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ARTICLE

Effects of bird feeder density on the foraging behaviors of a backyard songbird (the House Finch, *Haemorhous mexicanus*) subject to seasonal disease outbreaks

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Abstract: Provisioning of wildlife, such as backyard bird feeding, can alter animal behavior and ecology in diverse ways. For species that are highly dependent on supplemental resources, it is critical to understand how variation in the degree of provisioning, as occurs naturally across backyards, alters wildlife behavior and ecology in ways potentially relevant to disease spread. We experimentally manipulated feeder density at suburban sites and tracked local abundance, foraging behaviors, body mass, and movement in House Finches (*Haemorhous mexicanus* (P.L. Statius Müller, 1776)), the primary host of a pathogen commonly spread at feeders. Sites with high feeder density harbored higher local House Finch abundance, and birds at these sites had longer feeding bouts and total time on feeders relative to sites with low feeder density. House Finches at high-density feeder sites had lower residual body mass despite greater apparent feeder access. Finally, birds first recorded at low-density feeder sites were more likely to move to neighboring high-density feeder sites than vice versa. Because local abundance and time spent on feeders have both been linked with disease risk in this species, the effects of heterogeneity in bird feeder density on these traits may have important consequences for disease dynamics in this system and more broadly.

Key words: bird feeders, supplemental food, foraging behavior, House Finch, *Haemorhous mexicanus*, disease transmission.

Résumé : La mise à disposition de nourriture pour les animaux sauvages, par exemple par des mangeoires d'oiseaux dans les cours, peut modifier de différentes manières leurs comportements et leur écologie. Pour les espèces qui dépendent fortement de tels suppléments de ressources, il est extrêmement important de comprendre comment les variations spatiales du degré de cet approvisionnement se traduisent par des modifications du comportement et de l'écologie des espèces qui peuvent avoir une incidence sur la propagation de maladies. Nous avons manipulé expérimentalement la densité de mangeoires dans des sites suburbains et suivi l'abondance locale, les comportements d'alimentation, la masse corporelle et les déplacements de roselins familiers (*Haemorhous mexicanus* (P.L. Statius Müller, 1776)), l'hôte primaire d'un pathogène couramment propagé aux mangeoires. Les sites de forte densité de mangeoires étaient caractérisés par une plus grande abondance locale de roselins familiers, et les épisodes d'alimentation des oiseaux dans ces sites et la durée totale passée aux mangeoires étaient plus longs que dans les sites de faible densité de mangeoires. Les roselins familiers aux sites de forte densité de mangeoires présentaient une masse corporelle résiduelle plus faible, malgré leur plus grand accès apparent à des mangeoires. Enfin, les oiseaux d'abord observés dans des sites de faible densité de mangeoires étaient plus susceptibles de se déplacer vers des sites avoisinants de haute densité de mangeoires que l'inverse. Comme l'abondance locale et le temps passé aux mangeoires ont tous deux été liés au risque de maladie chez cette espèce, les effets de l'hétérogénéité de la densité de mangeoires sur ces caractères pourraient avoir d'importantes conséquences sur la dynamique des maladies dans ce système et plus largement. [Traduit par la Rédaction]

Mots-clés : mangeoires d'oiseaux, supplément de nourriture, comportement d'alimentation, roselin familier, *Haemorhous mexicanus*, transmission de maladies.

Introduction

The diverse impacts of anthropogenic food subsidies on wildlife populations and ecosystems are just beginning to be fully appreciated (Oro et al. 2013; Altizer et al. 2018). 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 has the potential to alter foraging behaviors in ways that can indirectly impact wildlife health. First, with increased resource availability, animals may engage in longer or more frequent feeding bouts, leading to increased nutritional condition (e.g., Jessop et al. 2012). In addition, these alterations in foraging behavior can augment direct and indirect contacts among individuals, facilitating exposure to pathogens (e.g., Flint et al. 2016). Thus, there is a growing interest in understanding how anthropogenic food supplementation impacts wildlife behavior and condition in ways ultimately relevant to disease dynamics (Becker et al. 2015; Altizer et al. 2018).

Changes in behavior in the presence of supplemental food are arguably one of the most universal responses of wildlife populations to supplemental food resources (e.g., Murray et al. 2016). Furthermore, heterogeneity in the availability of supplemental food over space and time is likely a general characteristic of supplemental food that has important implications for wildlife foraging behavior (e.g., Wehtje and Gompper 2011; Yoda et al. 2012;

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Stofberg et al. 2019). Although heterogeneity in supplemental food availability has been linked with downstream disease outcomes in some systems (e.g., Miller et al. 2003), it is important to explicitly examine how this heterogeneity alters animal behavior, particularly in ways relevant to disease spread for a given species (e.g., Thompson et al. 2008). Optimal foraging theory predicts that wildlife foraging in patchy habitats will maximize intake and efficiency while minimizing foraging costs including travel, handling time, and competition with conspecifics (e.g., MacArthur and Pianka 1966). For many taxa, sites with supplemental food often harbor higher local densities of individuals (e.g., Thompson et al. 2008; Corcoran et al. 2013), suggesting that the benefits of foraging in patches with supplemental food can outweigh potential costs associated with competition. From a disease transmission perspective, behavioral aggregation can augment rates of direct contact (e.g., Flint et al. 2016), and in some cases, indirect contact via feces and (or) environmental surfaces that harbor pathogens (i.e., fomites) (e.g., Murray et al. 2016). Supplemental food can also alter movement behaviors during foraging, often by reducing home ranges (e.g., Boutin 1990), which can augment local transmission but decrease pathogen spread across space. Finally, by altering resource availability and foraging behaviors, supplemental feeding can result in changes to host condition or nutritional balance, and thus, the ability of hosts to resist or tolerate pathogens once exposed (e.g., Budischak and Cressler 2018; Strandin et al. 2018).

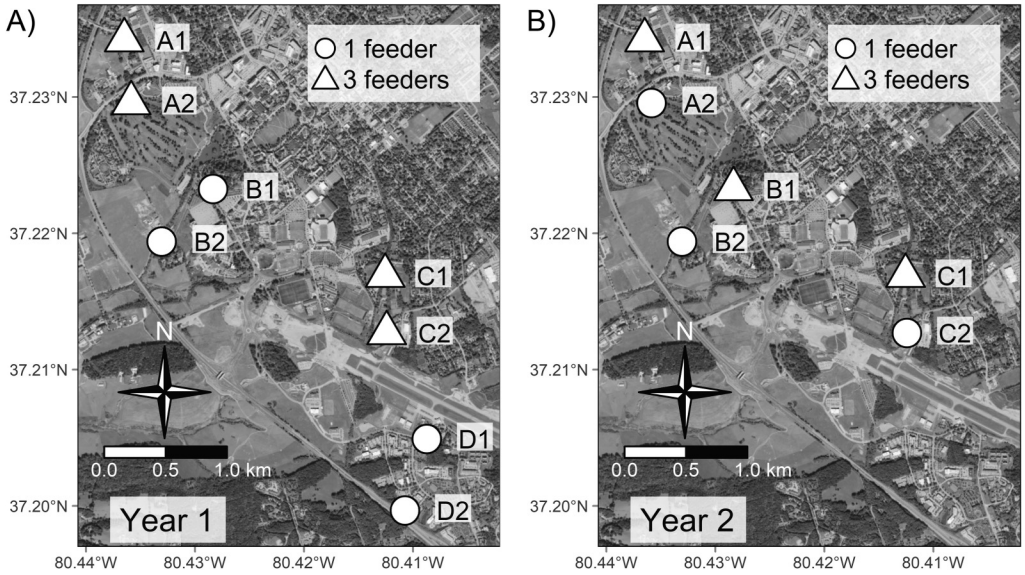
Backyard bird feeders are one of the most common forms of intentional human supplementation of wildlife worldwide (Cox and Gaston 2018). In the United States alone, an estimated 52 million households have at least one backyard bird feeder (U.S. Department of the Interior et al. 2011). Although a growing body of work has demonstrated far-reaching effects of supplemental food on the survival, abundance, and reproductive parameters of various bird species (Robb et al. 2008; Reynolds et al. 2017; Jones 2018; Lawson et al. 2018), less is known about the direct impacts of feeders on individual foraging behaviors, particularly in the non-breeding season. Roth and Vetter (2008) manipulated feeder presence for overwintering flocks of Dark-eyed Juncos (*Junco hyemalis* (Linnaeus, 1758)) and found that flocks with feeder access had smaller home-range sizes and reduced movement. In contrast, supplemental food did not alter home-range size or distribution in non-breeding flocks of Varied Tits (*Sittiparus varius* (Temminck and Schlegel, 1845)) (Kubota and Nakamura 2000). Because many foraging and movement behaviors can have key downstream impacts on disease dynamics (e.g., Adelman et al. 2015), it is important to understand how bird feeders alter behaviors that are directly relevant to disease spread for a given species. To date, two experimental studies have manipulated bird feeder presence and examined impacts on wild bird condition and disease prevalence (Wilcoxen et al. 2015; Galbraith et al. 2017*a*). Although these studies show that the presence of bird feeders can detectably alter bird condition and augment parasite prevalence, neither examined the potential behavioral mechanisms involved.

The use of radio-frequency identification device (RFID) technology has revolutionized the study of the foraging behavior of small birds (Bonter and Bridge 2011), allowing collection of high-resolution data on individual behavior at supplemental food sources. For example, Galbraith et al. (2017*b*) used RFID technology to measure feeding behavior across avian assemblages in New Zealand backyards, finding substantial individual and species-specific differences in feeder use. However, because this technology requires focal individuals to come within 10 cm of an antenna (Bonter and Bridge 2011), it is challenging to use RFID to quantify foraging behavior in the absence of any supplemental food, which provides the centralized location for antennae in studies of non-breeding birds. However, RFID technology can readily be used to quantify foraging behavior across sites that vary in the degree of supplemental feeding, specifically the number of bird feeders present. Variation in feeder number in a given patch (quantified here as "feeder density") is a particularly important characteristic to study, given the considerable heterogeneity in this trait across the landscape. For example, in North America, a subset of participants in the Cornell Lab of Ornithology's Project FeederWatch program report substantial variation in the number of backyard feeders that they provision in their yards (range of 1–147 feeders per yard; Dayer et al. 2019). Furthermore, those who feed birds in the United Kingdom harbor, on average, 5.7 feeders in their backyards (Schreiber 2010), with a separate study indicating that the number of backyard feeders provided by individual homeowners in the United Kingdom has significantly increased over time (Plummer et al. 2019). This heterogeneity in feeder density across sites is likely to have important consequences for backyard birds that rely heavily on anthropogenic food, such as House Finches (*Haemorhous mexicanus* (P.L. Statius Müller, 1776)).

House Finches are common backyard songbirds that are largely dependent on bird feeders throughout their introduced range in eastern North America (Badyaev et al. 2020). In fact, House Finch densities in the introduced range are positively associated with human population density and the presence of bird feeders (Mertz and Brittingham 2000; Fischer and Miller 2015). Bird feeders are also known to play an important role in the spread of *Mycoplasma gallisepticum* (MG), a common bacterial pathogen of House Finches (Dhondt et al. 2007*a*; Adelman et al. 2015). 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. Outbreaks of MG primarily occur in the non-breeding season, when House Finches form loose foraging flocks that use backyard bird feeders throughout much of their range (Altizer et al. 2004). In addition to serving as points of aggregation within and among flocks, feeders act as environmental fomites for indirect transmission of MG (Dhondt et al. 2007*a*; Adelman et al. 2015). A recent study found that the mean 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). Furthermore, in experimental epidemics in House Finch flocks, rates of transmission of MG were higher in captive flocks with a high density of bird feeders than in flocks of equal size with a lower feeder density (Moyers et al. 2018). However, effects of feeder density on free-living House Finch flocks that have access to numerous foraging patches are likely to differ.

In the present study, we hypothesized that habitat patches with experimentally enhanced feeder density would attract higher numbers of free-living House Finches and provide greater foraging opportunities for those individuals. To test this, we manipulated feeder density at eight otherwise similar sites on or near the Virginia Tech campus and tracked feeding behavior with RFID on all accessible feeder ports. We predicted that sites with higher feeder density would attract a higher local abundance of House Finches, which we measured by daily capture rate. We predicted that birds caught at sites with a higher density of feeders would also have higher residual body mass due to increased food access. Behaviorally, we predicted that birds at sites with higher feeder density would spend more time per day on bird feeders due to more available perches and that their bouts on feeders, on average, would be longer. We also predicted that House Finches would prefer sites with a higher density of feeders; thus, individuals would be more likely to move to a neighboring block of sites when those sites contained a higher rather than a lower feeder density. Finally, although our study was primarily focused on understanding how feeder density influences components of House Finch behavior potentially relevant for disease, we also examined the concentrations of MG-specific antibodies in birds at our sites. We predicted that House Finches caught at high-density feeder sites would harbor higher concentrations of MG-specific antibodies, indicating higher rates of exposure to MG.

Fig. 1. Experimental design of the feeder density manipulation study for year 1 (A) and year 2 (B), with pairs of sites starting with the same letter corresponding to separate "blocks". Shapes indicate the feeder density treatment that each block was given after manipulation. Because block D received almost no detectable House Finch (*Haemorhous mexicanus*) activity after manipulation, this block was conservatively removed from all analyses and was not included in year 2. The figure was created using the raster (Hijmans 2019), sf (Pebesma 2018), sp (Pebesma and Bivand 2005; Bivand et al. 2013), and tmap (Tennekes 2018) packages in R version 3.6.0 (R Core Team 2019). Site locations were based on GPS coordinates collected by the authors. The base map is from a four-band (red, green, blue, infrared) Digital Georectifed Image (raster) from the National Agriculture Imagery Program produced by the United States Department of Agriculture Farm Services Agency, Farm Production and Conservation Business Center, Aerial Photography Field Office, published on 13 June 2019. The raster image was retrieved from https://earthexplorer.usgs.gov/ on 10 April 2020.



Materials and 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, Virginia, USA (Figs. 1A and 1B), during the fall and winter (October–January) of two consecutive years (2016–2017 and 2017–2018). 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 4 weeks, half of the sites were manipulated to have a higher feeder density (three feeders per site), whereas the other half remained at a lower feeder density (one feeder per site). We did not include control treatments with no bird feeders present because wintering House Finches are rare to absent at sites without feeders (Mertz and Brittingham 2000). Thus, we would have been unable to study House Finch behavior, condition, or antibody levels at control sites due to the rarity or absence of the species at those sites. Furthermore, our primary interest was to measure differences in the degree of potential interaction with fomites (i.e., bird feeders), a known risk factor for disease transmission in this system (Adelman et al. 2015). Because control sites would have lacked fomites entirely, measuring behavior at these sites is not relevant to our overall question. Thus, our study manipulated the degree rather than the presence of supplemental feeding to understand how variation in feeder density across a landscape, as commonly occurs in suburban neighborhoods, may impact House Finch behavior and ecology in ways ultimately relevant to disease transmission.

In both years, sites that were closest to each other (0.4–0.7 km apart) were paired for experimental design purposes (Figs. 1A and 1B). 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. We placed our sites at distances largely within the range of daily House Finch foraging movements (up to 3 km per day; Dhondt et al. 2007*b*), because we were specifically interested in how variation in feeder density within House Finch home ranges influences House Finch foraging decisions (aka, our study aimed to mimic what House Finches might experience foraging in a neighborhood with variable feeder densities across backyards). The close distances between sites also allowed us to better standardize for variation in natural food availability and access to non-study feeders. The blocks (termed A, B, C, and D) spanned a northwest (NW) to southeast (SE) axis that we divided into two geographic areas (NW and SE) in year 1 only (Fig. 1A). There was considerable individual movement among sites and blocks (Tables 1 and 2), consistent with prior work on House Finch foraging ranges (Dhondt et al. 2007*b*). Nonetheless, the majority of birds (~73%) remained within the treatment block (high or low feeder density) where they were initially detected (Table 1). Because block D (sites D1 and D2 in Fig. 1A) had very low visitation by

Table 1. The number of total study sites (out of six maximum) and blocks (out of three maximum) visited in year 1 by the 79 individual House Finches (*Haemorhous mexicanus*) that met our RFID inclusion criteria.

	Number of birds (percentage of total)
Number of sites visited	
1	29 (36.7)
2	37 (46.8)
3	9 (11.4)
4	3 (3.8)
5	1 (1.3)
6	0 (0)
Number of blocks visited	
1	58 (73.4)
2	16 (20.3)
3	5 (6.3)

Table 2. The percentage of 79 House Finches (*Haemorhous mexicanus*) first detected at a block (A, B, or C) that were later detected at other study blocks.

	Block of initial detection (feeder density treatment)		
	Block A (high)	Block B (low)	Block C (high)
Block moved to			
A (high)	—	9/19 (47.4)	1/44 (2.3)
B (low)	2/16 (12.5)	—	2/44 (4.5)
C (high)	9/16 (56.3)	3/19 (15.8)	—

Note: Movements in shaded cells were all movements into high feeder density blocks (from blocks of either treatment type).

House Finches in year 1 (see the Results), this block was not used in year 2 and was removed from all statistical analyses.

In year 1, both sites within a block received the same experimental treatment (high or low feeder density). 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 NW and SE areas (Fig. 1A). Because only six sites were used in year 2, treatments were randomly assigned within blocks to account for geographic differences, such that one site within each block was a low-density feeder treatment and one site was a high-density feeder treatment (Fig. 1B). Thus, between years, half of the sites switched to a different feeder treatment, whereas the other 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 by two primary methods. First, we trapped at all sites twice weekly (see the Experimental timeline), ensuring that weekly trapping effort was equal across high-density and low-density feeder sites. Second, we continuously tracked feeding behaviors of all banded birds using 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 to occur in free-living House Finches (Altizer et al. 2004). Even though observed cases of disease in this study were limited (see the Results), we can use these results to understand the possible implications that changes in House Finch behavior and condition in response to feeder density may have on MG transmission.

Experimental timeline

In two consecutive fall seasons, tube-style feeders were put up at all sites and kept filled with black-oil sunflower (*Helianthus annuus* L.) seeds 1 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 1 month of baseline trapping and RFID data collection, we increased feeder density to three feeders, each spaced 3 m apart in a straight line parallel to the nearest tree line, at half of the sites. Thus, high-density feeder sites had a total of six available feeder ports equipped with RFID antennae, whereas low-density feeder sites had two available feeder ports equipped with RFID antennae. All feeders were kept full throughout the study, such that the food rarely to never fell below the level of all available feeding ports.

In both years, we trapped birds at each site twice weekly for 3–4 h beginning at sunrise. On any given day, trapping effort (both the number of hours that traps or nets were open and the total number of traps or nets) was equalized across treatments. We conducted most trapping using baited cage traps, but mist nets were also occasionally used to try and increase trapping success. When using baited cage traps, we set only one trap per site regardless of feeder-density treatment. While trapping at high-density feeder sites, the two extra feeders were covered 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 U.S. Fish and Wildlife Service band and a small (2 mm × 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* Linnaeus, 1758), which are comparable in size to House Finches (Nicolaus et al. 2008). Upon all initial and subsequent captures, we measured mass and tarsus length. Blood was drawn from all individuals who had not been captured previously or had not had their blood sampled within the prior 14 days. Using 26-gauge needles, blood samples (approximately 100 μL) were taken from the brachial vein and collected in heparin-coated capillary tubes. Capillary tubes were stored on ice until the plasma could be separated via centrifugation, typically within 2–4 h after sampling. Plasma was then separated out and stored in a –20 °C freezer until we ran enzyme-linked immunosorbent assays (ELISA) to quantify the concentration of MG-specific antibodies (as per Hawley et al. 2011). Finally, all birds were examined for clinical signs consistent with MG infection (i.e., conjunctivitis).

Birds were captured under Federal Bird Banding Permit 23513 and Virginia Department of Game and Inland Fisheries Bird Banding permits (056090 and 061440). All animal procedures were in accordance with U.S. regulations regarding animal care and were approved by Virginia Tech's Institutional Animal Care and Use Committee prior to the initiation of the work.

Statistical analyses

We observed very low House Finch activity at sites D1 and D2 in year 1, with only one bird captured at either site after 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 been 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. Therefore, our final data set for analysis included six sites per year, with an unbalanced design in year 1 after the elimination of sites D1 and D2 and a balanced design in year 2 with three low-density feeder sites and three high-density feeder sites (Figs. 1A and 1B).

Although our sites were not fully statistically independent in the sense that birds could and did move between them, our unit of replication for all analyses except capture rate was the individual, and the endpoints of primary interest (behavior, residual body mass) are temporally dynamic and thus representative of the treatment experienced at the time of sampling. Antibody responses to MG are the least dynamic; thus, we likely had low statistical power to detect relationships between feeder treatment and antibody response in our study. Nonetheless, the majority of individuals in our study (~73%; Table 1) remained within a single treatment block or moved to a block of identical feeder-density treatment (~9%; Table 2), such that ~82% of birds that met our RFID inclusion criteria (see below) used the same feeder density throughout the study. This suggests our treatments were largely independent while also allowing us to examine movements between them. Finally, for the analyses of capture rate where site was the unit of replication, we had two years of data, whereby half of the sites switched feeder treatments between years (see Experimental design).

We calculated residual body mass as a surrogate for "body condition" to account for variation in structural size (Brown 1996). We regressed body mass at capture onto tarsus length and took the residuals of the relationship as our metric of residual body mass. Because residual body mass can be misleading (e.g., Green 2001),

we also modeled raw body mass alone. The effects of treatment on both metrics (residual and raw body mass) were modeled for all birds captured after manipulation using linear mixed-effects models (LMMs). We included feeder-density treatment, year of capture, the pairwise interaction between year and treatment, and time of day of capture (which is known to influence body mass) as fixed effects and capture site and individual ID as random effects. For this and all other models (except capture rate, where our dependent variable was not an individual-level metric), we initially included sex and its interaction with treatment as fixed effects. However, because sex alone or in interaction with treatment was never significant ($p > 0.05$), we removed it from our final models.

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 an LMM including feeder-density treatment, year of capture, and the pairwise interaction between year and treatment as fixed effects and capture site as a random effect.

To assess the effect of treatment on foraging behavior and bird movement, we quantified feeding bouts, time spent on feeders, and movement among sites using RFID data. For these analyses, we only included individual birds with RFID detections for >1 unique day and for a minimum total of 10 unique feeder bouts over the course of the study. We defined a bout as any time a House Finch was recorded on the same feeding port continuously for a minimum of 3 s. To account for missed RFID reads, we defined multiple bouts by the same individual at the same port only if there was a 4 s 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 a single individual from this analysis 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, as well as no reads at our low-density feeder sites in that year, all RFID analyses were limited to year 1 of the study.

We conducted analyses of mean time spent on feeders per day using LMMs and $\log_{10}$ transforming the response variable. We conducted analyses of feeding bout duration using generalized linear mixed models (GLMM) with a gamma distribution and a log link. For both models, we included feeder-density treatment as a fixed effect and site and individual ID as random effects to account for repeated detections of the same individuals and variation among sites.

We also used RFID data to explore whether feeder density influenced House Finch movement among blocks in year 1. We accounted for our unbalanced design in year 1 and the spatial arrangement of sites by first considering that birds initially observed in block B had the option of two movements to neighboring blocks, either to the north or to the south (Figs. 1A and 1B), whereas birds initially observed in block A or block C could only move in one direction to reach a neighboring block. Thus, for our first movement analysis, birds in block B were replicated in our data set, with each potential movement considered to be independent. However, we included individual ID as a random effect in our model to account for statistical non-independence of movements by the same individual. We then analyzed the probability (0 or 1) of an individual moving to a neighboring block using a GLMM with a binomial distribution and a logit link with the first feeder-density treatment visited as a fixed effect. For our second movement analysis, we considered raw rates of movement alone (Table 2) to ensure that our assumptions about the ability of birds in block B to move in either direction were not driving our results and to allow us to examine movements between non-neighboring blocks. Here, we statistically analyzed movements of birds initially observed only in block A or block C (both peripheral blocks, which controls for spatial arrangement) to ask whether birds from these blocks were more likely to later be observed at a closer block with lower feeder density (block B, which neighbored both block A and block C; Figs. 1A and 1B) or a farther block of similarly high feeder density (block A or block C). We defined the latter type (i.e., movement to the farther block of similarly high feeder density) as a "leapfrog" movement, given that birds had to pass over block B to move between block A and block C (Figs. 1A and 1B). We used a likelihood ratio χ^2 test to compare the proportion of birds initially detected in block A or block C who were observed to make leapfrog (from block A to block C or from block C to block A) versus neighboring movements.

For analyses of disease risk, we analyzed the concentration of MG-specific antibodies using an LMM, with feeder-density treatment as a fixed effect and individual ID as a random effect. Due to low physical recapture rates in this species, the vast majority of blood samples collected were from individuals that did not meet our RFID inclusion criteria. Thus, we were unable to include foraging behavior metrics as covariates in our antibody model.

We performed all analyses using R (R Core Team 2019) and the lme4 package (Bates et al. 2015), and all graphs show visualizations of raw data.

Results

Sample size

Over the course of 2 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 2 days of the study. Among those birds, we had >11 000 recorded feeding bouts.

Capture rates

On average, high-density feeder sites (HD) had almost twice as many captures per day relative to low-density feeder sites (LD) ($n = 69$ days; treatment HD estimate ± SE = 1.30 ± 0.86 and treatment LD estimate ± SE = 0.79 ± 1.50; $F_{[1,69]} = 5.59$, $p = 0.018$; Fig. 2). 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; $F_{[1,69]} = 1.87$, $p = 0.17$).

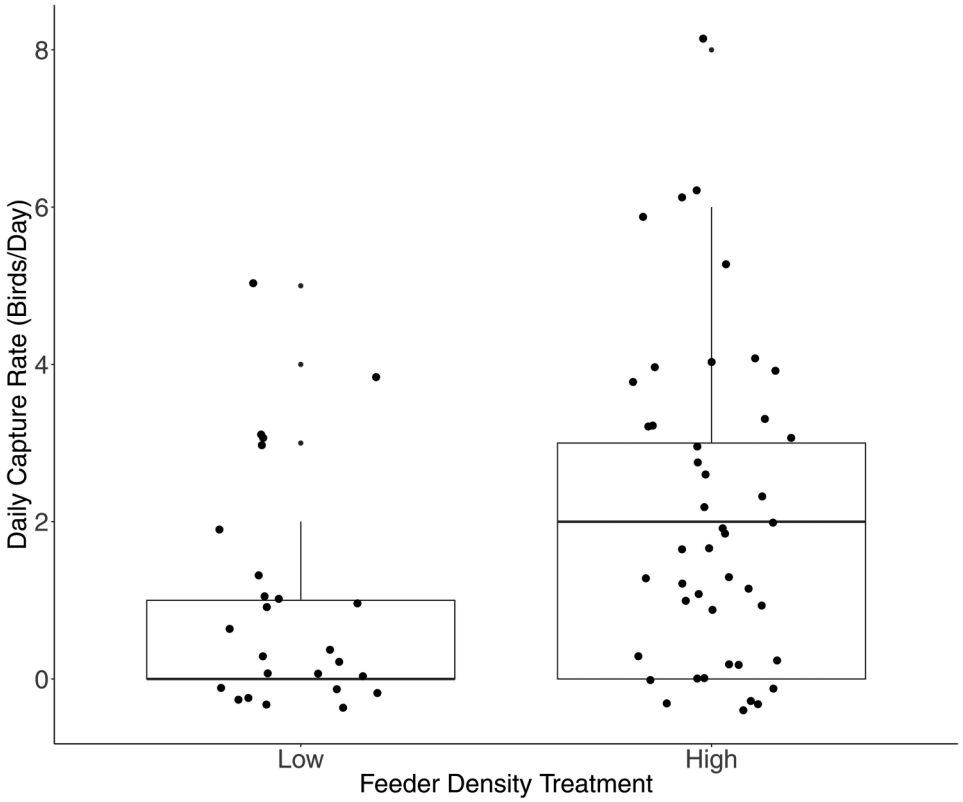
Body condition

On average, individual body condition was three times lower among birds captured at high-density feeder sites than at low-density feeder sites ($n = 128$; treatment HD estimate ± SE = –2.36 ± 1.04 and treatment LD estimate ± SE = 1.38 ± 0.95; $F_{[1,128]} = 4.85$, $p = 0.028$; Fig. 3). Year 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 ($F_{[1,128]} = 2.99$, $p = 0.08$). Results for feeder treatment were equivalent when raw rather than residual body mass was modeled ($p = 0.025$).

Foraging behaviors

Feeding bouts at high-density feeder sites were, on average, twice as long as those at low-density feeder sites ($n = 87$; treatment HD estimate ± SE = 2.15 ± 0.11 and treatment LD estimate ± SE = 1.02 ± 0.14; $F_{[1,79]} = 67.09$, $p < 0.001$; Fig. 4A). Similarly, feeder density strongly predicted the mean time per day spent on feeders, with birds at high-density feeder sites spending approximately three times as much time on feeders per day than birds at low-density feeder sites ($n = 87$; treatment HD estimate ± SE on $\log_{10}$-transformed response = 1.89 ± 0.06 and treatment LD estimate ± SE on $\log_{10}$-transformed response = 1.41 ± 0.10; $F_{[1,79]} = 17.4$, $p < 0.0001$; Fig. 4B).

Fig. 2. Daily capture rates (defined as the number of individuals caught per day at a given site) of House Finches (*Haemorhous mexicanus*) were higher at sites with high feeder density (n = 44 capture days) relative to sites with low feeder density (n = 25 capture days). Capture effort (both the total amount of time per day that traps or nets were open and the total number of days trapped at a site) was equivalent for sites with high and low feeder densities throughout the study. However, two sites with low feeder density (D1 and D2) were eliminated from the study post hoc to be conservative, resulting in unequal capture days across treatments despite equivalent effort (see the Materials and methods; note that inclusion of removed sites would only strengthen the treatment effect shown here). The thick horizontal line indicates the median, the box encompasses the 25th to 75th percentiles of the data, and the whiskers extend to points within 1.5 times the inter-quantile range.



Movements between treatments

House Finches that first visited the low-density feeder block were almost four times more likely to visit a neighboring block (i.e., one of different feeder density) at some point during the experiment than House Finches who first visited a high-density feeder block (n = 98; treatment HD estimate ± SE = −2.69 ± 0.73 and treatment LD estimate ± SE = 1.90 ± 0.70; $F_{[1,98]}$ = 8.72, p = 0.0064; Fig. 5). Similarly, when between-block movements were examined only for birds initially observed in the two peripheral blocks (block A or block C), birds were significantly more likely to make leapfrog movements to another high-density feeder block (i.e., from block A to block C or from block C to block A) than to move to the closer, neighboring block (i.e., block B) with low feeder density (Table 2; n = 120 potential movements from n = 60 individuals; likelihood ratio χ^2 = 4.44, p = 0.035). This result was driven by birds initially detected in block A, since birds from block C were rarely detected at other study blocks (Table 2).

MG-specific antibody concentrations

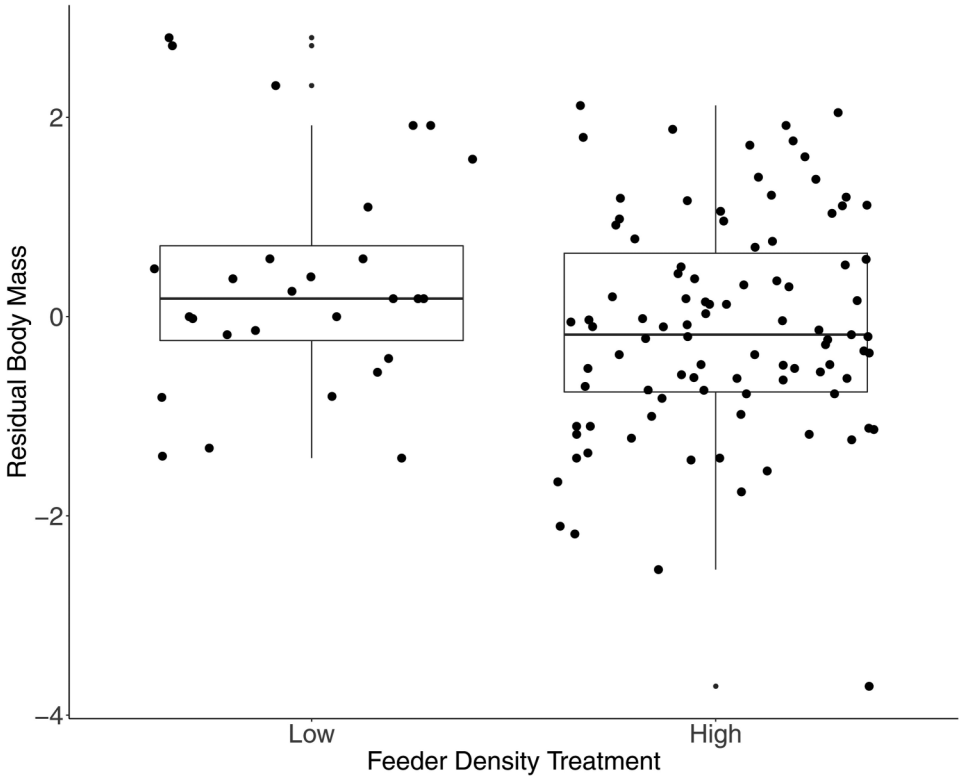
Disease prevalence was low overall, with only 5.2% of House Finches captured after manipulation with visible signs of disease. Potentially as a result of this low prevalence, we did not observe an effect of feeder density on the concentration of circulating MG-specific antibodies (n = 106; $F_{[1,106]}$ = 0.01, p = 0.91).

Discussion

This study experimentally examined how heterogeneity in the degree of anthropogenic feeding among sites, which is inherently variable for many supplemental food systems such as backyard bird feeding, affects the behavior and condition of a wild bird species that is largely dependent on supplemental food during the non-breeding season. We found that bird feeder density was associated with increased local abundance of House Finches and amount of time spent feeding, but decreased body condition. Given the importance of local abundance (Altizer et al. 2004) and time spent foraging at feeders (Adelman et al. 2015) for the acquisition and spread of a contagious bacterial pathogen in this species, our results suggest that variation in 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, House Finches at sites with higher feeder density had significantly longer mean feeding 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 sites with few feeders. 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 they do not record the amount of food consumed 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

Fig. 3. Residual body mass was lower for House Finches (*Haemorhous mexicanus*) captured at sites with high feeder density (n = 99) than at sites with low feeder density (n = 29). The thick horizontal line indicates the median, the box encompasses the 25th to 75th percentiles of the data, and the whiskers extend to points within 1.5 times the inter-quantile range.

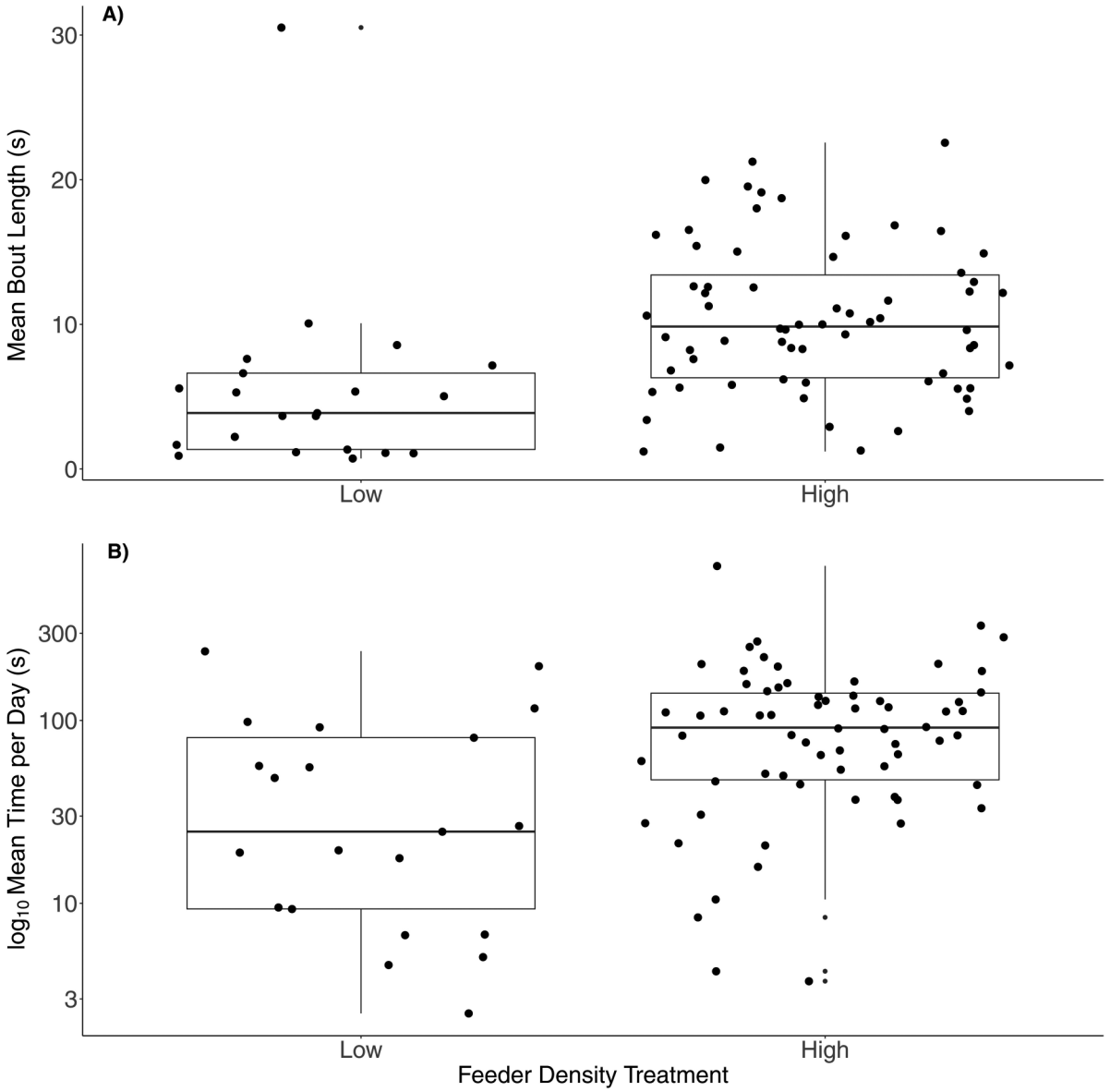


House Finches at low-density feeder sites. Our finding that body condition was lower at high-density feeder sites (see below), however, is not consistent with higher food intake at these sites. Nevertheless, given that past work identified time spent on bird feeders as the strongest predictor of an individual's risk of acquiring mycoplasmal conjunctivitis (Adelman et al. 2015), our results suggest that House Finches foraging at high-density feeder sites may be at higher risk of disease.

Feeder density had a significant effect on local House Finch foraging movements as well. Prior studies have shown that supplemental feeding can reduce local movements and thus contract home ranges (e.g., Boutin 1990; Roth and Vetter 2008). Because our study blocks were each approximately 1 km apart (Figs. 1A and 1B) and past work indicates that House Finches readily move up to 3 km between roosting and feeding locations in the non-breeding season (Dhondt et al. 2007*b*), we examined whether the feeder density treatment in the block where finches were initially detected 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, indicating that House Finches move from areas of low to high feeder availability more readily than the opposite. Similarly, we found that House Finches first detected at one of our two peripheral blocks were more likely to make leapfrog movements of almost 3 km in length to another high-density feeder block than they were to move to a neighboring block of lower feeder density. Thus, rather than feeders resulting in contracted home ranges as occurred in Dark-eyed Juncos (Roth and Vetter 2008), House Finches appear to sufficiently prefer sites with a higher number of feeders that they travel farther to forage at those sites. One caveat of the use of RFID technology, where detections of individual movement rely on the presence of an antenna at a site, is that we were unable to determine to what extent House Finches in our study used other sources of supplemental food (e.g., feeders at nearby private residences). Future work using other tracking methods such as radio transmitters would allow movements to sites other than those directly monitored in our study to be accounted for, providing a more complete picture of the extent to which House Finches trade off travel distance with patch quality when foraging. Overall, 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). Thus, more research is needed to understand how variation in the presence, extent, or quality of supplemental bird food alters local movements of House Finches, as studied here, as well as larger scale movements across the landscape.

We also examined the potential effects of feeder density on House Finch condition, measured by residual body mass. In contrast to our predictions and one prior study on a suite of bird species in North America (Wilcoxen et al. 2015), we found that House Finches at high-density feeder sites had poorer residual and absolute body mass than finches at low-density feeder sites. Notably, the sites used in Wilcoxen et al. (2015) experienced a severe drought during much of the study, which may partly explain the discrepancy with our results, if feeders only result in elevated residual body mass under challenging environmental conditions. Similar to our results, prior work by Galbraith et al. (2017*a*) found that House Sparrows (*Passer domesticus* (Linnaeus, 1758)) captured at sites with experimental bird feeders in New Zealand had lower scaled mass indices than House Sparrows at sites without supplemental food, though this difference was specific to season. Patterns of lower body mass in the presence of higher degrees of supplemental food are somewhat surprising, particularly given our behavioral results that House Finches at high-density feeder sites had longer foraging bouts and spent more time on feeders

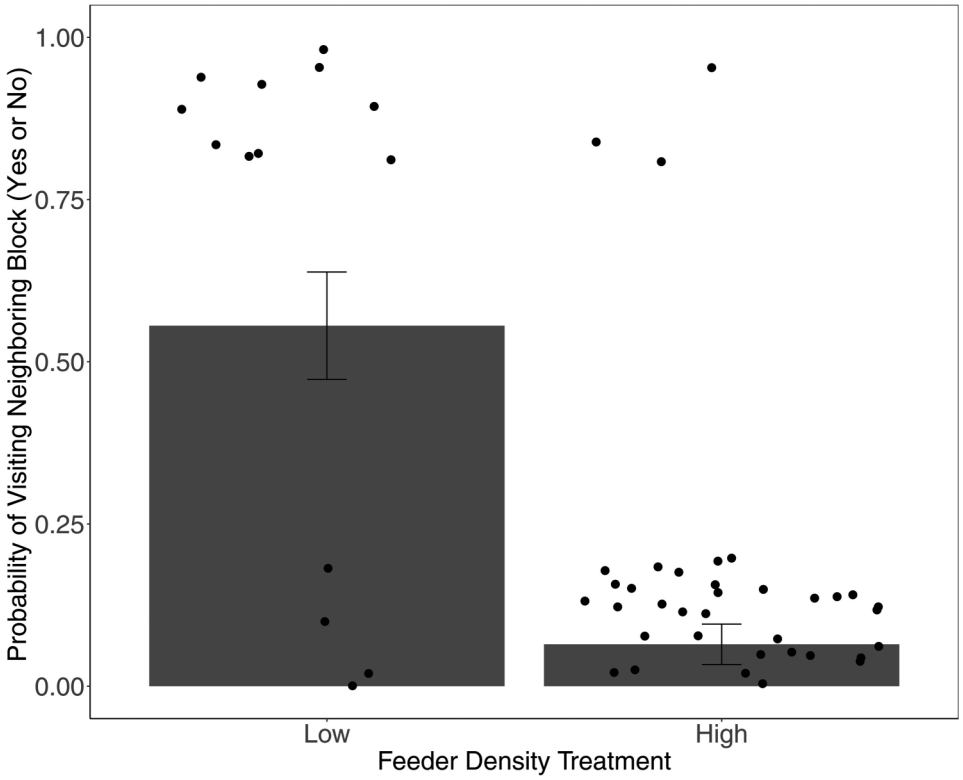
Fig. 4. Mean bout lengths (A) and mean time per day on feeders (B) were significantly longer for House Finches (*Haemorhous mexicanus*) at sites with high feeder density (n = 66) relative to those at sites with low feeder density (n = 21). The thick horizontal line indicates the median, the box encompasses the 25th to 75th percentiles of the data, and the whiskers extend to points within 1.5 times the inter-quantile range. Mean values for both foraging variables were quantified for the 79 unique individuals that met our RFID inclusion criteria. For the small subset (n = 4) of these individuals who used sites with both high and low feeder densities, mean values from both feeder treatments were included in the analysis (with non-independence accounted for in the model), resulting in a total sample size of n = 89 for each analysis.



per day. However, there are several possible mechanisms that can underlie patterns of lower mass with higher degrees of supplemental food. First, small wintering birds are predicted to lower their body mass when food availability is stable (Lima 1986) owing to trade-offs between the need to store body fat to counteract food unavailability and the risk of predation when body mass is too high to readily escape (Rogers 2015). In line with this idea, experiments in European Starlings (*Sturnus vulgaris* Linnaeus, 1758) found that food-deprived individuals had increased body mass because they had stored more fat (Witter et al. 1995). The reduced movement that we detected 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, leading them to retain a lower body mass relative to House Finches at low-density feeder sites. 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 residual body mass are more likely to seek out high-density feeder sites. Finally, our index of condition should be interpreted with some caution because the use of residual body mass as a condition index has been previously criticized due to a number of assumptions, including likely non-linearity in the relationship between structural size and body mass (e.g., Green 2001; Peig and Green 2010). Although the use of residual body mass has been shown to be robust to these assumptions in several small-mammal species (Schulte-Hostedde et al. 2005; but see McGuire et al. 2018) and one songbird species (Ardia 2005), future work should examine whether absolute or residual body mass is predictive of relative fat stores in wintering House Finches.

We used capture rate as a proxy for local site abundance and found significantly higher capture rates at high-density feeder

Fig. 5. House finches (*Haemorhous mexicanus*) initially detected at sites with low feeder density (n = 36) via RFID were more likely to visit a neighboring experimental block (of distinct feeder density) than House Finches initially detected at sites with high feeder density (n = 62). Raw means of movement (yes or no) and standard errors that are normal approximations of the binomial proportion interval are presented. Although only the 79 unique individuals that met our RFID inclusion criteria are represented, individuals that were initially observed in the centrally located block B (n = 19) were uniquely able to move to neighboring blocks in either direction; thus, each type of movement was included separately in the analysis for these 19 individuals to account for the unbalanced design (see the Statistical analyses).



sites. Thus, there appear to be more House Finches, on average, present around high-density feeder sites than low-density feeder sites. These results are consistent with prior field correlations showing significantly higher House Finch abundance at sites where feeders are present versus absent (Mertz and Brittingham 2000). Interestingly, the higher number of individuals at high-density feeder sites in our study 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; 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. 2004; Hochachka and Dhondt 2000, 2006), the increased local abundance of House Finches at high-density feeder 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 were unable to draw definitive conclusions about MG transmission due to low overall prevalence of MG during the study and low physical recapture rates of House Finches, which limited the majority of our antibody sample collections to fairly early in the feeder-density manipulation period. We observed few instances of visible pathology (5.2%) during the treatment period in both years. Given the low apparent prevalence of MG and the timing of blood sample collection in our study, the measured antibody concentrations may reflect exposure during prior epidemics, rather than during our experimental manipulations. 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.

Overall, our results suggest that variation in 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. Although our study was unable to detect differences in MG prevalence across feeder density, the striking differences in foraging behaviors that we know are important to transmission in this species (Adelman et al. 2015) suggest that variation in feeder density may have important implications for MG spread in regions or years with higher MG prevalence than occurred in our study. Because House Finches spend more time on feeders at high-density sites and because high-density feeder sites appear to be more attractive to birds foraging nearby, backyards with many bird feeders could act as hubs of disease outbreaks through two mechanisms. First, sites with many feeders appear to draw in larger numbers of House Finches, fueling higher local densities of susceptible individuals (Altizer et al. 2004). Second, high-density feeder sites facilitate individual behaviors (i.e., more time on bird feeders) that past work showed to be associated with a higher risk of acquiring and spreading MG (Adelman et al. 2015). However, further work is needed to determine whether the behavioral differences associ-

ated with high bird feeder density in our study actually translate into differences in disease risk in House Finches. Given the enormous popularity and inherent heterogeneity of backyard bird feeding (e.g., Plummer et al. 2019) and other forms of supplemental feeding of wildlife (e.g., Yoda et al. 2012), it is critical that future work explore how heterogeneity in supplemental food availability over space and time impacts wildlife behavior and ecology in ways relevant for fitness.

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