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Mycoplasmal Conjunctivitis and the Behavior of Wild House Finches (*Carpodacus mexicanus*) at Bird Feeders

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Parasite infections can influence host foraging behavior, movement, or social interactions. House finches (*Carpodacus mexicanus*) in the US are susceptible to a recently emerged strain of the bacteria, *Mycoplasma gallisepticum*. Infected birds develop mild to severe conjunctivitis that could affect their foraging or social behavior. We videotaped house finches with and without conjunctivitis at a bird feeding station in Atlanta, GA to determine whether birds with conjunctivitis differed in feeding duration, efficiency, total food intake, or aggressive interactions. We observed 105 house finch feeding bouts (of which 41% were of birds with conjunctivitis). Infected birds spent more time at the feeding station and had smaller average and minimum flock sizes. House finches with conjunctivitis also showed lower feeding efficiency than noninfected birds in terms of seeds obtained per attempt and number of seeds eaten per unit time. However, because of their longer feeding bouts, birds with conjunctivitis consumed similar total numbers of seeds as birds without conjunctivitis. Finally, house finches with conjunctivitis were displaced from feeder perches less frequently than noninfected individuals and 75% of all observed displacement events consisted of an infected bird displacing a noninfected bird. Differences in flock sizes and feeding behavior of birds with and without mycoplasmal conjunctivitis could influence the fitness effects and transmission of this bacterium in wild house finch populations.

Key words: Infectious disease; Host behavior; *Mycoplasma gallisepticum*; Feeding behavior; Aggression

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Infection by pathogens can influence the behavior of animals, often in ways that increase disease transmission (Moore, 1984, 2002). These behavioral changes induced by parasites have been documented in a variety of species, including birds (Lindström, Van der Veen, Legault, & Lundström, 2003; Moore, 2002). In some cases, changes in host behavior following infection might increase parasite transmission opportunities, especially if they increase the probability of contact between diseased and healthy animals (Bakker, Mazzi, & Zala, 1997; McClain, Magnuson, & Warner, 1988; Moore, 1984). In other cases, behavioral changes resulting from parasite infection can decrease transmission opportunities. For example, common greenfinches (*Carduelis chloris*) infected with Sindbis virus are less active and move shorter distances, which could increase their risk of predation and hence reduce parasite prevalence (Lindström et al., 2003). Indeed, reduced host activity is a common physiological response to parasite infections in birds and other animals that should generally lower host contact rates and limit disease spread (Ewald, 1994).

House finches (*Carpodacus mexicanus*) in eastern North America are susceptible to a newly emerged strain of the poultry bacterium, *Mycoplasma gallisepticum* (MG), that has caused density-dependent declines in house finch abundance of up to 60% in recent years (Dhondt, Tessaglia, & Slothower, 1998; Fischer, Stallknecht, Luttrell, & Dhondt, 1997). A recent large-scale study of house finches across eastern North America showed that seasonal outbreaks occur each year, with prevalence increasing during the fall and winter months (Altizer, Hochachka, & Dhondt, 2004). Birds infected with MG develop red, swollen tissues with discharge around one or both eyes that can last for 6 weeks or longer (Kollias et al., 2004; Luttrell, Stallknecht, Fischer, Sewell, & Kleven, 1998; Roberts, Nolan, & Hill, 2001). The social nature of house finches and their propensity to aggregate at backyard bird feeders during the fall and winter months is thought to increase transmission opportunities of this pathogen among individual birds (Hartup, Mohammed, Kollias, & Dhondt, 1998). Severe physical signs, including conjunctival edema, closed eyelids, and depressed motor activity could negatively affect the foraging behavior or locomotion of infected birds.

House finches and mycoplasmal conjunctivitis are rapidly becoming a model system for studying the ecology of wildlife diseases, in part because infection with MG is readily apparent (Hartup, Bickal, Dhondt, Ley, & Kollias, 2001; Ley, Swarthout, Sydenstricker, Kollias, & Dhondt, 2003), and also because house finches are easy to observe at backyard bird feeders. Recent studies have demonstrated negative effects of this disease on host survival (Faustino et al., 2004), population size (Hochachka & Dhondt, 2000), body condition (Altizer, Davis, Cook, & Cherry, in press), and male plumage (Nolan, Hill, & Stoehr, 1998). Effects of MG on host foraging and social behavior also seem likely, but have not been explicitly tested to date. Because house finches spend a large amount of time at bird feeders during the fall and winter months, when disease transmission is likely to occur, comparison of feeding behaviors of birds with and without MG could identify parasite-induced changes in host behavior that might be important to disease spread. For example, if birds infected with MG spend more total time at bird feeders and contaminate feeders with infectious material, this could increase bacterial transmission to uninfected birds.

In this study we videotaped house finches visiting a backyard bird feeding station during a period of high prevalence of conjunctivitis to quantify the feeding behavior of birds with and without actual signs of infection. Specifically, we compared total feeding duration, feeding efficiency, feeding rate, total food intake, and perch displacement (i.e., where birds were forcibly displaced from their feeder perch by another bird). We also examined flock sizes associated with focal individuals with and without conjunctivitis. Because infected birds might experience impaired vision and lower physical activity (Kollias et al., 2004), we predicted that house finches with physical signs of conjunctivitis would remain longer at bird feeders than those without conjunctivitis, would be associated with lower average flock sizes, and would not be as efficient at procuring seeds as birds without conjunctivitis.

Methods

Feeding Station and Video Recording

The feeding station for this study was located in a suburban backyard near Atlanta, GA (USA). The feeding station consisted of two tube-style bird feeders mounted on a post, with five feeding ports in each feeder (Fig. 1). Each port had a small perch below it. Both feeders were kept filled with sunflower seeds, a favored food of house finches (Hill, 1993). We used a Sony Digital Handycam (Model DCR-TRV520 NTSC with 450× digital zoom) to record birds visiting the feeding station between October 5 and 14, 2002. All recording was conducted between 0900 and 1100 h. Recent studies showed that September and October are months with the highest prevalence of MG in this location (Altizer et al., in press), so recording during this time period allowed us to observe large numbers of birds with and without conjunctivitis. All recording was conducted on clear days for 1–2-h time intervals, between 0900 and 1200 h. Later, we transferred the video to a desktop computer to record behavior.

The use of video to record behaviors of birds at feeders is well established (Popp, 1986, 1989); it is especially useful for documenting behaviors of flocking birds and where slow-motion replays are often necessary. One drawback with this technique is that because birds can enter and exit the field of view of the camera during a given recording session, some birds might be observed more than once. To reduce this possibility, we captured and uniquely color-banded as many house finches as possible at this site prior to the recording dates of this study. Although we did not mark all birds, we identified at least 51 separate individuals across all videos, thus reducing the level of pseudoreplication caused by repeated observations of the same individuals.

Data Collected

For each individual house finch that entered the video camera's field of view (Fig. 1), we recorded the sex and presence of physical signs of conjunctivitis, which was readily observed in the birds' eyes. Sex was assigned based on the presence or absence of male plumage coloration. Because our study was conducted in October, most of the juvenile males had begun to molt into their adult male plumage by this time (A. K. Davis, personal observation). Further, although we did not assign infection status based on isolation or culture of MG, past data have shown a high correspondence between MG prevalence and the presence of clinical signs among wild birds (Hartup et al., 2001; Ley et al., 2003). Moreover, greater than 97% of a subset of house finches (*N* = 87) that were captured over a 2-year period at this site with no physical signs of conjunctivitis also tested negative for MG based on eye swabs examined via culture and PCR methods (D. H. Ley, unpublished data). Similarly, over 85% of a subset of birds captured with clinical conjunctivitis also tested positive for MG based on eye swabs (*N* = 75).

Figure 1. Feeder configuration for videotaping house finches. Each feeder had a total of five feeding ports (one port per feeder was removed) and was kept filled with sunflower seeds.

For each bird, we recorded the total time spent at each feeder port (feeding duration), the number of times the bird inserted its beak into the feeder port (pecks), and the number of seeds eaten (determined when pieces of seed were observed falling from the beak of the focal bird). We also recorded whether the bird left the feeding station on its own, was displaced by another house finch, or if the bird was scared away (e.g., by a larger bird species, squirrel, etc.). For birds that were displaced by another house finch we recorded the infection status of the displacer. Because a large body of research has shown a positive relationship between flock sizes and feeding rates (Barnard, 1980; Beauchamp, 1998; Beauchamp, & Livoreil, 1997), we recorded the number of other house finches feeding at the same time as the focal individual, including the flock size at the start of each feeding bout, the maximum flock size, and the minimum flock size during the bout. It should be noted here that since there were only five available feeding ports in each feeder, the number of house finches we observed at one time in our video was rarely greater than 10 individuals. Therefore, our flock size indices, while useful for this study, may not represent the true flock sizes of house finches in our area.

Data Analysis

We first used a multivariate analysis of variance to examine how flock size at feeders covaried with the sex and infection status of individual birds (ANOVA model: flock size = sex + infection status). Four separate measures of flock size (mean, minimum, maximum, and starting flock size) were used as dependent variables. Flock sizes were log-transformed prior to analysis to normalize the error variance. Because the two-way interaction effect between sex and infection status did not approach significance (i.e., $p > 0.75$), we did not include this interaction term in the final model.

To examine factors affecting feeding performance we conducted a multivariate ANOVA using each of the following dependent variables: feeding duration (log-transformed time at feeder), feeding efficiency (seeds eaten per peck), feeding rate (seeds eaten per minute), pecking rate (number of pecks at the feeder port per minute), and total seeds eaten (log-transformed). Only data for birds that made at least one peck were included in analyses. We originally tested the full ANOVA model (feeding parameter = sex + infection status + flock size + sex*infection status), with log-transformed average flock sizes included as a covariate. Because no test involving flock size or the sex*infection status interaction approached significance (i.e., $p > 0.25$), our final model excluded these two effects. All tests were performed using SPSS statistical software (SPSS, 2001).

Results

Flock Sizes and Infection Status

A total of 105 individual feeding bouts were observed over 6 days from approximately 9 h of recorded video. Mean flock sizes for all 105 individual feeding bouts ranged from 0.33 to 6.33 house finches (not counting the focal individuals). Birds with conjunctivitis were associated with significantly smaller minimum [$F(1, 104) = 6.891$, $p = 0.01$] and average flock sizes [$F(1, 104) = 4.10$, $p = 0.046$] (Fig. 2), but there was no difference in flock size between males and females. Moreover, there was no difference in the maximum and initial flock sizes of noninfected and infected birds (Fig. 2).

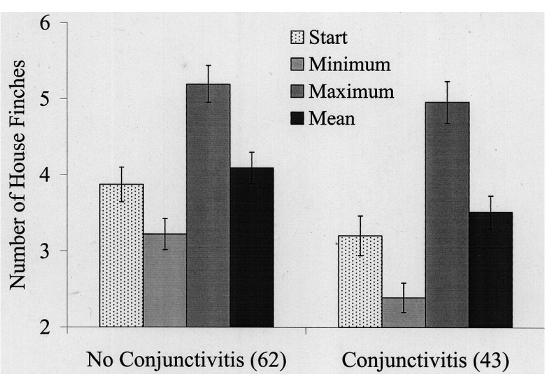

Figure 2. Flock sizes associated with house finches with and without conjunctivitis as observed in videos. Initial flock size is the mean flock size at the beginning of all feeding bouts. Also shown are the minimum and maximum flock sizes during the entire feeding bout, and the mean of all three flock sizes. Sample sizes shown in parentheses. Error bars are standard errors.

Conjunctivitis, Sex, and Feeding Behavior

Across all individual feeding bouts, 47 birds were recorded as females and 58 were males. Feeding bouts of female house finches were significantly longer (mean = 3.6 ± 0.37 min) than those of males (mean = 1.9 ± 0.26 min) [$F(1, 98) = 4.69$, $p = 0.033$]. Further, females tended to consume more seeds than males (14.6 ± 1.41 vs. 10.8 ± 1.34 seeds on average) per feeding bout [$F(1, 98) = 4.22$, $p = 0.042$]. With respect to conjunctivitis, 62 (59%) of the bouts we observed were from birds without conjunctivitis and 43 (41%) were from birds with conjunctivitis. Consistent with our expectations, house finches with conjunctivitis stayed at feeders an average of 2.12 min longer per bout than those without conjunctivitis [$F(1, 98) = 6.87$, $p = 0.01$] (Fig. 3A). Both efficiency [seeds eaten/peck: $F(1, 98) = 52.2$, $p < 0.001$] and feeding rate [seeds eaten/min: $F(1, 98) = 41.4$, $p < 0.001$] were significantly higher in birds without conjunctivitis than those with conjunctivitis (Fig. 3B, C). By comparison, there was no significant difference in the total number of seeds eaten during the entire feeding bout by birds with and without conjunctivitis (Fig. 3D), so that house finches with conjunctivitis consumed an average of 13.5 ± 1.39 seeds per feeder visit whereas finches without conjunctivitis consumed 11.8 ± 1.37 seeds per visit. There was no difference in number of pecks per minute between birds with and without conjunctivitis (Fig. 3E).

Displacement From Perches

Of all house finches that left the feeding station on their own or were displaced ($n = 66$), 42.4% had conjunctivitis. Among birds without conjunctivitis, 37% were displaced by another house finch, whereas 17% of birds with conjunctivitis were displaced by another house finch. This association between infection status and whether of not the bird was displaced by another finch showed a nonsignificant trend [$\chi^2(1) = 2.83$, $p = 0.092$]. Moreover, of the 19 house finches that were displaced, 75% were displaced by a house finch with conjunctivitis.

Discussion

Our data indicate that house finches infected with MG (as indicated by the presence of physical signs of conjunctivitis) behaved differently than nonin-

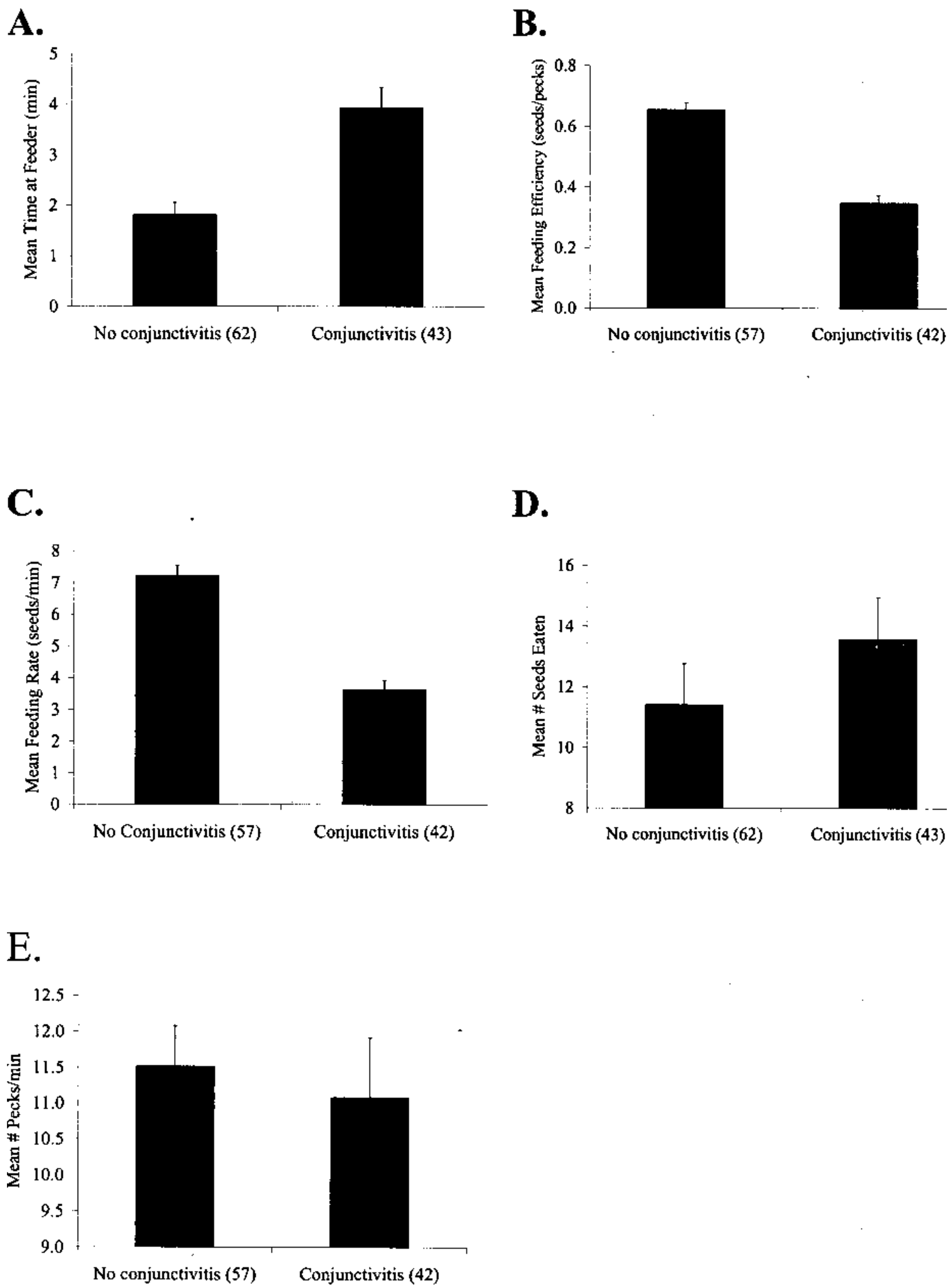

Figure 3. (A) average duration (in minutes) of feeding bouts; (B) average feeding efficiency (number of seeds eaten/number of feeder port pecks); (C) average feeding rate (seeds eaten/minute); (D) average number of seeds eaten per feeding bout; and (E) average number of pecks/min of house finches with and without conjunctivitis. Sample sizes shown in parentheses. Error bars represent standard errors.

fected birds at bird feeders. Infected birds were less efficient at procuring seeds than noninfected birds, perhaps because of their impaired vision. Thus, infected birds consumed fewer seeds per attempted peck than birds without conjunctivitis, and their seed intake rate per minute was much lower than healthy birds. Because infected birds made as many attempts at procuring seeds (pecks/min) as noninfected birds, we conclude that their lower seed intake rate was a consequence of their reduced efficiency in handling or consuming the seeds.

Previous studies have estimated that house finches are required to consume an average of one seed every 3 min to meet their energy requirements during a given 24-h period (Benkman, & Pulliam, 1988). However, their diverticular pouches, which allow them to store uneaten seeds for short intervals, enable finches to concentrate their feeding bouts and store seeds to be eaten later. In our study, birds without physical signs of conjunctivitis consumed an average of 12 seeds per 1.8-min feeding bout, which suggests that they were filling their storage pouches rather than actually eating the seeds.

Because birds with conjunctivitis were less efficient at obtaining seeds, it is likely that they were forced to remain longer at the bird feeders to consume the same total number of seeds as noninfected birds. These longer feeding bouts of infected birds could translate to greater opportunities for parasite transmission through increased contamination of feeder ports that are subsequently contacted by susceptible birds. However, longer feeding bouts of house finches with conjunctivitis could also be caused by reduced physical activity or movement resulting from infection. Previous studies of captive house finches and other bird species with experimental or natural infections showed that reduced activity levels are a common result (Lindström et al., 2003; Tell, Woods, Foley, Needham, & Walker, 2003). Finally, infected house finches with impaired vision might also have remained at feeding stations because of a lower probability of relocating feeding stations. Thus, birds with severe conjunctivitis were often seen struggling to locate perches and hovering around feeders, as though they were unable to visualize landing sites (A. K. Davis, personal observation). This could also explain the greater levels of aggressive behavior among infected individuals. Infected birds might have more actively defended their own perches and neighboring perches to avoid losing their feeding position (but see alternative explanation below).

Flock sizes of house finches also depended on whether or not focal birds exhibited physical signs of conjunctivitis. Initial and maximum flock sizes did not differ between the two groups, indicating that infected birds did not arrive with fewer birds, and were frequently joined by large flocks during their feeding bouts. However, the minimum flock sizes of infected birds were notably lower than for birds without conjunctivitis, consistent with the observation that infected house finches remained at feeders long after other individuals left (A. K. Davis, personal observation).

The fact that females spent nearly twice as long at the feeding station than males was surprising, but it is consistent with previous studies of the prevalence of mycoplasmal conjunctivitis. A recent epidemiological study of house finches infected with MG in Atlanta, GA showed that during severe outbreaks, prevalence and severity of physical signs was higher among juvenile females than any other age-by-sex category (Altizer et al., in press). Although we could not distinguish juvenile and adult birds from the videos in the present study, house finch flocks during the fall months are dominated by juveniles (Hill, 1993). If the majority of female birds in our videos were juveniles, then their longer feeding durations could increase their risk of exposure to the MG bacterium through contacts with other infected birds or by visiting contaminated feeding ports. Our finding of females remaining longer at feeders than males could also indicate a higher energetic demand in females at this time of year, or it may be a consequence of female dominance in this species (Brown, & Brown, 1988; McGraw, & Hill, 2002).

As a final point, it is important to note that several possible explanations could account for behavioral differences between house finches with and without conjunctivitis. It is not clear whether parasite-induced changes in host behavior are driven by selection on parasite transmission or are a side effect of pathology or the hosts' response to infection (Levri, 1999; Poulin, 1995). Moreover, ecological correlations between infection status and behavior could be due to parasite effects on host activity, but could also result from hosts that behave in certain ways (e.g., spending more time at feeders, or engaging more frequently in displacement behaviors) being more likely to acquire infections. For example, it is possible that the reason we observed so many displacement events involving an infected bird replacing an uninfected bird could be because individual house finches that frequently displaced other birds from perches were themselves more likely to encounter the bacterium. Thus, differences in behavior between noninfected and infected birds could point to host traits that increase exposure or susceptibility to the bacterium, or to the direct consequences of infection for individual birds, and distinguishing between these two hypotheses would require more detailed studies of captive or wild individuals before and after infection.

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