Age, sex, and season affect the risk of mycoplasmal conjunctivitis in a southeastern house finch population

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Abstract: House finches (*Carpodacus mexicanus* (Muller, 1776)) in eastern North America have been affected by annual epidemics of an eye disease caused by the bacterium *Mycoplasma gallisepticum* since 1994. To identify factors associated with seasonal changes in prevalence and variation in host susceptibility, we monitored mycoplasmal conjunctivitis among wild house finches in a region of high prevalence in southeastern North America. We captured 888 birds between August 2001 and December 2003 and observed seasonal outbreaks characterized by rapid increases in prevalence from August to October each year. During periods of high prevalence, infection probability was significantly higher among juveniles than adults, and the severity of conjunctivitis among juvenile females was greater than for any other host category. We found no evidence linking moulting status to elevated infection risk among adult birds. Finally, house finches with conjunctivitis were in poorer condition than birds with no clinical signs of infection, particularly among those with severe infections. Results from this study are consistent with recent reports of seasonal and regional variation in mycoplasmal conjunctivitis and suggest that annual changes in host reproduction, behaviour, and age structure might be important determinants of the timing and magnitude of local epidemics.

Résumé : Depuis 1994, les roselins familiers (*Carpodacus mexicanus* (Muller, 1776)) de l'est de l'Amérique du Nord sont affectés par des épidémies annuelles d'une maladie de l'oeil, causée par la bactérie *Mycoplasma gallisepticum*. Nous avons suivi l'évolution de la conjonctivite mycoplasmique chez des roselins familiers sauvages dans une région de forte prévalence de la maladie dans le sud-est de l'Amérique du Nord afin d'identifier les facteurs associés aux changements saisonniers de la prévalence et à la variation de la vulnérabilité des hôtes. Nous avons capturé 888 oiseaux entre août 2001 et décembre 2003 et nous avons observé des recrudescences saisonnières de la maladie caractérisées par une augmentation rapide de la prévalence d'août à octobre chaque année. Durant les périodes de forte prévalence, la probabilité d'infection est significativement plus élevée chez les jeunes que chez les adultes et la sévérité de la conjonctivite chez les jeunes femelles est plus grande que chez toute autre catégorie d'hôtes. Nous ne trouvons aucune indication qui relie l'état de la mue à un risque accru d'infection chez les oiseaux adultes. Enfin, les roselins souffrant de conjonctivite, particulièrement si l'infection est sévère, sont en plus mauvaise condition physique que ceux qui n'ont pas de signes cliniques. Les résultats de notre étude s'accordent avec les signalisations récentes de variations saisonnières et régionales dans la conjonctivite mycoplasmique et ils indiquent que les changements annuels dans la reproduction, le comportement et la structure en âge des hôtes peuvent être d'importants facteurs déterminants du moment ou de l'importance des épidémies locales.

[Traduit par la Rédaction]

Introduction

Emerging infectious diseases have increasingly become a focus in ecology and conservation biology, and over the past two decades introduced pathogens have been linked with catastrophic declines in amphibians, seals, lions, sea otters, and other wildlife populations (reviewed in Harvell et al. 1999; Daszak et al. 2000; Lafferty and Gerber 2002). Among birds, avian pox and malaria contributed to marked losses in Hawaiian forest birds (van Riper et al. 1986). More recently, American crows and related species in North America have died in unusually large numbers following the emergence of West Nile virus (Mostashari et al. 2003). Understanding the determinants of host susceptibility to novel pathogens, including host age and behaviour and environmental variables, will therefore become increasingly important for wildlife conservation (Friend et al. 2001; Cleaveland et al. 2002). Yet despite detailed studies of human pathogens and sophisticated host–pathogen models, we know relatively little about factors affecting disease risk in wild animal populations (but see Hudson et al. 1992; Begon et al. 1999; Altizer et al. 2000).

We studied a local population of house finches affected by a recently emerged bacterial disease caused by *Mycoplasma gallisepticum* (MG) to identify factors associated with temporal and within-population variation in disease risk. Following initial reports of infected house finches at feeders

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during the winter of 1993–1994, this novel strain of a domestic poultry pathogen spread rapidly throughout eastern North America (Ley et al. 1996; Dhondt et al. 1998). Within 4 years post introduction, this pathogen caused density-dependent declines in house finch abundance of up to 60% (Hochachka and Dhondt 2000). Upon exposure to MG, individual house finches rapidly develop mild to severe conjunctivitis that persists for many weeks (Luttrell et al. 1998), and hosts that reach advanced stages (where one or both eyes swell shut) probably die from exposure, predation, or starvation.

Because wild house finches are easy to capture and handle, are ubiquitous and well studied, and are susceptible to a bacterial infection that produces highly visible outward signs, they are rapidly becoming a model system for understanding infectious disease dynamics in wild avian systems (e.g., Dhondt et al. 1998; Nolan et al. 1998; Hochachka and Dhondt 2000). Moreover, close correspondence between clinical signs and bacterial infection indicates that conjunctivitis provides a reliable estimate of MG presence in wild house finches (Hartup et al. 2001*a*). However, despite recent analyses of temporal dynamics and captive studies of infected house finches, few studies have identified host characteristics associated with infection risk or disease severity in wild house finch populations, perhaps because previous efforts have focused on locations where or times when prevalence was low (e.g., Hartup et al. 2000; Roberts et al. 2001*b*; but see Hartup et al. 2001*b*).

Previous monitoring studies based on field data from New York and New Jersey, in addition to citizen science reports, demonstrated that mycoplasmal conjunctivitis exhibits both seasonal and multi-year fluctuations in prevalence (Hartup et al. 2000; Hartup et al. 2001*a*; Altizer et al. 2004), with increasing prevalence during the fall and winter (September–February) and extremely low prevalence during the breeding season (April–July). These regular epidemics of mycoplasmal conjunctivitis could be caused by a combination of factors, including the recruitment of a large number of immunologically naive juveniles into the population at the end of the summer, providing a larger base of susceptible hosts. The flocking behaviour of house finches at bird feeders in the fall and winter could further increase host contact and parasite transmission rates, thus triggering seasonal epidemics (Hartup et al. 1998). Alternative explanations for fall epidemics include increased adult susceptibility brought on by late-summer moulting, which has been shown to be energetically costly (Lindström et al. 1993) and might increase susceptibility to infectious disease (e.g., Ginn and Melville 1983; but see Svensson and Merila 1996). Thus, adult house finches undergoing a complete prebasic moult at the end of the summer could be at higher risk of MG infection because of reduced temperature insulation or energetic trade-offs with immune defenses.

Our goal was to examine factors affecting host susceptibility during seasonal outbreaks of mycoplasmal conjunctivitis in a wild house finch population in the southeastern United States, where prevalence based on citizen science monitoring has been shown to be high (Altizer et al. 2004). We used field capture data collected over three successive fall/winter outbreaks to examine whether characteristics of individual birds, including age, sex, and moulting status, were associated with the presence and severity of infection. We also examined house finch condition in relation to disease severity to assess the potential fitness consequences of mycoplasmal conjunctivitis and to identify which classes of hosts experience the most severe effects of this disease. On the basis of events that coincide with the timing of annual epidemics, we predicted that juveniles and moulting birds captured during intervals of high prevalence would be at greater risk of infection and would exhibit more severe clinical signs and poorer body condition following infection.

Methods

House finches were trapped at six sites in Atlanta, Georgia, within a 20-km radius of Emory University, between August 2001 and December 2003. Birds were captured using either wire mesh cages around tube-style bird feeders (after Hill 2002) or standard mist nets (30 mm mesh, 9 m long) placed near bird feeders. Birds were banded with a unique combination of one US Fish and Wildlife aluminum leg band and three coloured leg bands for later identification. The sex of each bird was determined from the dimorphic plumage of the species (Hill 1993), although most juvenile birds could not be sexed during the summer months (May–August). Birds captured between April and December were classified as hatch-year (HY) or after hatch-year (AHY) according to the date of any previous capture and the bird's status on that date, the degree of ossification in the skull, the tail shape (Pyle 1997), or the extent of plumage wear (Hill 1993). From January to March, all birds were classified as AHY. Birds that could not be reliably aged at the time of capture (19.8% of all captures) were classified as unknown.

For each bird, we measured mass in grams (using an electronic balance) and length of the right tarsus in millimetres. A body condition index (hereafter called BCI) based on pectoral muscle development around the carina (breastbone) was assigned as follows: 1 = severely sunken muscle tissue, 2 = moderately sunken tissue, 3 = muscle approximately level with the carina, and 4 = muscle protruding above the level of the carina (Gosler 1991). We also scored the amount of visible subcutaneous fat in the furculum using a scale of 0–4, following Hartup et al. (2001*a*): 0 = no visible fat, 1 = furculum <33% full, 2 = furculum 33%–66% full, 3 = furculum filled, and 4 = outward bulging furculum.

For all birds showing clinical signs of mycoplasmal conjunctivitis, we assigned each eye a score of 0–3 based on the severity of conjunctivitis following Roberts et al. (2001*a*). A score of 0 represented no signs of conjunctivitis; eyes with minor swelling or redness were assigned a score of 1; eyes with moderate swelling and discharge received a score of 2; and severely swollen eyes (those that were nearly or completely swollen shut) were classified as 3. Although we did not assign infection status on the basis of isolation or culture of *M. gallisepticum*, past data has shown a high correspondence between MG prevalence and the presence of clinical signs among wild birds (Hartup et al. 2001*a*). Moreover, more than 97% of a subset of house finches captured in this study that had no physical signs of conjunctivitis (N = 87) tested negative for MG when eye swabs were examined via culture and polymerase chain reaction methods (D.H. Ley, unpublished data). Similarly, more than 85% of a subset of

captured birds that had clinical conjunctivitis (N = 75) tested positive for MG.

Animal protocols described herein were approved by Emory University's Animal Care and Use Committee and were used in accordance with the principles and guidelines of the Canadian Council on Animal Care. Banding permits were granted by the US Bird Banding Laboratory (permit No. 23141) and the Georgia Department of Natural Resources (permit No. 29-WMB-02-176). All birds were released within 30 min of capture at the site of collection and then observed to ensure that they flew to a nearby perch. Birds that showed signs of handling stress (shivering, gaping, or listlessness; North American Banding Council 2001) were immediately released and data collection was terminated. To limit accidental transmission of disease between captured birds, cloth holding bags were sterilized in 20% chlorine bleach solution between each use. Additionally, instruments and tools were sterilized using 95% ethanol, and research personnel washed their hands with antibacterial soap between handling of individual birds.

Data analysis

Assigning infection status

We summarized the infection status of individual birds in two ways: first, according to whether or not the bird showed any signs of MG (presence/absence) and second, on the basis of the mean severity of infection in both eyes. Infection severity categories were as follows: 0 = no clinical signs; 1 (mean eye score between 0.5 and 1.0) = low infection severity; 2 (mean eye score between 1.5 and 2.0) = moderate disease severity; and 3 (mean eye score ≥2) = severely infected birds. The highest severity group (class 3) included birds that were blind or nearly so in both eyes, whereas the moderate severity group (class 2) included birds whose vision was probably impaired but not blocked.

Correlates of infection status

We used logistic regression to examine host characteristics associated with increased risk of MG infection during annual outbreaks. Our analysis focused on three periods of high prevalence (August 2001 to January 2002, October 2002 to February 2003, and July 2003 to September 2003), because >88% of birds with conjunctivitis in our data set were captured during these time intervals, and prevalence during these months was greater than or equal to the grand mean prevalence of 16% (Fig. 1). We examined how host age, sex, and moulting status covaried with disease risk, measured as both the presence/absence of infection and the degree of severity. Because only a small proportion of juvenile house finches undergo a complete prebasic moult (Hill 1993), we restricted our analysis of moulting status to adult birds only and further focused on months when both moulting and conjunctivitis were observed (August, September, and October). Finally, because the two trapping methods (mist net versus feeder traps) might have captured different subsets of birds, we included capture method as a final effect in logistic regression analyses.

Infection status and host condition

We evaluated the association between mycoplasmal conjunctivitis and host condition using data from the same three periods of high prevalence described above. Principal component analysis (PCA) was used to obtain a composite measure of host condition based on three host properties: unstandardized residuals from a linear regression of body mass on tarsus length, muscle condition (BCI), and fat scores. Within the subset of birds examined, these three variables were positively and significantly correlated (e.g., all two-way Pearson's correlation coefficients were positive and significant at a level of 0.05 or greater). The first principal component (PC-1) from a factor analysis explained 45.3% of the total variance, and birds with high PC-1 values had greater muscle development, more subcutaneous fat, and weighed more relative to their body size than birds with negative scores (component coefficients: BCI = 0.41, subcutaneous fat = 0.76, and residuals from regression of mass on tarsus length = 0.79). Using PC-1 as a composite measure of host condition, we used analysis of variance (ANOVA) to examine general associations between condition and disease severity, age, and sex.

To more closely examine the causal relationship between infection and host condition, we performed a second set of analyses using data from the subset of birds that had been initially captured without clinical signs between 15 July and 15 December and that were recaptured 10–60 days later. We chose this time frame because past studies have shown that infected hosts usually develop eye infections within 7–14 days after exposure and because clinical signs often persist for 6 weeks or longer (Roberts et al. 2001*a*). Thus, the 10–60-day time frame represented an interval over which transition to an infected state was likely to be observed during peak infection periods. Birds in this subsample were divided into two groups according to whether or not they exhibited clinical signs upon recapture. We first used analysis of variance to examine whether the body condition of birds upon initial capture was associated with their subsequent infection status. We then used a repeated measures ANOVA to examine how body condition changed between capture events and whether this change depended on infection group, age, or sex. These two final analyses were designed to discriminate between the possibility that mycoplasmal conjunctivitis leads to loss of body condition versus the likelihood that birds in poorer condition are more likely to develop conjunctivitis.

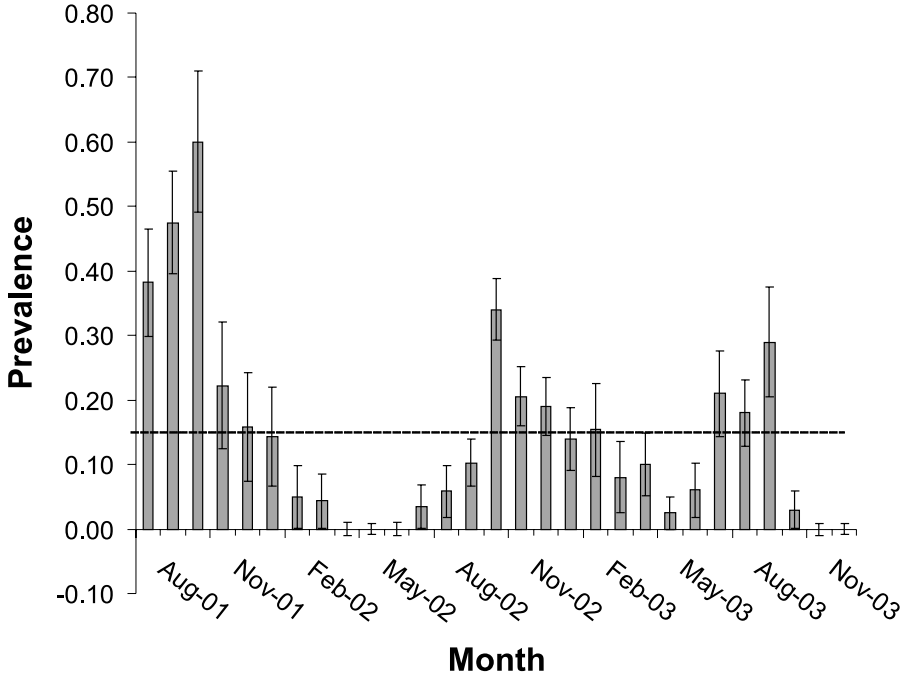
Results

Overall patterns

A total of 888 house finches were captured and banded between 16 August 2001 and 30 December 2003, with a total of 1079 capture events. We excluded individual birds captured more than once during the same month from prevalence estimates and analyses unless the infection status of those birds had changed within that month. Of the birds that could be sexed, 57% were males and 44% were females. A total of 704 birds could be reliably aged, and of these, 51% were adults (AHY) and 49% were juveniles (HY).

Throughout the entire 29-month period, 16% ± 1.0% (SE) of the house finches showed clinical signs of mycoplasmal conjunctivitis. Among 176 infected captures, 62% exhibited mild infections, 29.5% showed moderate clinical signs, and 8.5% were severely infected. Prevalence of conjunctivitis

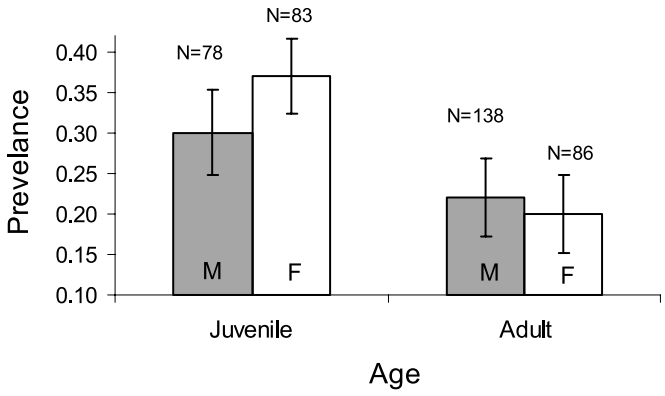
Fig. 1. Monthly changes in the proportion of house finches (*Carpodacus mexicanus*) with mycoplasmal conjunctivitis from August 2001 to December 2003. Monthly sample sizes ranged from 19 to 97 birds. Error bars represent SEs. The dotted line shows grand mean prevalence across the entire 29-month study period (16%).



showed strong seasonal variation. Prevalence was low during the late spring and summer months, and increased during late summer or fall (Fig. 1). Maximum prevalence was higher in 2001 (60% ± 11% SE) than in 2002 (34% ± 5% SE) or 2003 (29% ± 9% SE) and peaked in September or October each year.

Of all birds initially captured, 18% were later recaptured at least once during the entire study period. Among birds captured during periods of high prevalence, the probability of being recaptured at any future date throughout the entire study period covaried with infection severity upon initial capture, but this association was not statistically significant (χ^2 = 3.07, df = 3, p = 0.382). Across all birds within this subset, those initially captured with no (N = 387) or mild clinical signs (N = 90) were associated with a probability of future recapture of 0.21; those with moderate conjunctivitis (N = 32) had a probability of future recapture of 0.13; and no birds captured with severe conjunctivitis (N = 7) were later recaptured.

Fig. 2. Association between age, sex, and the proportion of house finches with clinical signs of mycoplasmal conjunctivitis during three periods of high prevalence (described in Methods). Bars represent SEs. Samples sizes are indicated above each bar.

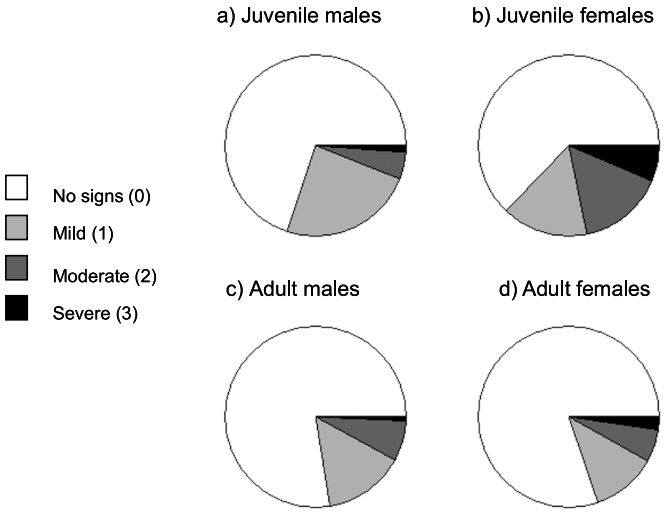


Disease risk and host characteristics

The presence and severity of infection varied with age and sex during three annual periods of high prevalence. Mean prevalence was higher among juvenile birds (33%, N = 231) than adults (21%, N = 225). The proportions of male and female birds with clinical signs were similar (25% vs. 26%, respectively) when examined across all individuals. However, prevalence of conjunctivitis was higher in juvenile than in adult birds (Fig. 2). Logistic regression analysis (model: infection status = age + sex + age × sex + trap + age × trap + sex × trap) revealed a significant association between infection probability and age (Wald χ^2 = 4.7, df = 1, p = 0.030) but not sex (Wald χ^2 = 1.1, df = 1, p = 0.299). The effect of trapping method was also highly significant (Wald χ^2 = 8.6, df = 1, p = 0.003), with prevalence of conjunctivitis higher among birds captured with mist nets (37% of 144 captures) than among those captured with feeder traps (22% of 461 captures), perhaps because of an effect of disease on the ability of birds to visually detect mist nets. No two-way interactions between age, sex, or trapping method approached significance at the 0.05 level.

The severity of clinical signs was higher among females than among males, and this was primarily due to a relatively high proportion of juvenile (HY) female birds with moderately severe infections (Fig. 3). In fact, the association between infection severity and sex was significant when using data from all birds (χ^2 = 7.963, df = 3, p = 0.047) and juvenile birds alone (χ^2 = 9.28, df = 3, p = 0.026), but not when

Fig. 3. Association between age, sex, and infection severity during three periods of high prevalence of mycoplasmal conjunctivitis (described in Methods). Categories for severity (based on clinical signs of mycoplasmal conjunctivitis in both eyes) are explained in the Methods. Error bars represent SEs. Sample sizes for each category were as follows: hatch-year (HY) males, 83; HY females, 78; after hatch-year (AHY) males, 138; and AHY females, 86.



tested using data from adult birds only (χ^2 = 1.55, df = 3, p = 0.671). Thus, juvenile females experienced the highest mean severity of clinical signs among all age and sex categories.

Among adult birds captured from August to October (N = 123), the mean (±SE) prevalence of infection for moulting birds (19.0% ± 4.7%) was similar to the mean prevalence for non-moulting birds (23.0% ± 5.8%). A separate logistic regression analysis (model: infection status = moult + sex + trap + all two-way interactions) showed that moulting status (Wald χ^2 = 0.22, df = 1, p = 0.639), sex (χ^2 = 1.38, df = 1, p = 0.240), and the two-way interaction (χ^2 = 0.132, df = 1, p = 0.717) were not significantly associated with the infection status of adult birds. Furthermore, no main effect or two-way interaction involving trapping method approached significance at the 0.05 level.

Infection status and host condition

We used PC-1 scores as a measure of body condition, with positive values representing individuals that were in better than average condition and negative values representing individuals that were in poorer condition. The ANOVA showed that the severity of clinical signs was significantly associated with variation in body condition (Table 1). Thus, house finches with more severe clinical signs had progressively poorer measures of body condition. This effect was more severe for females than for males, but the sex × severity interaction was not statistically significant (Fig. 4).

To further examine the association between condition and infection status, we used data from a subset of initially uninfected, recaptured birds, as described in the Methods. These birds were divided into two categories: group "0" birds were those that were uninfected at both initial capture and subsequent recapture dates (N = 31), and group "1" birds were those that were initially captured without clinical signs but were later recaptured with conjunctivitis (N = 19). The ANOVA showed no difference in the initial condition of birds as a function of the main effects of their infection group ($F_{[1,38]}$ = 0.024, p = 0.878), sex ($F_{[1,38]}$ = 0.017, p = 0.897), or age ($F_{[1,38]}$ = 0.024, p = 0.095; model: condition = group + age + sex). In fact, birds that later developed clinical signs of MG (group 1) had slightly higher initial mean PC-1 values than those that remained uninfected (Fig. 5).

Table 1. Analysis of variance table showing effects of age (hatch-year versus after hatch-year), sex, *Mycoplasma gallisepticum* infection severity, and all two-way interactions on a composite measure of body condition of house finches (*Carpodacus mexicanus*).

Effect	MS	df	F	P
Age	1.94	1	2.06	0.152
Sex	1.97	1	2.10	0.148
Severity (0–3)	5.67	3	6.06	0.001
Age × sex	1.01	1	1.07	0.302
Age × severity	1.17	1	1.24	0.295
Sex × severity	0.48	1	0.51	0.677
Error	0.941	362		

Note: The composite measure of body condition, PC-1, was estimated from a principal component analysis of body mass relative to body size, fat scores, and muscle condition, as explained in the Methods. Infection severity was measured on a scale of 0–3, as described in the Methods.

A repeated measures ANOVA that treated condition scores from birds at first and second capture events as within-subject effects showed that the interaction between capture event and infection group was statistically significant (Table 2). Thus, PC-1 values for birds that did not develop clinical signs were similar on the first and second capture dates, but PC-1 values for birds that transitioned to the infected class declined sharply (Fig. 5). No other main effects or interactions tested in this model were statistically significant (Table 2).

Discussion

Consistent with a recent analysis based on citizen science data (Altizer et al. 2004), mycoplasmal conjunctivitis among house finches captured in Atlanta, Georgia, showed extreme seasonal variation, with markedly high prevalence between late summer and early winter. During one epidemic peak in October 2001, 60% of captured house finches exhibited eye infections, an exceptionally high proportion relative to those found in other recent field studies (e.g., Hartup et al. 2000; Roberts et al. 2001*b*). Maximum disease prevalence occurred during the months of September or October across all 3 years and declined to low or undetectable levels during the late spring and summer months. Fall epidemics of mycoplasmal conjunctivitis have been noted in several recent studies (Hartup et al. 2001*b*; Roberts et al. 2001*a*, 2001*b*) and could be due to a combination of factors, including annual variation in house finch reproduction, flock size, and feeder use, or seasonal factors that affect host susceptibility or pathogen transmission.

These rapid increases in conjunctivitis during the fall could be caused by the recruitment of immunologically na-

Fig. 4. Association between *M. gallisepticum* infection severity (based on clinical signs of mycoplasmal conjunctivitis in both eyes) and overall body condition (PC-1) shown separately for male and female house finches. Body condition was estimated from a principal component analysis as explained in the Methods. Error bars show SEs.

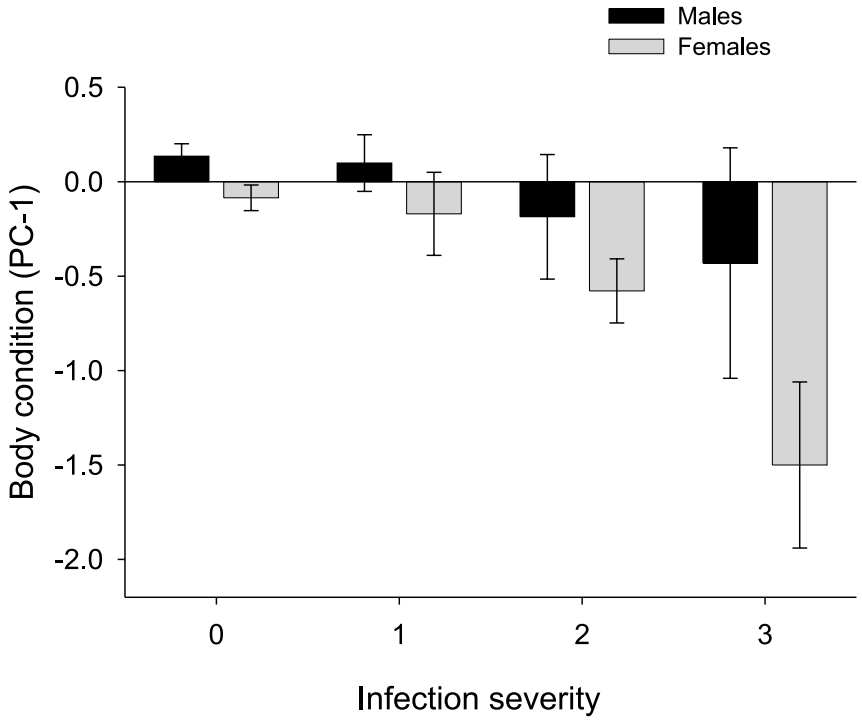
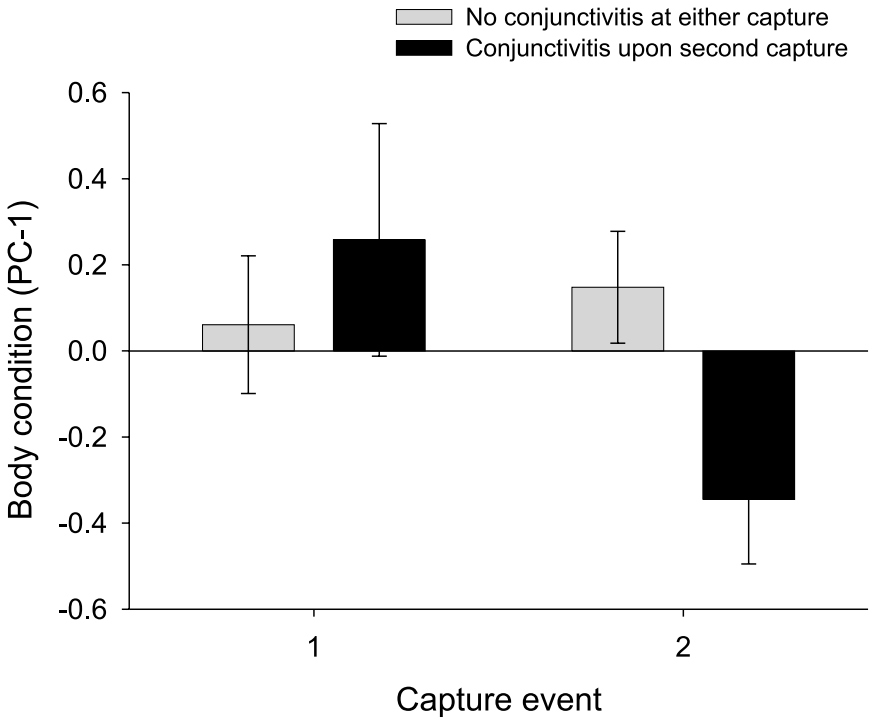


Fig. 5. Association between *M. gallisepticum* infection status and house finch body condition (based on PC-1, as described in Methods and Results) in a subset of birds that were initially captured during fall months without conjunctivitis and recaptured 10–60 days later. Error bars represent SEs. Sample size = 31 for birds recaptured without clinical signs (grey) and 19 for birds recaptured with conjunctivitis (black).



ive juveniles into the population towards late summer. This hypothesis is supported by studies of nematode outbreaks in Soay sheep showing that the magnitude of late-summer peaks in worm larvae numbers on pasture depended on the number of lambs produced earlier that year (Gulland and Fox 1992). If such recruitment is important to disease spread

Table 2. Repeated measures analysis of variance table showing effects of capture/recapture event (as a within-subject effect) and interactions with transition group, age, and sex (as between-subject effects) on the principal component analysis measure of house finch body condition (PC-1).

Effect	MS	df	*F*	*P*
Capture event	2.084	1	0.684	0.014
Group × capture event	1.937	1	6.263	0.017
Age × capture event	0.092	1	0.297	0.589
Sex × capture event	0.676	1	2.185	0.149
Error	0.309	33		

Note: Samples were drawn from house finches initially captured without clinical signs that were later recaptured either with (group 1) or without (group 0) clinical signs of mycoplasmal conjunctivitis, as described in the Methods. Only the main effects of capture event, infection group, age, sex, and two-way interactions were included in the statistical model. ANOVA results for all between-subject effects alone were not significant at the 0.05 level and are therefore not shown.

in the house finch – MG system, the majority of new infections each fall should occur among juvenile birds. Not unexpectedly, we found that age was a significant predictor of infection risk and that prevalence and severity of mycoplasmal conjunctivitis were notably higher among juvenile than among adult birds. Moreover, juvenile house finches are known to form large roving flocks at the end of the summer breeding period and congregate in large numbers at bird feeders (Hill 1993), both of which might increase the spread of MG among hatch-year birds. In a similar study, patterns of MG prevalence over a 12-month period in Alabama suggested that young birds might be more susceptible to MG than adults (Roberts et al. 2001*b*), although analyses were limited by extremely low observed prevalence (only 49 of 1214 captured birds were infected).

Previous studies in avian systems suggest that reproductive effort and breeding stress can lower host immunity or increase rates of parasitism (e.g., Moreno et al. 2001; Møller and Petrie 2002), and this effect might be more extreme in females than in males. However, neither our study nor previous studies (Hartup et al. 2000, 2001*a*) have found a significant main effect of sex on disease risk during the fall months, and among adult birds captured in the present study, prevalence of MG was lower among females than males. Thus, evidence to date does not support a strong role for breeding stress in generating differential prevalence among adult males and females, although further studies are needed to evaluate potential effects of reproductive investment on subsequent infection status of both sexes.

We might have expected females to be infected more frequently than males because in all *Carpodacus* spp., females are dominant to males during the fall and winter (Brown and Brown 1988; Belthoff and Gauthreaux 1991; McGraw and Hill 2002), spending more time at bird feeders and engaging in more aggressive encounters. If transmission of MG occurs through contacts with bird feeders or aggressive contacts with other birds at feeders (Hartup et al. 1998), females should have a greater probability of contracting the disease. Although we did not observe a significant main effect of sex on overall infection probability, we did note an association between age, sex, and infection status. Thus, both prevalence and severity were highest among juvenile females (Figs. 2 and 3), suggesting that this class of house finches is either physiologically more susceptible or more likely to encounter greater doses of the bacterium through transmission events during the fall.

An additional factor related to host biology that could contribute to annual epidemics is increased host susceptibility brought on by late-summer moulting stress. Moulting has been shown to be energetically costly in some bird species (Lindström et al. 1993) and might increase susceptibility to disease owing to increased stress or reduced body insulation (Ginn and Melville 1983; Svensson and Merila 1996). Whereas adult house finches moult once annually, from early July to mid-October (Hill 1993), most juvenile house finches do not undergo a complete prebasic moult during the fall of their first year. During months when both infected and moulting birds were observed, our study produced no evidence that the moulting status of adult birds at the time of capture was associated with the presence of mycoplasmal conjunctivitis, and prevalence was slightly lower among moulting versus non-moulting adults.

Finally, recent analyses have shown that a second annual rise in the incidence of conjunctivitis among house finches occurs during the months of February and March, coincident with the timing of mate pair formation prior to the breeding season (Hartup et al. 2001*a*; Altizer et al. 2004). It has been hypothesized that this second peak in prevalence results from increased contacts among potential mates or aggressive contacts among males, or that it might also be related to effects of testosterone on male immunocompetence and disease susceptibility. However, we found no evidence for a late-winter rise in incidence, suggesting that the presence of this annual pattern is inconsistent among locations or years.

Condition, based on a composite measure consisting of residual body mass, fat reserves, and muscle development, was poorer among house finches with clinical signs of conjunctivitis than among uninfected hosts. Among infected birds, condition declined with increasing severity of clinical signs, so that birds with mild infections had body condition similar to that of uninfected birds, but those with severe infections were in poorer than average condition. This pattern might reflect a reduced ability of severely infected birds to effectively forage or fly following complete or near blindness caused by extreme conjunctival swelling and discharge.

Our results pointed to a potentially stronger link between infection severity and condition among females than among males (Figs. 3 and 4). Infected juvenile females were more likely to develop severe symptoms, and the decline in body condition of females as a function of disease severity was more pronounced than in males. This result could be caused by a relationship between dominance, stress, and disease severity, given that female house finches (both juveniles and adults) are behaviourally dominant to males. However, the pattern we observed counters a previous study documenting a sex ratio skew following a severe initial outbreak in 1996 in Alabama (Nolan et al. 1998), from which the authors concluded that males were more susceptible to MG than females owing to a decline in the proportion of birds that were male over a 9-month period.

The association between infection severity and host condition could have been caused by greater infection risk among birds in poorer condition. However, separate analyses using

data from house finches recaptured during periods of high prevalence of infection indicated that this was not the case. In fact, the condition of birds upon initial capture was unrelated to their subsequent infection status, whereas the change in condition upon recapture depended strongly on whether or not birds developed clinical signs (Fig. 5).

The proportion of house finches with mycoplasmal conjunctivitis in Atlanta, Georgia, was high relative to estimates from field studies in the northeastern United States (Hartup et al. 2000, 2001*a*, 2001*b*). In New York state, for example, Hartup et al. (2000) captured 196 house finches, of which only 9.7% were infected. In Mercer County, New Jersey, Hartup et al. (2001*a*) captured 1651 house finches over 60 months, and only 11.3% were infected. These observations are in agreement with a large-scale regional comparison of maximum and mean prevalence of MG, suggesting that epidemics are most severe in southeastern North America (Altizer et al. 2004). One possible explanation is that high prevalence of infection in juveniles combined with a longer breeding season in the South could be a major driving force behind the extreme fall southern epidemics. An alternative possibility is that pathogen transmission is greater in the Southeast owing to a longer duration of infectiousness (if, for example, infected hosts live longer because of a milder climate and greater food availability) or longer persistence of pathogen infectious stages outside of the host (for example, on bird feeders). Future studies addressing regional differences in house finch behaviour, survival, and pathogen transmission might identify which of these factors most strongly influences observed epidemiological patterns.

The difference we observed in the magnitude of the fall epidemics between 2001 and subsequent years in Atlanta, Georgia, was also consistent with the timing of multi-year cycles described by a recent large-scale analysis of citizen science data from eastern North America (Altizer et al. 2004). This analysis identified both seasonal and multi-year cycles in the prevalence of conjunctivitis throughout the house finch's eastern North American range, with cycles of higher amplitude in the Southeast. These citizen science data indicated that in the fall of 2001 a seasonal prevalence peak coincided with a multi-year prevalence peak in the southeastern region (Altizer et al. 2004), consistent with the extremely high prevalence (60%) we observed among house finches captured during fall 2001 in Atlanta.

An important and yet unanswered question in epidemiology concerns what factors trigger regular, seasonal outbreaks of infectious diseases in both humans and wild animal populations (Dowell 2001). Our study confirmed that seasonal fluctuations in the occurrence of MG in a wild house finch population were characterized by rapid increases in prevalence during the fall months, potentially coinciding with seasonal changes in juvenile recruitment or social behaviour. Higher prevalence among juvenile birds indicates that seasonal recruitment could elevate the local density of susceptible hosts within populations. Greater infection severity among juvenile females than among males further suggests that dominance interactions at feeders might play a role in disease transmission or host susceptibility. An important possibility is that seasonal changes in house finch ecology and behaviour could sustain longer term cycles of MG and could influence its population-wide persistence. Thus, seasonal factors affecting disease dynamics, including annual recruitment of susceptible juveniles and variation in host social behaviour, might have overriding importance for large-scale spatial and temporal patterns of disease prevalence in this and other avian host–pathogen systems.

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