

Sickness behaviour acting as an evolutionary trap? Male house finches preferentially feed near diseased conspecifics

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Host behaviour towards infectious conspecifics is a crucial yet overlooked component of pathogen dynamics. Selection is expected to favour individuals who can recognize and avoid infected conspecifics in order to reduce their own risk of infection. However, evidence is scarce and limited to species employing chemical cues. Here, we experimentally examine whether healthy captive house finches (*Carpodacus mexicanus*) preferentially forage near a same-sex, healthy conspecific versus one infected with the directly transmissible pathogen *Mycoplasma gallisepticum* (MG), which causes lethargy and visible conjunctivitis. Interestingly, male house finches strongly preferred feeding near diseased conspecifics, while females showed no preference. This sex difference appeared to be the result of lower aggression rates in diseased males, but not in females. The reduced aggression of diseased males may act as an ‘evolutionary trap’ by presenting a historically beneficial behavioural cue in the context of a new environment, which now includes a recently emerged, potentially fatal pathogen. Since MG can be directly transmitted during feeding, healthy males may inadvertently increase their risk of contracting MG. This behaviour is likely to significantly contribute to the continued persistence of MG epidemics in wild populations.

Keywords: house finch *Carpodacus mexicanus*; *Mycoplasma gallisepticum*; disease avoidance; aggression; pathogen transmission; foraging behaviour

1. INTRODUCTION

Pathogen transmission is a costly and sometimes deadly consequence of conspecific interaction, particularly for group-living organisms (Møller *et al.* 1993). Selection should therefore favour individuals who can recognize and avoid conspecifics infected with directly transmitted pathogens (Loehle 1995). However, surprisingly little is known as to whether and how individuals alter their behaviour in response to infected conspecifics, particularly outside the context of mate choice where avoidance behaviours carry both direct and indirect benefits (e.g. Rosenqvist & Johansson

1995). To date, evidence for behavioural avoidance of infected conspecifics, documented in both bullfrog tadpoles (Kiesecker *et al.* 1999) and social lobsters (Behringer *et al.* 2006), appears to result from chemical cues. Many types of pathogens, however, result in visible changes in their hosts ranging from behavioural modifications (lethargy, posture) to physical signs (e.g. inflammation, lesions, hair loss; Loehle 1995). Birds, in particular, rely heavily upon visual cues for behavioural decisions. However, no study outside of the context of mate choice has examined whether individuals use visible cues in order to avoid diseased conspecifics and reduce their own risk of infection.

House finches (*Carpodacus mexicanus*) suffer from the directly transmissible bacterial pathogen *Mycoplasma gallisepticum* (MG) which causes visible conjunctival symptoms and behavioural changes (Kollias *et al.* 2004). Since its emergence in 1994 (Ley *et al.* 1996), MG has caused annual seasonal epidemics in eastern North American house finches. MG-infected finches have significantly lower overwinter survival rates (Faustino *et al.* 2004) and the initial epidemic resulted in detectable population declines (Hochachka & Dhondt 2000), suggesting that MG has sufficient fitness consequences to select for avoidance of infected individuals. Furthermore, MG epidemics occur during periods of gregarious flocking (Altizer *et al.* 2004), and flocking behaviour increases disease prevalence (Hosseini *et al.* 2004). Therefore, free-living house finches in eastern North America regularly encounter visibly infected conspecifics while feeding.

Here, we use an experimental feeding choice arena to investigate whether healthy house finches preferentially feed near a healthy conspecific or one exhibiting behavioural and physical signs of MG infection. In addition, we examined behavioural differences between healthy and diseased house finches to determine potential cues healthy individuals may use to alter their preference towards conspecifics.

2. MATERIAL AND METHODS

Experimental cages were divided into three compartments with a small food dish on either side of two wire-mesh dividers, allowing adjacent individuals to interact and aggressively displace each other without physical contact (figure 1 inset; electronic supplementary material S1). Focal individuals (17 males; 22 females) in the middle compartment were tested once against a unique, same-sex combination of one healthy (out of five males and six females) and one diseased conspecific (out of five males and 12 females) placed in either side compartment. Diseased conspecifics were experimentally inoculated with MG as part of an ongoing infection experiment and all showed visible conjunctival lesions (electronic supplementary material S2).

Trials were recorded on video between 8.00 and 15.30 EST in March 2009. Focal birds were food-deprived for 3 h prior to trial commencement in order to ensure standardized motivation to feed (table 1). During the first 20 min following focal bird entry (T_0 ; table 1), we quantified at 30 s intervals the conspecifics' levels of activity and aggression (table 2) towards the focal bird (i.e. (i) total number of interactions, and percentage of interactions where conspecific (ii) showed aggression and (iii) won). Next, the focal bird was provided with both food sources ($T + 0.5$ h; table 1) and its feeding behaviour quantified for 60 min at 30 s intervals by scoring when and where it was feeding.

We analysed sources of variation in focal bird feeding preference (i.e. time feeding near healthy–diseased conspecific) using a general linear model including sex, differences in conspecific behaviour (healthy–diseased for activity, aggression and wins) and the two-way interactions with sex. Second, we analysed conspecific behaviour (activity, aggression and wins; table 2) as a function of sex, treatment

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0020> or via <http://rsbl.royalsocietypublishing.org>.

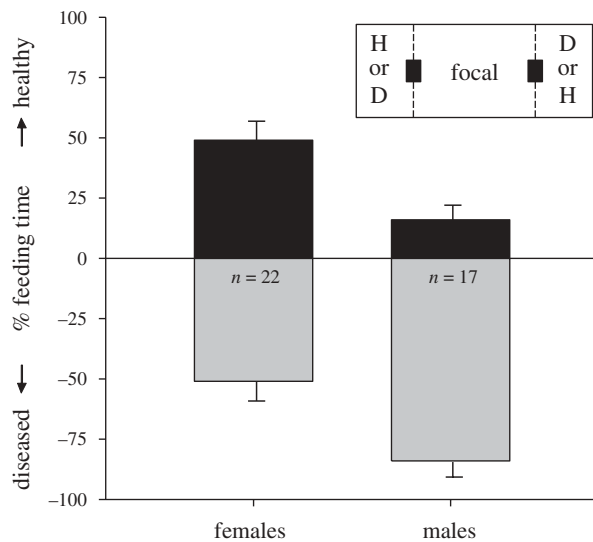


Figure 1. Mean (\pm s.e.) percentage of time spent feeding by focal house finches near a healthy ('H'; black bars) or diseased conspecific ('D'; grey bars). The inset shows the experimental set-up with the placement of mesh barriers (dashed lines) and food dishes (black squares).

Table 1. Experimental timeline.

time	action	food present?	
		focal bird	conspecifics
$T - 3$ h	remove food of focal bird in its home cage	no	yes
$T - 0.5$ h	move conspecifics to experimental cage	no	yes
T_0	move focal bird to experimental cage start observation of conspecific behaviour	no	yes
$T + 0.5$ h	provide focal bird with food in both food dishes start observation of focal bird feeding preference	yes	yes
$T + 1.5$ h	end of observation		

(healthy versus diseased) and their interaction using general linear mixed models including trial as a random effect. For further details on the statistical analyses, see electronic supplementary material 3.

3. RESULTS

(a) Focal bird behaviour

Feeding preferences significantly differed by sex ($F_{1,34} = 8.63$, $p = 0.006$; figure 1): male focal house finches strongly preferred to feed near diseased conspecifics ($t_{16} = 6.15$, $p < 0.001$), whereas females fed for similar amounts of time near each conspecific ($t_{21} = 0.51$, $p = 0.62$). Focal bird feeding preference was negatively related to the difference in wins between healthy and diseased conspecifics (figure 2; $F_{1,34} = 5.54$, $p = 0.024$), but unrelated to difference in activity ($F_{1,34} = 0.19$, $p = 0.67$) or aggression ($F_{1,34} = 0.50$,

Table 2. Definitions of scored behaviour.

behaviour	definition
activity level	total number of movements between perches, floor or sides of the compartment
aggressive interaction	peck, attack (i.e. a fast, direct flight towards the other bird that is perched next to the cage divider) or combat (i.e. both birds repeatedly peck and aggressively vocalize at each other, often when hovering in mid-air) between focal bird and conspecific
winning an interaction	displacement with a winner and a loser (i.e. loser moves away while winner stays put)

$p = 0.49$). All pair-wise interactions between behavioural differences and sex were non-significant (all $p > 0.74$).

(b) Conspecific behaviour

The effect of being healthy or diseased on conspecific behaviour varied with sex for the percentage of wins (figure 2; sex \times treatment; $\chi^2_1 = 5.06$, $p = 0.024$), but not for activity ($\chi^2_1 = 0.67$, $p = 0.41$) or aggression level ($\chi^2_1 = 0.41$, $p = 0.52$). Healthy males won a higher percentage of interactions with the focal bird than diseased males ($\chi^2_1 = 9.19$, $p = 0.002$), while this difference was absent in females ($\chi^2_1 = 0.24$, $p = 0.62$; electronic supplementary material, figure S4c). Regardless of sex, healthy conspecifics were more active than diseased ones ($\chi^2_1 = 42.75$, $p < 0.001$; electronic supplementary material, figure S4a), and there was no difference in aggression ($\chi^2_1 = 1.83$, $p = 0.18$; electronic supplementary material, figure S4b).

4. DISCUSSION

Behavioural changes such as lethargy, often referred to as 'sickness behaviours', are generalized responses to infection (Hart 1988) that may serve as informative cues for avoidance of conspecifics infected with a broad range of pathogens. However, in this study, healthy male house finches responded to a sickness behaviour—the reduced potential to win—by increasing time spent feeding near diseased individuals: the more likely the healthy conspecific in a given trial was to win aggressive interactions with the focal bird, the stronger the feeding preference towards the less competitive, diseased conspecific. These results suggest that healthy males seek to avoid costly social defeats, which have been shown to dynamically suppress immune responses in this species (Hawley 2006), by foraging in the vicinity of individuals with the lowest potential for winning aggressive interactions. This study is the first demonstration of individuals using visual cues (i.e. behaviour) to alter their behaviour towards diseased conspecifics, although the additional use of chemosensory cues (Hagelin & Jones 2007) cannot be excluded by our experimental design.

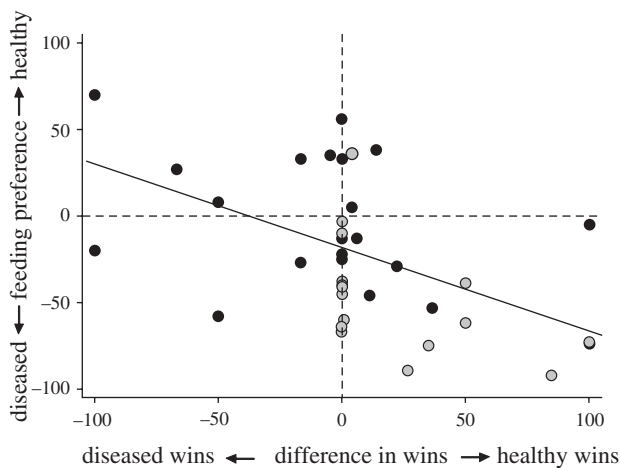


Figure 2. The extent of focal house finch feeding preference (i.e. feeding time near healthy–diseased conspecific; *y*-axis) for diseased conspecifics was related to the reduced percentage of wins (*x*-axis) by diseased male ($n = 17$; grey dots), but not female conspecifics ($n = 22$; black dots). As there was no interaction between sex and difference in wins (healthy–diseased conspecifics), the sexes were pooled for the regression analysis (solid line). The dashed lines indicate no feeding preference (horizontal) or no difference in wins (vertical).

The sickness behaviour of infected male house finches may act as an ‘evolutionary trap’ by presenting a historically beneficial cue (i.e. reduced aggression) in the context of a new environment (Schlaepfer *et al.* 2002), in this case, a recently emerged pathogen. Before the emergence of MG in house finches, the risk of exposure to pathogens carried by non-aggressive individuals may have been outweighed by the benefits of access to resources, whereas the behavioural cue is now likely to carry fitness costs (Faustino *et al.* 2004). Since associations between this host and the pathogen have been of relatively short evolutionary duration (approx. nine finch generations), sufficient time for the selection of avoidance of infected conspecifics may not yet have passed.

Why did we detect a feeding preference for diseased conspecifics only in male house finches? Our results indicate that this difference was not driven by focal bird behaviour: focal males and females responded similarly to differences in aggression, since the interaction between sex and differences in wins on feeding preference was non-significant. Therefore, in mixed-sex flocks, which are the rule during non-breeding in house finches, we expect females to be just as likely as males to prefer feeding in the proximity of infected, non-aggressive males. Instead, the detected sex-specific feeding preference resulted from behavioural differences in the conspecific house finches: infected male conspecifics were significantly less likely to win aggressive interactions than healthy male conspecifics, driving male focal birds to prefer feeding in their vicinity. Female conspecifics, however, showed no change in the potential to win with MG infection. It remains unknown why the potential to win interactions differed between healthy and diseased males and females in our study. Previous studies suggest that the suppression of sickness behaviours depends on life-history trade-offs

and can, for instance, vary with body condition (Owen-Ashley *et al.* 2006). Since female house finches tend to be dominant in aggressive interactions (Brown & Brown 1988), the motivation for infected females to maintain social status may be higher than for infected males. Alternatively, the physiological costs of infection and/or social defeat may be higher for male house finches.

Infection-induced behavioural changes are prevalent among host–pathogen systems (Moore 2002) and can alter the ability of a disease to invade and persist in a population (Lloyd-Smith *et al.* 2004). The population-level consequences for the observed behavioural changes towards infected house finches are likely to be critical for MG dynamics. Transmission experiments indicate that MG deposited on a feeder is only infectious for short (12 h or less) timescales (Dhondt *et al.* 2007). Therefore, house finches that associate in close proximity with infectious individuals while feeding may be most likely to contact viable MG and contribute to the continued persistence of MG epidemics in wild populations. The extent to which infection-induced behavioural changes such as those observed here drive transmission dynamics and epidemic persistence in host–pathogen systems is an area ripe for further exploration.

All housing protocols and experimental procedures were approved by Virginia Tech’s Institutional Animal Care and Use Committee prior to the commencement of research.

We thank Tamara Feters and Grace Martin for help analysing video observations, Laila Kirkpatrick and Bambi Jarrett for help with bird care and Cas Eikenaar, Erik Osnas and three anonymous referees for useful feedback on the manuscript. This work was supported by NSF-EF 0622705 under the NSF-NIH Ecology of Infectious Diseases programme.

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