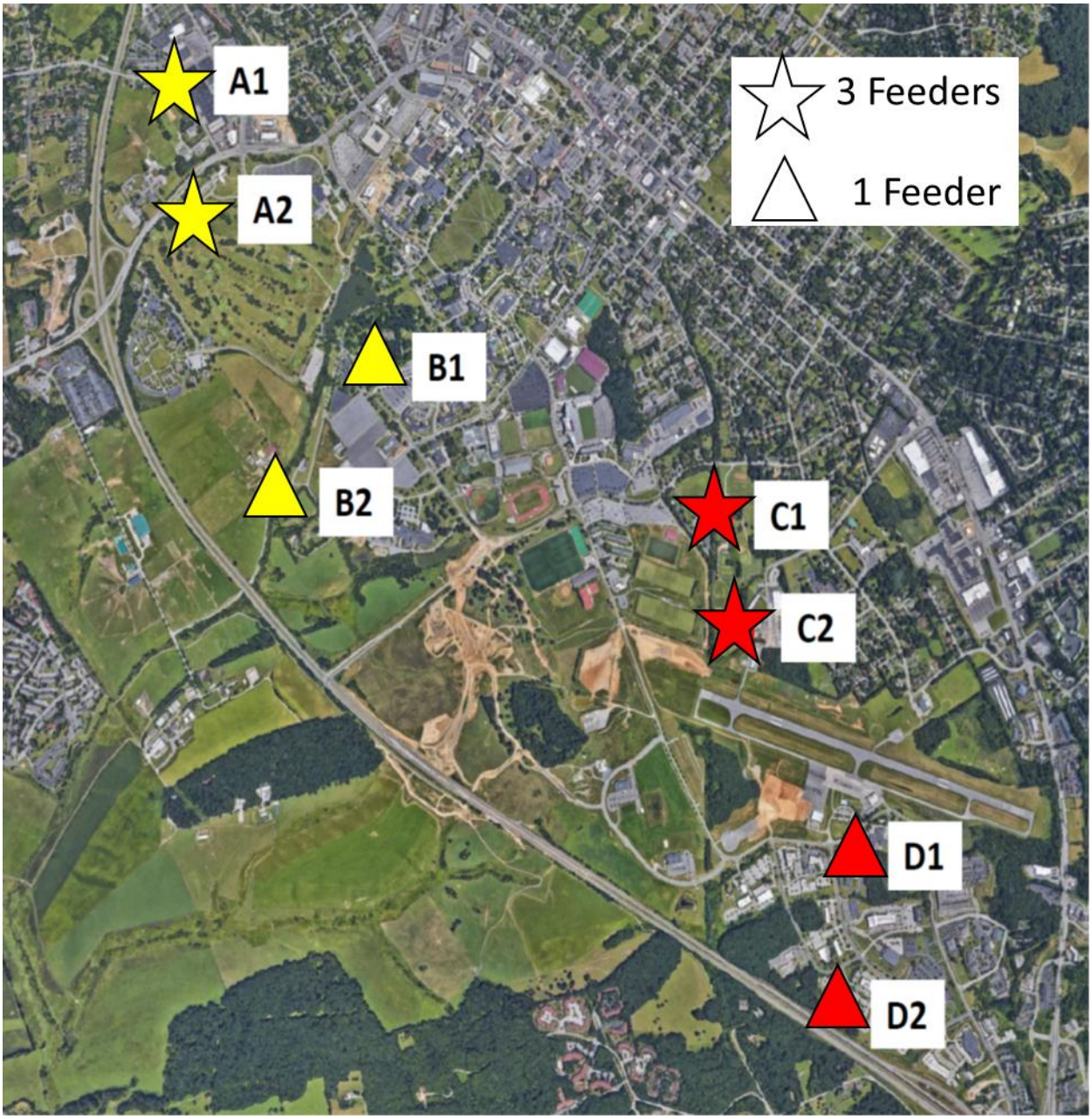


Figure 1a. Experimental design of field study for year 1, with pairs of sites starting with the same letter corresponding to separate "blocks". Shapes indicate the feeder density treatment each block was given post-manipulation. The experimental design initially accounted for geographic variation by assigning the two blocks within either the northwest (yellow) or southeast (red) to separate treatments. However, block D received almost no detectable house finch activity post-manipulation, and thus this site was eliminated from all analyses.

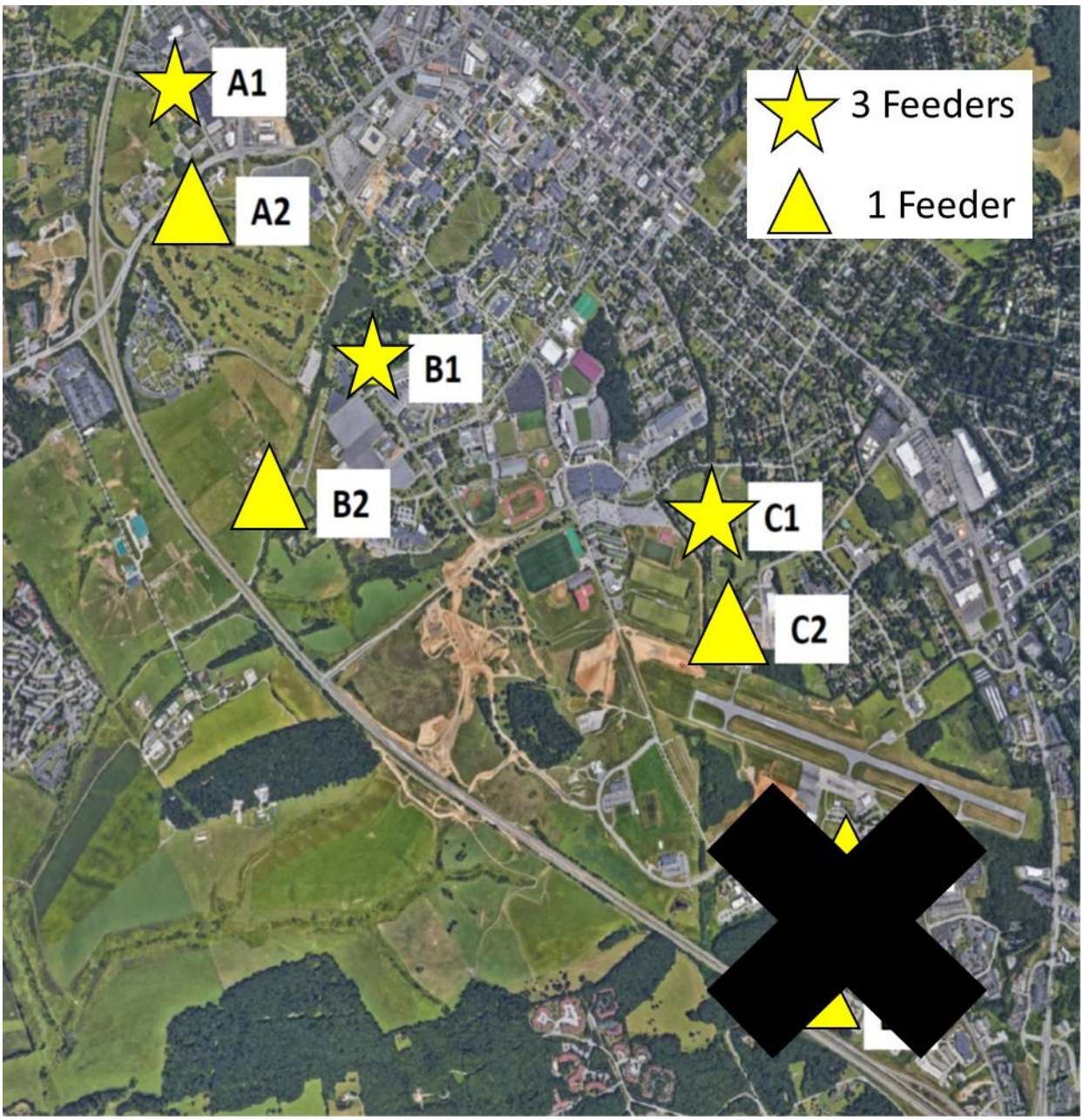
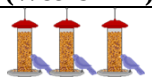


Figure 1b. Experimental design of field study for year 2, with pairs of sites starting with the same letter corresponding to separate "blocks". In this year, geographic variation was controlled for by assigning sites (represented by number) within the same block to different feeder density treatments. The D block was removed from the study in this year due to low activity in year 1.

Year 1:

SITES	Pre-manipulation (Weeks 1-4)	Post-manipulation (Weeks 4-12)
N=4 A1, A2 C1, C2		
N=4 B1, B2 D1, D2		

Year 2:

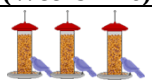
SITES	Pre-manipulation (Weeks 1-4)	Post-manipulation (Weeks 4-16)
N=3 A1, B1, C1		
N=3 A2, B2, C2		

Figure 2. Experimental timeline for both years. The pre-manipulation column shows the number of feeders at all sites during the pre-manipulation phase of the experiment, and the post-manipulation column shows the number of feeders at each site post-manipulation. Letters indicate the blocks based on site proximity, and numbers indicate the specific site within that block.

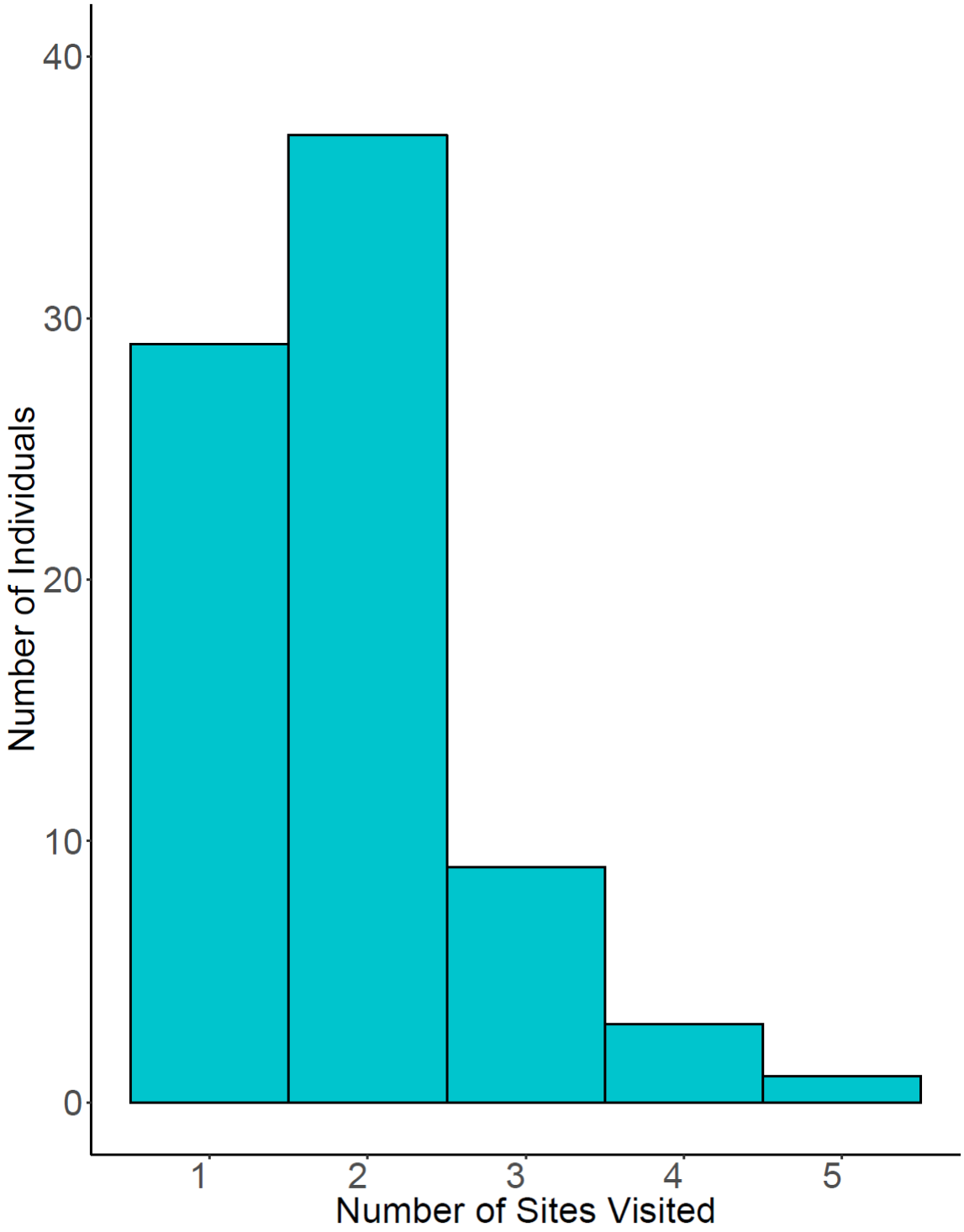


Figure 3. Distribution of the number of sites visited by individual house finches in year 1, out of 6 total sites (A1-A2, B1-B2, and C1-C2). This analysis only includes individuals that were detected on more than one day and had at least 10 separate feeding bouts post-manipulation.

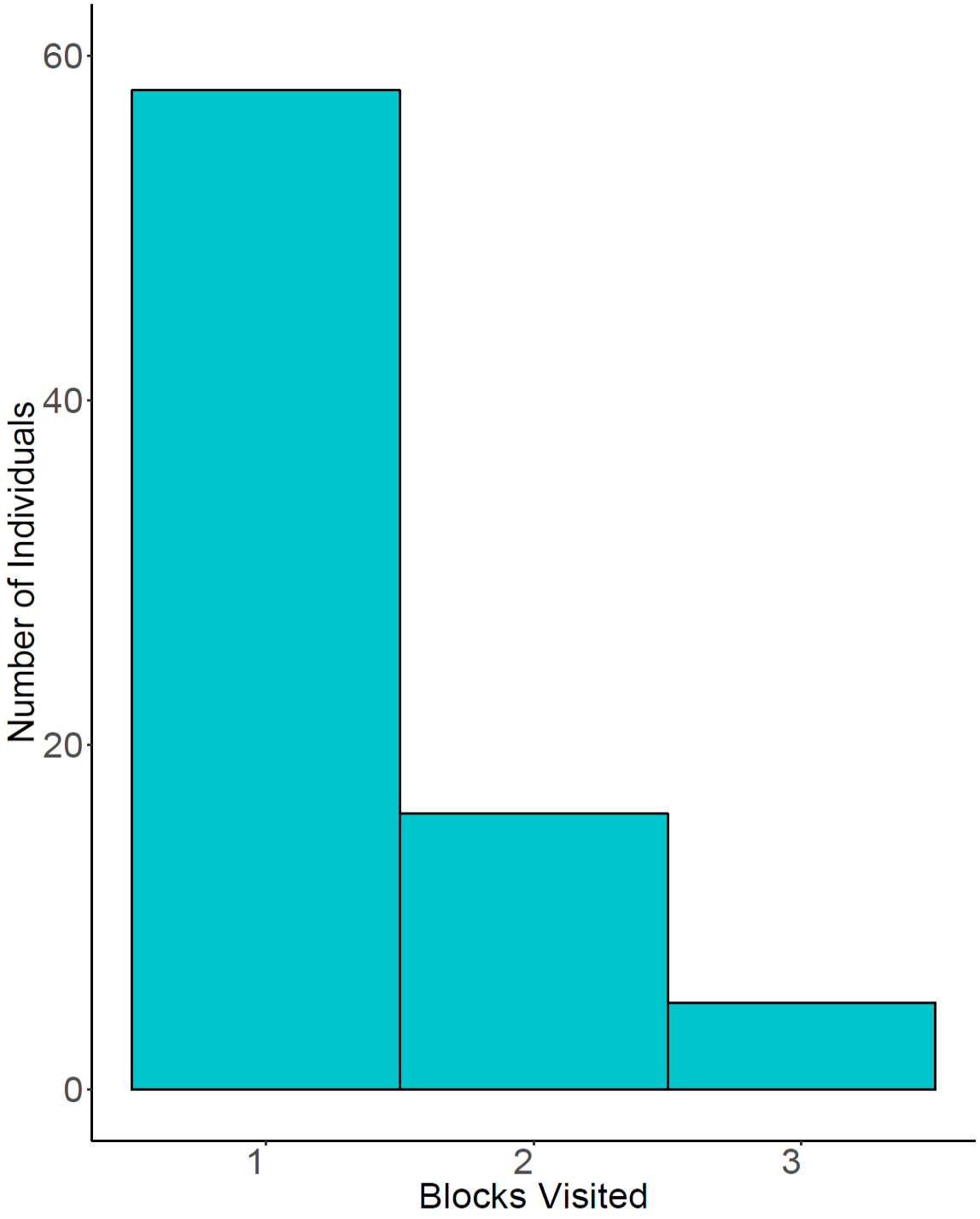


Figure 4. Distribution of the number of blocks visited by individual house finches in year 1, out of three total blocks (A, B, or C). This analysis only includes individuals that were detected on more than one day and had at least 10 separate feeding bouts post-manipulation.

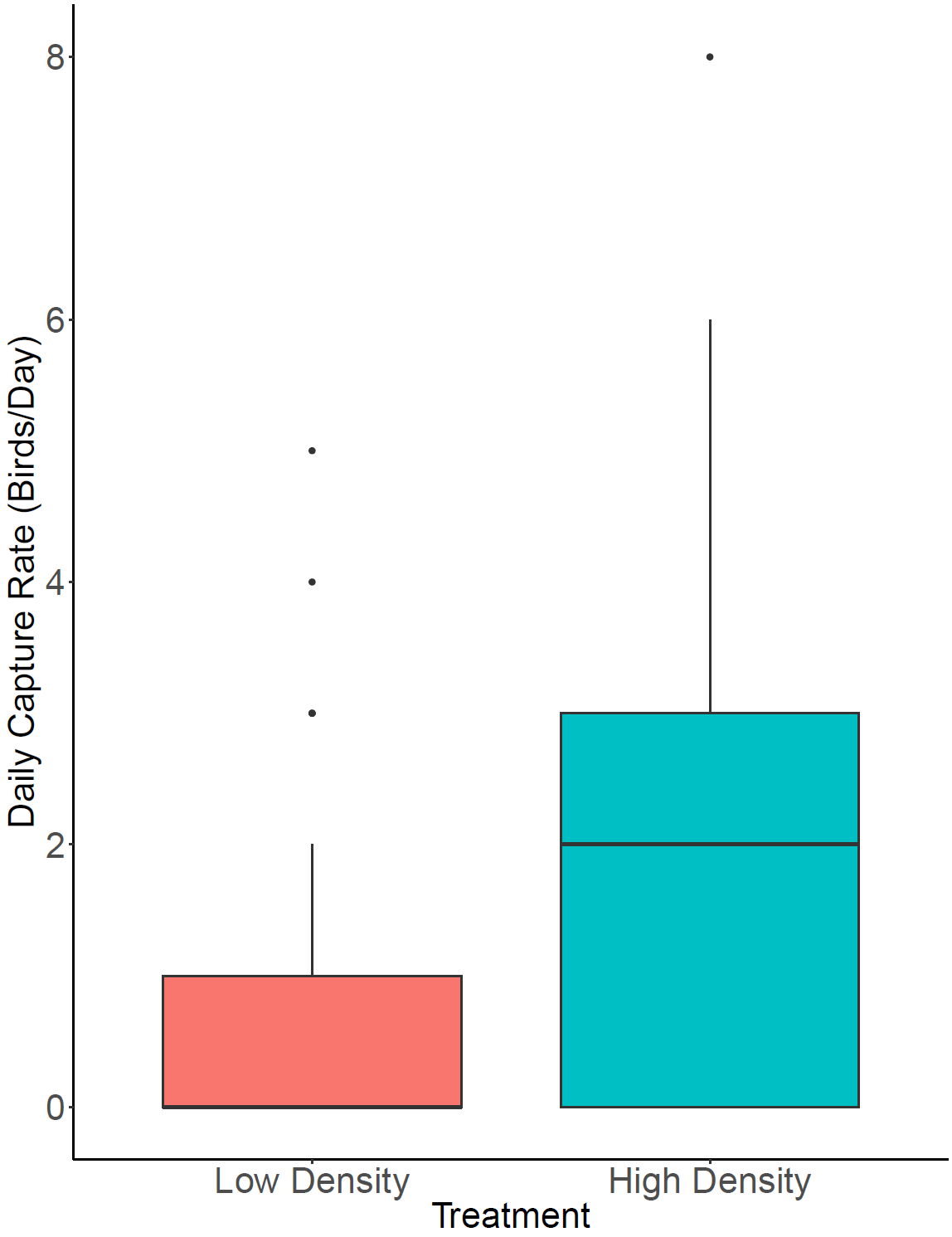


Figure 5. Daily capture rates (defined as the number of birds caught per day at a given site) post-manipulation in years 1 and 2. Across both years, capture rates were higher at sites with three feeders (blue bar) relative to sites with one feeder (red bar).

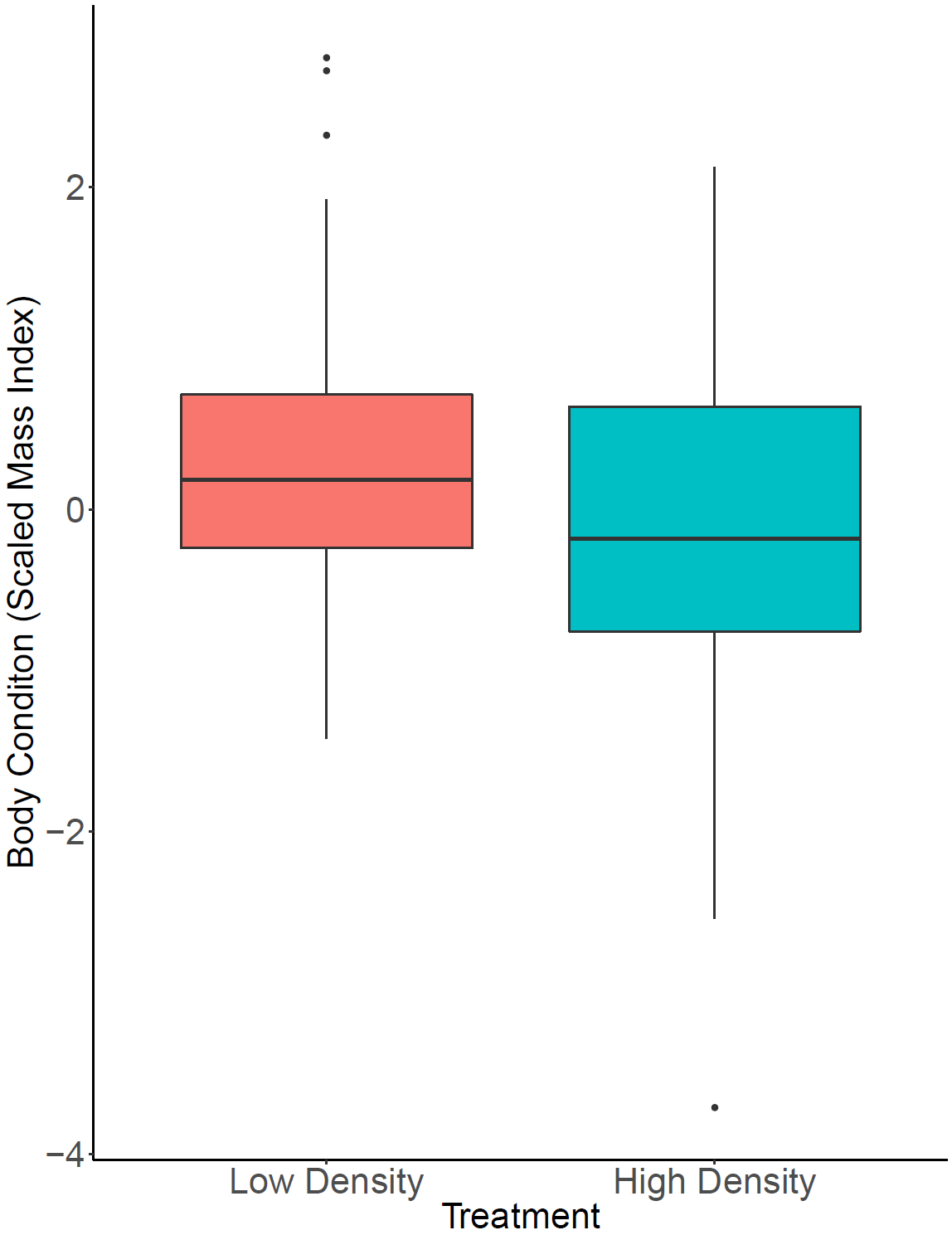


Figure 6. Body condition, quantified here as scaled mass index, post-manipulation in years 1 and 2. Across both years, body condition was lower at three feeder sites (blue bar) than at one feeder sites (red bar).

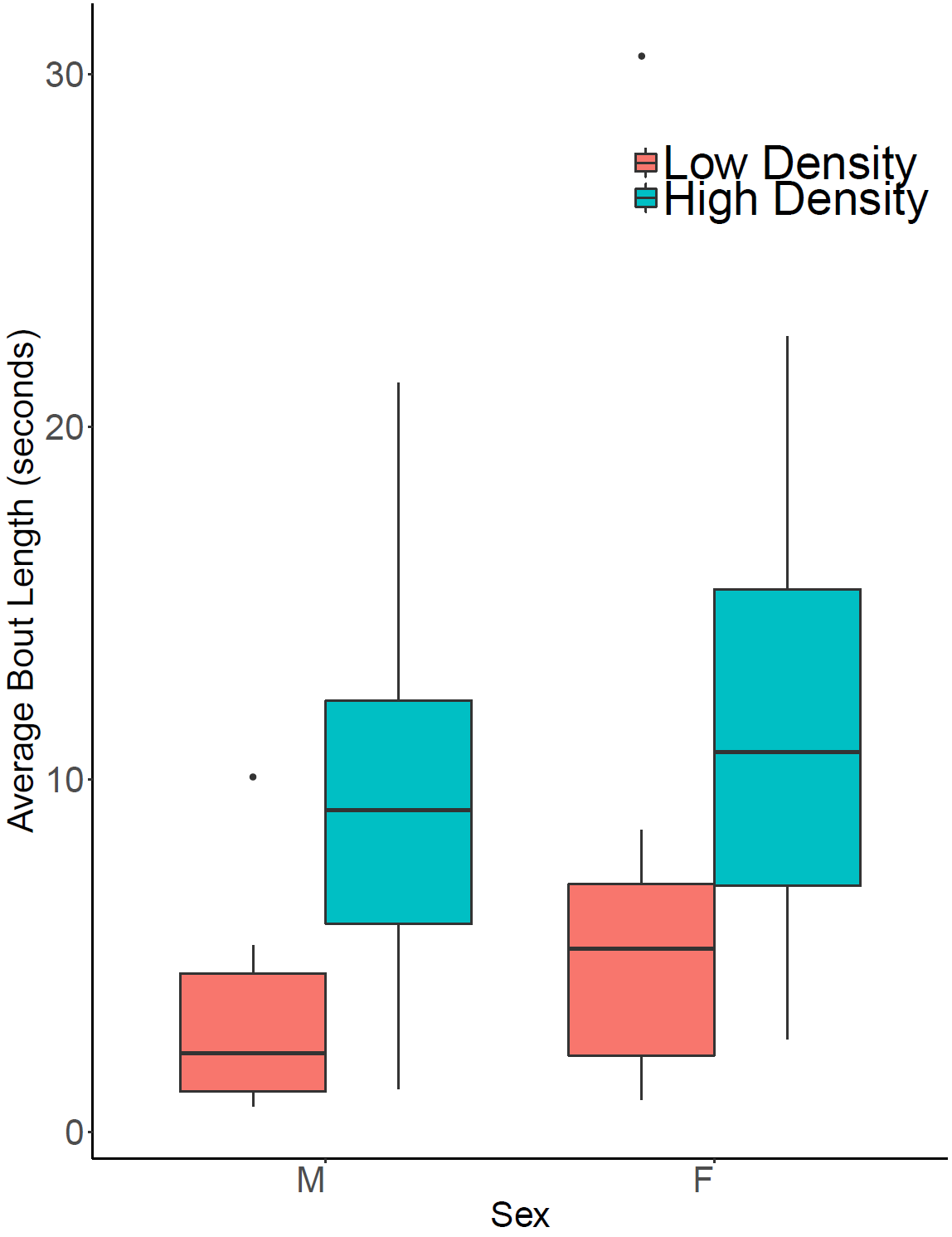


Figure 7. Average bout length in seconds for house finches in year 1 that were detected on more than one day and had at least 10 separate bouts post-manipulation. Bouts at three feeder sites (blue bars) were longer than bouts at one feeder sites (red bars), and males had shorter average bout lengths than females at one feeder sites.

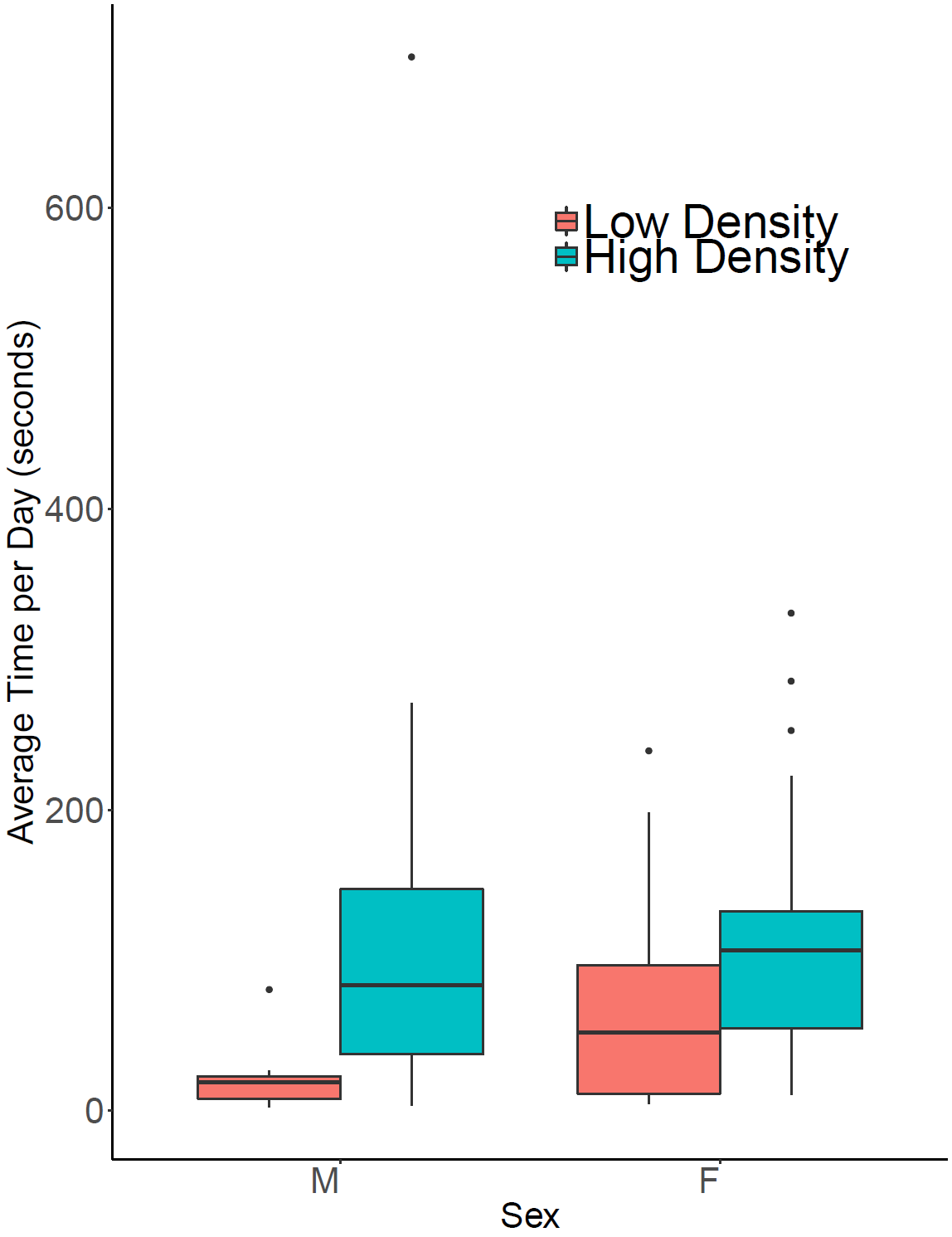


Figure 8. Average time per day on feeders for house finches in year 1 that were detected on more than one day and had at least 10 separate bouts post manipulation. Average time per day on feeders was longer at three feeder sites (blue bars) than at low feeder sites (red bars). Males had shorter average bout lengths than females at low feeder sites.

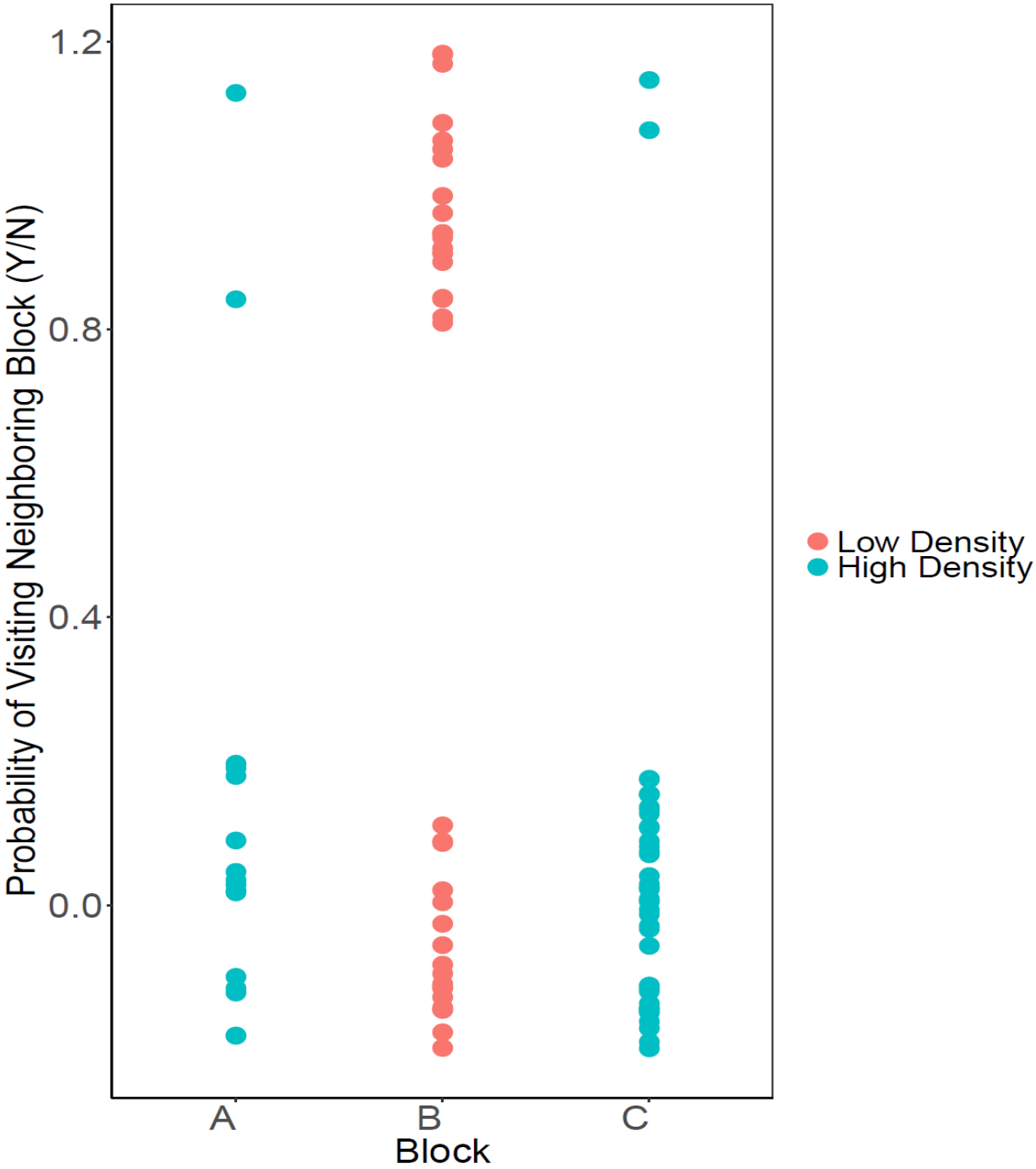


Figure 9. The probability of an individual house finch visiting a neighboring experimental block based on the first block that they visited in year 1. The neighboring block was always a different treatment than the first block visited. To account for the fact that birds in block B had neighboring blocks in both directions (Fig. 1*a*), which could artificially inflate their likelihood of visiting a neighboring block, visits to block A versus C from block B were considered separate events and thus coded as separate rows in our dataset. However, bird ID was included as a random effect to account for the statistical non-independence of these separate events. Probabilities are either 1 or 0, points represent individual birds and are jittered for visibility.

3. CONCLUSION

The goal of this research was to determine how the density of bird feeders at a site influences the over-wintering ecology and feeding behavior of free-living house finches, a highly feeder-dependent species affected by a common bacterial pathogen that is transmitted at feeder ports. The density of bird feeders at a site had many notable effects on the abundance, behavior, and physiology of house finches in late fall and winter. First, sites with the high-density feeder treatment had increased daily capture rates for house finches relative to low-density feeder sites, indicating higher local abundance of individuals at sites where more bird feeders are present. Second, house finches using sites with the high-density feeder treatment had significantly longer bouts on feeders and spent more time on feeders per day, but despite this greater resource access, had poorer body condition. Finally, feeder density treatment influenced the local movements of house finches: individuals that initially visited sites with a low-density of feeders were more likely to later visit nearby sites with a high-density of feeders present, whereas birds initially detected at high-density feeder sites were more likely to only use high-density feeder sites.

Overall, these results demonstrate that the density of bird feeders at a site can have far-reaching consequences for wild birds. With the popularity of wild bird feeding in the United States and many other developed countries (Reynolds et al. 2017), it is critical to investigate how heterogeneity in bird feeding practices mediates the effects of bird feeders on wild bird populations. Although there are currently no published data on variation in feeder density among backyards, there is likely to be substantial heterogeneity in the density of feeders present per site across the landscape. Our results indicate that this heterogeneity can have far-reaching consequences for wildlife ecology and behavior, at least for a bird species that is largely dependent on anthropogenic food in many parts of its range. As we continue to explore the

diverse effects of anthropogenic food sources on ecosystems, our results suggest that we need to consider not only whether supplemental food is present or not, but how that food is being distributed to wildlife.

Our results also suggest that individuals within a species may not always respond equally to supplemental feeding, which to date, is an area that has not been closely examined. Specifically, we found that sex interacted significantly with feeder density to predict several foraging behaviors, suggesting that males and females may in some cases respond differently to the density of feeders at a site. Future work should explore how sex and other sources of individual variation can influence responses of wildlife to supplemental feeding, as well as the mechanisms underlying these differential responses.

Although our goal was to understand how feeder density influences house finch ecology and behavior in ways relevant to disease spread, we were unable to directly determine whether feeder density altered the risk of disease. We captured very few house finches with signs of mycoplasmal conjunctivitis after manipulating the density of feeders, which suggests that disease prevalence was quite low at the time of study. Thus, it is perhaps not surprising that we did not find any effect of feeder density on the likelihood of exposure to Mg in our study. However, past work has shown that the amount of time spent per day on feeders is an important predictor for disease acquisition (Adelman et al. 2015), and thus, our results suggest that disease risk may be higher for birds foraging at sites with a high-density of feeders, where they were able to spend significantly longer amounts of time feeding in our study. Further, the increased local abundance of house finches at high-density feeder sites should facilitate disease spread. Finally, house finches at high-density feeder sites had lower body condition on average, which might further exacerbate disease spread (Becker et al. 2015). However, it remains unknown whether body

condition in house finches has any notable effects on immune function or disease susceptibility, and thus this is an important direction for future studies on this system.

Our work is one of a growing set of studies across taxa examining how supplementary feeding influences local movements of wildlife. Theory suggests that local movements of animals based on variation in patch quality can have important effects on disease dynamics by facilitating or dampening the ability of a disease to persist across the landscape (Becker and Hall 2016). Sedentary behavior around anthropogenic food sources has been shown to occur in American white ibis (*Eudocimus albus*) (Murray et al. 2018) and in monarch butterflies (*Danaus plexippus*). The latter have formed more sedentary populations due to anthropogenic planting of milkweed species that do not die back over winter (Altizer et al. 2011). More research is needed to understand how variation in the presence, extent, or quality of anthropogenic resources alters local or landscape movements of wildlife, as well as the consequences of these changes for disease dynamics.

In conclusion, this study is one of the few experimental field studies on anthropogenic resource provisioning on a wild population. More complex manipulations of feeder abundance, access, type of feeder, and food type could further help determine the mechanisms behind the behaviors observed in this study (Altizer et al. 2018). Larger studies looking across broader geographic areas and observing more bird species could also help to broaden the scope of mechanisms that may be impacting the house finch – Mg system around bird feeders. The results of this study can help drive not only disease ecology, but behavioral ecology in new directions in understanding how supplemental feeding by humans, both intentional and unintentional, impacts wild populations behaviorally and physiologically.

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