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Transmission-relevant behaviours shift with pathogen infection in wild house finches (*Carpodacus mexicanus*)

D.M. Hawley, A.K. Davis, and A.A. Dhondt

Abstract: Host individuals who are infected with a pathogen may alter their behaviour in ways that influence transmission. We observed a marked population of house finches (*Carpodacus mexicanus* (Muller, 1776)) in Ithaca, New York, to test whether individuals change their behaviour at feeding stations when infected with a prevalent bacterial pathogen, *Mycoplasma gallisepticum* (MG). We found that house finches with conjunctival lesions consistent with MG infection fed for longer bouts of time than individuals without conjunctivitis. Furthermore, the same individuals that were observed both with and without conjunctivitis during 3 years of study were more likely to feed alone and associated in significantly smaller flocks when conjunctivitis signs were present. These results suggest house finches alter their foraging and social behaviour at feeding stations when visibly infected with MG. Since MG transmission is thought to primarily occur at feeders, these changes in host behaviour likely have important consequences for MG transmission dynamics.

Résumé : Les hôtes individuels qui sont infectés par un agent pathogène peuvent modifier leur comportement de manière à en affecter la transmission. Nous avons observé une population de roselins familiers (*Carpodacus mexicanus* (Muller, 1776)) à Ithaca, New York, afin de vérifier si les individus changent leur comportement dans les mangeoires lorsqu'ils sont infectés avec une bactérie pathogène commune, *Mycoplasma gallisepticum* (MG). Les roselins familiers portant des lésions à la conjonctive compatibles avec une infection à MG ont des épisodes alimentaires plus longs que les individus sans conjonctivite. De plus, les mêmes individus, qui ont été observés au cours des 3 années de l'étude avec et sans conjonctivite, ont plus tendance à se nourrir en solitaires ou en groupes significativement plus petits lorsqu'ils possèdent des symptômes de conjonctivite. Ces résultats indiquent que les roselins familiers modifient leurs comportements alimentaires et sociaux dans les mangeoires lorsqu'ils sont manifestement infectés au MG. Puisque l'on croit que la transmission de MG se fait principalement aux mangeoires, ces changements de comportement de l'hôte ont vraisemblablement des conséquences importantes sur la dynamique de la transmission de MG.

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Introduction

Host behaviour can respond to pathogen infections in ways that influence transmission (Kulkarni and Heeb 2007). Although many pathogens alter host behaviour to adaptively increase their transmission (Poulin 1994), the majority of behavioural changes appear to be host-induced side effects of infection that may either help or hinder pathogen transmission (Moore 2002). The initial studies of "sickness behaviour", or changes in host behaviour following pathogen infection, were primarily done on mammals and lizards (reviewed in Johnson 2002), and only recently have pathogen-associated behavioural changes been examined in wild birds (Righi and Gauthier 2002; Lindström et al. 2003). Understanding how host behaviour shifts in response to pathogen infection is critical for identifying the factors that influence pathogen transmission in wild bird populations.

House finches (*Carpodacus mexicanus* (Muller, 1776)) are a particularly interesting species for asking questions about pathogen infection and host behaviour. The eastern North American population of this species was recently colonized by a bacterial pathogen, *Mycoplasma gallisepticum* (MG), that causes mild to severe conjunctival swelling (Ley et al. 1996), as well as marked increases in lethargy (Kollias et al. 2004). Since the initial observations of house

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finches with mycoplasmal conjunctivitis in 1994, the pathogen spread rapidly throughout eastern North America (Dhondt et al. 1998) and reduced the expanding eastern house finch population by up to 60% (Hochachka and Dhondt 2000). Several lines of evidence suggest house finch behaviour at feeders is important to the spread of MG, which can occur either directly or indirectly (= fomite transmission). First, MG infection is most prevalent during the nonbreeding season when house finches are highly gregarious (Hill 1993), and the prevalence of MG increases with flock size in some geographic regions (Altizer et al. 2004). Second, heterospecifics who feed sympatrically with house finches show occasional MG lesions or antibodies, suggesting secondary transmission occurs regularly at feeders (Hartup et al. 2000, 2001*b*). Third, an epidemiological study (Hartup et al. 1998) found significant associations between certain types of feeders and mycoplasmal conjunctivitis presence in house finches. Finally, infection of naïve house finches via MG-contaminated feeders has been demonstrated experimentally and the infectivity of feeder-deposited MG declines rapidly with time (Dhondt et al. 2007). Taken together, these results suggest house finch behaviour at feeders likely plays an important role in MG transmission, and any change in feeding behaviour among infected birds could have important impacts on MG transmission and resulting disease dynamics.

Given the close correlation between the visible eye lesions and the confirmed presence of MG in the eye by polymerase chain reaction (Hartup et al. 2001*a*), simple feeder observation of disease can be used to identify individuals who are likely infected with MG. In this study, we examine whether MG infection, as measured by the presence of visible eye lesions, alters two components of house finch behaviour that might directly impact the ability of MG to spread at feeders: (1) the amount of time infected individuals spend feeding and (2) the number of flock mates with which infected individuals are associated. A single previous study in Atlanta, Georgia, showed house finches with mycoplasmal conjunctivitis fed for longer periods of time and associated in smaller flocks than individuals without signs of conjunctivitis (Hotchkiss et al. 2005). However, this study did not observe marked individuals, and was therefore limited by potential pseudoreplication and the inability to eliminate the alternative hypothesis that house finches which feed for longer periods of time or associate in smaller flocks are more likely to acquire mycoplasmal conjunctivitis. Our study uses repeated observations of marked individuals to infer the effect of mycoplasmal conjunctivitis on house finch behaviour.

We use two sets of field observations to address our questions. First, we observed marked house finches in the nonbreeding season and compared the feeding behaviour of individuals with and without physical signs of conjunctivitis. Second, we used flock-size observations of marked individuals who were observed both with and without conjunctivitis to examine whether the same individuals associated in smaller flocks when disease signs were present. House finch flocks have a loose social structure but are highly fluid in membership, leading to rapid shifts in flock size and composition at a feeding station (A. Dhondt and C. Jennelle, unpublished data). With the flock-size observations, we were able to use an individually based approach to more directly test the impact of disease on dynamic changes in social behaviour.

Materials and methods

Capture and marking

House finches are small (20 g), sexually dichromatic, passerine birds that regularly visit feeding stations throughout eastern North America (Hill 1993). Since 1999, we have captured house finches in Tompkins County, New York (42°51′N, 76°34′W), using mist nets and hand-built cylindrical wire-mesh cage traps under permits from the New York State Department of Environmental Conservation (No. LCP 99-039) and the US Fish and Wildlife Service (PRT 802829). We marked individuals using unique combinations of three plastic coloured bands and a single nine-digit numbered aluminium leg band (Bird Banding Laboratory, Laurel, Maryland). We conducted all procedures involving live animals in accordance with protocol 00-90 approved by the Cornell University Institutional Animal Care and Use Committee.

Feeding observations

In January–April 2001, we observed marked house finches at a feeding site (Cornell Laboratory of Ornithology Observatory) in Tompkins County, using a spotting scope and (or) binoculars from a blind observation window. The feeding station consisted of three tube feeders filled with sunflower seeds, in a total area approximately 5 m^2 large. From 0800 to 1200 eastern standard time (EST), we began observing house finches as soon as they approached the feeding station and recorded their behaviour until they were no longer visible. We recorded each individual's behaviour at 30 s intervals by observing whether the individual was (*i*) feeding or (*ii*) perching nearby. We also recorded sex, conjunctivitis status (the presence of conjunctivitis in either eye), and the number of times an individual moved between the feeder and the nearby perches. We quantified the proportion of time spent feeding as the proportion of total 30 s intervals that an individual was on the feeder and the movement rate as the number of movements between feeders or perches divided by the total number of 30 s intervals at the feeding station.

Flock-size observations

We used a separate data set to examine changes in flock size within individuals who were observed both with and without conjunctivitis. As part of an ongoing mark–recapture effort to quantify survival rates in our local population (for further details see Faustino et al. 2004), we conducted standardized resightings of marked house finches from October to April in 2000–2003 at four identical feeding stations in Tompkins County. During a weekly 3 h interval between 0800 and 1200 EST, we recorded an individual's colour band combination, sex, conjunctivitis status, and flock size (the number of other house finches within a 1 m radius of the feeding station). We did not quantify individual feeding behaviour during standardized resightings. For the flock-size analysis, we removed any colour band combinations from

Table 1. Foraging behaviour of house finches (*Carpodacus mexicanus*) with and without physical lesions of mycoplasmal conjunctivitis (mean ± SE).

	Sample size	Total no. of 30 s intervals at the observation site	Proportion of time spent feeding (%)	Total no. of 30 s intervals spent feeding	Movement rate
No conjunctivitis	55	7.95±0.49	47±3	3.32±0.26	0.47±0.18
Conjunctivitis	18	10.12±1.71	64±7	6.37±1.41	0.36±0.25

Note: Movment rate is the number of movements between feeders or perches divided by the total number of 30 s intervals at the feeding station.

the database that were incomplete or inconsistent with our banding data (Milligan et al. 2003).

Statistical analysis

We analyzed the feeding observations in JMP® version 5.1 (SAS Institute Inc. 2002) and the flock-size analyses in SAS® version 9.1 (SAS Institute Inc. 2003). For the feeding observations, we independently examined the effect of sex and the presence of conjunctivitis on the following variables: total time spent at the feeding station (number of 30 s intervals), total time intervals spent feeding, proportion of time intervals spent feeding, and the movement rate. Because none of our dependent variables fit a normal distribution (Shapiro–Wilk hypothesis test, $P < 0.05$) and sample sizes were unequal across groups, we used nonparametric Wilcoxon rank sum two-sample tests for all comparisons. However, we present the mean ± SE of unranked values to facilitate interpretation of the data. Finally, since observation month did not significantly affect any of the feeding behaviours (Kruskal–Wallis, all $\chi^2 < 5.53$, df = 3, $n = 73$, all $P > 0.14$), we averaged multiple observations of the same individual to avoid pseudoreplication. Therefore, only a single value for each individual was included in the feeding analyses with the exception of two individuals who were observed both with and without conjunctivitis during separate observation periods. For these individuals, we included a single average value within each conjunctivitis state for all behavioural variables. Finally, we applied sequential Bonferroni corrections (Holm 1979) to our feeding behaviour hypothesis tests to reduce the probability of type I error while maintaining sufficient statistical power (Rice 1988).

We extracted 37 individuals from the flock-size data set that were observed both with and without conjunctivitis to ask whether the presence of conjunctivitis was associated with changes in flock sizes at the level of the individual. If we observed the same individual more than once in a single observation day ($n = 83$), we averaged observed flock-size values within that day. Individuals were observed on a total of 236 observation days within the 30 month study period; a few ($n = 5$) were observed only twice (once with and once without conjunctivitis), while the majority of individuals ($n = 29$) were observed between 3 and 11 times. Three individuals were observed >20 times, with a maximum value of 32 independent observations for a single marked individual. Overall, this gave us a powerful data set for examining how flock sizes change with mycoplasmal conjunctivitis at the level of the individual.

We natural log transformed observed flock-size values to meet the assumptions of parametric statistics; because of a large number of birds observed alone (flock size = 1), the transformed flock sizes showed significant negative kurtosis (two-tailed t test, $t_\infty = 5.23$, $P < 0.001$; Sokal and Rohlf 1998). Therefore, we restricted our parametric analysis to birds observed in groups (flock size ≥2) and conducted a separate logistic analysis that included birds observed alone. Taken together, we asked the following two questions about changes in house finch social behaviour. (1) Are individuals more likely to feed alone when displaying signs of conjunctivitis? (2) When observed in a social group (flock size ≥2), are individuals more likely to feed with fewer individuals when conjunctivitis signs are present? To address the first question, we conducted a logistic regression on the probability of being observed alone using the Glimmix macro in SAS® version 9.1, including individual as a random effect and month as a fixed effect because house finch flock sizes vary by season. For the second question, we performed a mixed general linear model on birds observed in groups (flock size ≥2), including individual as a random effect and month as a fixed effect. We also included an order term (1, conjunctivitis – no conjunctivitis; 2, no conjunctivitis – conjunctivitis) in our model to test whether individuals that were observed without conjunctivitis first ($n = 23$) showed the same directional shifts in behaviour as those observed with conjunctivitis first ($n = 14$). Because our data contained different numbers of observations for each individual, we applied the Satterthwaite approximation, which does not assume equal variances, to calculate the denominator degrees of freedom for our mixed model. Finally, we used the likelihood ratio test to evaluate the significance of the overall model compared with a null model.

Results

Feeding observations

We observed 73 individually marked house finches (18 with conjunctivitis, 55 without conjunctivitis) for the duration of their visit at the feeding station. We did not detect any significant differences between male and female house finches across any of the foraging behaviours: the total time intervals at the observation site, the proportion of time spent feeding, or the movement rate (Wilcoxon two-sample test; all $Z < 0.37$, df = 1, $n = 71$, $P > 0.72$). House finches with conjunctivitis spent the same number of total time intervals at the observation site as individuals without conjunctivitis (Table 1; $Z = 0.5$, $n = 73$, $P_{\alpha=0.05} = 0.61$). However, house finches with conjunctivitis fed for significantly longer bouts of time ($Z = 2.4$, $n = 73$, $P_{\alpha=0.025} = 0.02$) and therefore spent a larger proportion of their time at the observation site feeding (Table 1; $Z = 2.6$, $n = 73$, $P_{\alpha=0.0166} = 0.01$) than individuals without conjunctivitis. Furthermore, individuals with conjunctivitis moved less frequently between the feeder and the nearby perches than individuals without conjunctivitis ($Z = –2.5$, $n = 73$, $P_{\alpha=0.0125} = 0.01$).

During the feeding component of the study, we observed

Fig. 1. Change in flock size for 37 house finches (*Carpodacus mexicanus*) observed with and without mycoplasmal conjunctivitis (n = 37). The majority (27/37) of house finches associated in smaller average flock sizes when conjunctivitis lesions were present. The values represent the difference in average flock size for each individual, since many individuals were observed more than once in a single conjunctivitis state.

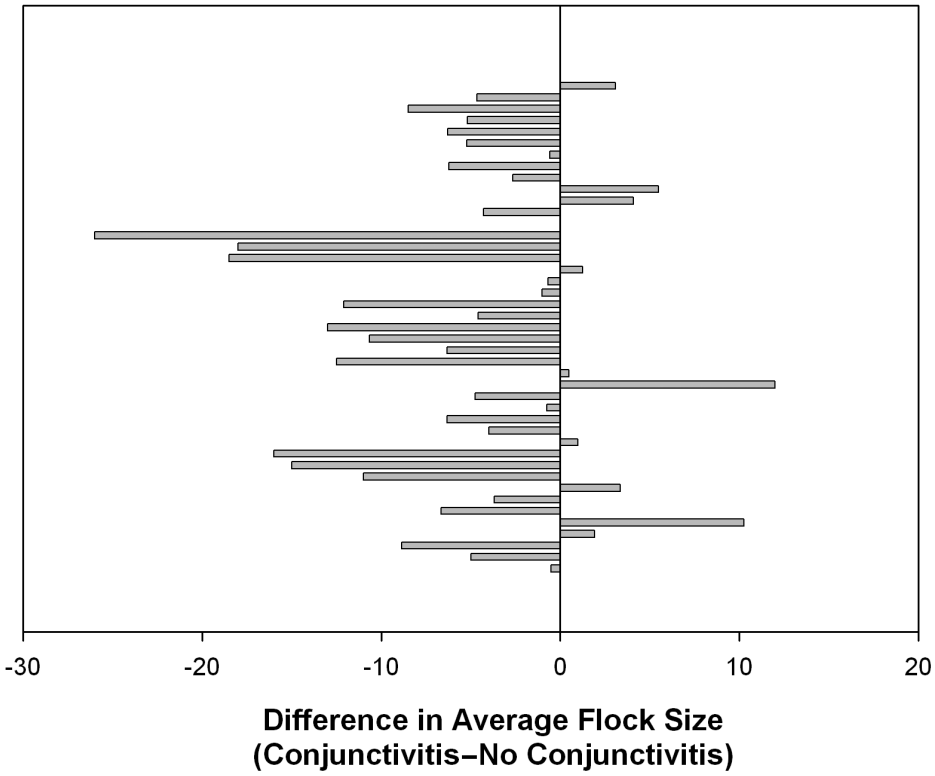

Table 2. Mixed model results for the effect of month, order (see Materials and methods), and conjunctivitis status on natural log transformed flock sizes (whole model likelihood ratio test, χ^2 = 122.9, df = 4, P < 0.001).

Model effects	ddf	F	P
Month	216	0.09	0.764
Order	31.3	2.18	0.150
Conjunctivitis status	216	4.57	0.033

Note: This analysis controls for random variation associated with individual identity. ddf is the denominator degrees of freedom.

two individuals both with and without conjunctivitis. Consistent with the results seen in the larger data set, these two individuals changed behaviour in the predicted direction: they spent a larger proportion of time feeding (88% ± 13%) and moved at a lower rate (0.32 ± 0.15) when mycoplasmal conjunctivitis was present than when conjunctivitis was absent (proportion of time feeding 28% ± 11%; movement rate 0.59 ± 0.13).

Flock-size observations

We identified 37 individually marked house finches in the flock-size data set that were observed multiple times both with and without conjunctivitis. Individuals were significantly more likely to be observed feeding alone when conjunctivitis lesions were present (Fig. 1; $F_{[1,196]}$ = 17.91; $P_{\alpha=0.025}$ < 0.0001; individual and month included in the model). Furthermore, when house finches fed in groups (flock size ≥2), they associated in significantly smaller flocks when conjunctivitis was visible (Table 2). On average, birds with conjunctivitis associated with two fewer flock mates (7.00 ± 0.87) than birds without conjunctivitis (9.14 ± 0.64).

Discussion

Our results indicate that house finches displaying signs of mycoplasmal conjunctivitis change their behaviour in several ways: they feed for longer periods of time, move less often between feeders and nearby perches, are more often observed feeding alone, and associate in smaller flocks. The individually based nature of our analyses provides evidence consistent with the idea that the observed changes in house finch behaviour are direct consequences of MG infection. The individuals that were observed both with and without conjunctivitis during our feeding (n = 2) and flocking (n = 37) observations changed behaviour in the direction predicted by the hypothesis that MG infection causes individuals to spend more time feeding and associate in smaller flocks. However, direct causation can only be proven with experimental manipulation and further study must confirm whether or not the observed changes in behaviour are truly direct consequences of infection. In particular, the feeding observations of only two individuals are highly circumstantial, and further within-individual changes in foraging behaviour must be documented to conclude that MG infection

per se is responsible for the observed differences in the time spent feeding or movement rate. Finally, our reliance on visible disease to identify infected individuals require both sets of results to be interpreted with some caution, as the scope of our conclusions are limited to house finches displaying observable lesions.

The longer feeding bouts observed for infected birds in this study do not appear to fit the general characterization of "sickness behaviour" as reviewed by Johnson (2002). A marked decrease in food intake is a common result of pathogen infection, and in some cases, anorexia may provide direct or indirect benefits to an infected animal (Johnson 2002). Several possibilities may explain why house finches with conjunctivitis fed for longer bouts of time: decreased foraging efficiency, reduced social competition for food, or some combination of these factors. A decrease in feeding efficiency may occur in infected birds owing to the visual impairment caused by the inflammatory lesions of conjunctivitis (Kollias et al. 2004). In fact, Hotchkiss et al. (2005) found house finches with conjunctivitis were half as efficient at procuring seeds and had to spend twice as long at feeders to obtain the same number of seeds as individuals without signs of conjunctivitis. Alternatively, the longer feeding bouts of house finches with conjunctivitis may be an indirect consequence of reduced social competition for food from surrounding flock mates. The smaller flock sizes of house finches with conjunctivitis and their propensity to feed alone are both consistent with decreased social competition while feeding. Although we did not record aggressive interactions in this study, Hotchkiss et al. (2005) found a tendency for house finches with conjunctivitis to receive less aggression while at feeders, consistent with the idea that social competition may be less intense for birds with conjunctivitis. Furthermore, a study of house finches housed individually showed no difference in the amount of time spent feeding before or after infection with mycoplasmal conjunctivitis (Kollias et al. 2004), suggesting the longer feeding bouts of infected birds may not occur in the absence of social interactions. The observed changes in foraging behaviour among birds with conjunctivitis in the wild likely result from a combination of decreased foraging efficiency and reduced competition for food from flock mates.

The flock-size analyses revealed two interesting changes in social behaviour that were associated with the presence of MG: the same house finch individuals were more likely to feed alone and were observed in significantly smaller flocks when conjunctivitis lesions were present. The propensity to feed alone among house finches with conjunctivitis might reflect an inability to keep up with flock movements, which can cover extensive distances in Ithaca, New York (A. Dhondt, unpublished data). Depressed motor activity is a universal component of sickness behaviour that has been shown to interfere with the predator escape response in virus-infected European greenfinches (*Carduelis chloris* (L., 1758); Lindström et al. 2003). The slower rate at which house finches with conjunctivitis moved around the feeding station is consistent with depressed motor activity during infection. Similarly, an experimental study of captive house finches showed a marked 50% reduction in activity levels only 4 days following inoculation with MG (Kollias et al. 2004). Although depressed activity levels almost certainly play a role in the propensity of diseased house finches to feed alone, additional mechanisms must be invoked to explain the observed reductions in flock size among group-feeding birds with conjunctivitis. Diseased individuals may be behaviourally subordinate and might actively avoid large flocks where they have fewer opportunities to feed. Second, healthy individuals may actively exclude diseased birds from social groups, particularly given the visible nature of the disease lesions. We are unable to distinguish between these alternatives with our data set, but the results of our individually based analysis are consistent with the hypothesis that the differences in flock size are a direct consequence of MG infection.

Our results suggest changes in house finch behaviour that result from mycoplasmal conjunctivitis may have contrasting effects on MG transmission via contaminated feeders. We expect the longer amount of time that house finches with conjunctivitis spend at feeders should increase the probability of MG being deposited, where it remains infectious to naïve house finches for only up to 12 h at artificially high doses (Dhondt et al. 2007). On the other hand, the lower number of flock mates that infected house finches are associated with will decrease the probability of nearby susceptible individuals contacting a viable dose of MG on the feeder, and therefore should decrease MG transmission (Ewald 1994). Unfortunately, we have no information regarding the relative proportion of indirect feeder transmission vs. direct transmission of MG in wild house finches, or the extent to which direct contact between individuals may shift with the observed changes in behaviour. The relative impact of each behavioural change on resulting transmission rates will depend on many factors, including flock turnover rates at feeders, direct contact rates among infected and healthy flock mates, and the likelihood of viable MG transmission resulting from a direct vs. indirect encounter. However, the results suggest overall mycoplasmal infection may alter house finch behaviour in ways that both increase and decrease the probability of transmission.

Given the short duration of this host–pathogen association (approximately 13 years), we expect the observed behavioural changes in house finches to most likely be due to side effects of infection rather than evolutionary adaptation on the part of the host or pathogen (Poulin 1995). However, microbes are quickly evolving owing to their large population sizes and short generation times (Lederberg 1997), and therefore may have the capacity to manipulate host behaviour in adaptive ways over rapid evolutionary time scales. As this host and pathogen continue to associate, it will be particularly interesting to track whether house finch behaviour in response to mycoplasmal conjunctivitis changes over time.

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