



Sex, size, and plumage redness predict house finch survival in an epidemic

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Mycoplasma gallisepticum is a well-known disease of poultry, but until 1994 it had not been observed in passerine birds. From 1994 to 1996, tens of millions of house finches (*Carpodacus mexicanus*) are believed to have died in an epidemic of mycoplasmal conjunctivitis, similar to 'pinkeye' in humans. The outbreak of *Mycoplasma gallisepticum* affected finches of both sexes, but disproportionately killed males, shifting the sex ratio from male-biased to female-biased. This differential male mortality is consistent with a cost of testosterone, which is a key prediction of the immunocompetence handicap hypothesis. Males and females that survived the epidemic weighed significantly less and had significantly shorter wing chords, tarsi, and bills than did individuals before the epidemic. Male survivors also had significantly redder plumage than males that did not survive, supporting the idea that plumage brightness serves as an indicator of condition, as proposed by the honest advertisement model of sexual selection.

Keywords: house finch; *Carpodacus mexicanus*; sexual selection; differential mortality; epidemic; *Mycoplasma gallisepticum*

1. INTRODUCTION

Natural selection normally occurs due to subtle differences in survival and reproduction related to certain phenotypes. Generally, the process is slow, requiring numerous generations for appreciable change in traits to accumulate. Less frequently, a catastrophic event may lead to strong selection and rapid change in morphology, but such rapid evolution has rarely been demonstrated in nature. Hermon Bumpus (1899) described an episode of mass mortality in a population of house sparrows (*Passer domesticus*) during a severe winter storm, initiating nearly a century of research on traits favoured by intense selection during catastrophic events (Elton 1927; Johnston & Haines 1957; Price & Grant 1984; Jones 1987). Still relatively unstudied, however, are the effects of epidemic outbreaks of lethal pathogens on traits of wild animals. In 1996, we witnessed an epidemic of *Mycoplasma gallisepticum* as it swept through a colour-banded population of house finches (*Carpodacus mexicanus*). We compared the mean morphological and plumage characteristics of a house finch population before and after the epidemic.

The house finch is a small, sexually dichromatic cardueline finch averaging 13 cm in length and 20 g in mass (Hill 1993a). Males exhibit carotenoid-based plumage coloration on their head, breast and rump, with colours ranging from pale yellow to bright red (Michener & Michener 1931; Hill 1993b). There is little geographical variation in body size or male plumage coloration among eastern USA populations of house finches (Hill 1993a; G. E. Hill, unpublished data). Plumage redness is dependent on good

nutritional condition at the time of moult (Hill 1992; Hill & Montgomerie 1994), making plumage colour an honest signal of male condition.

Mycoplasma gallisepticum is a well-known disease of poultry, but until 1994 it had not been observed in passerine birds (Yoder 1991). In 1994, however, wild house finches with characteristic swollen, crusty eyelids began to be seen at bird feeders in the mid-Atlantic states (Fischer *et al.* 1997; figure 1). Many dead and dying birds were reported to disease control agencies and to wildlife rehabilitation clinics. *M. gallisepticum* was isolated from affected tissues in these birds (Ley *et al.* 1996; Luttrell *et al.* 1996), but only rarely from individuals not showing clinical signs of conjunctivitis. Each of those studies concluded that infection by *M. gallisepticum* was the cause of the epidemic occurrence of conjunctivitis in house finches. By June 1996, cases were being reported from all states and provinces east of the Great Plains and from the eastern provinces of Canada (Fischer *et al.* 1997).

In late 1995, we first observed infected house finches at our feeders on the campus of Auburn University, in east-central Alabama. From June to September of 1996, 60% of the house finches captured for banding and observed at our feeders showed symptoms of mycoplasmal conjunctivitis. The infected birds represented a cross-section of the house finch population, including both sexes and adults as well as hatch-year birds. We assume that most of those individuals died of their infections. The Breeding Bird Survey, carried out by the Biological Resources Division of the United States Geological Survey, estimated annual house finch population growth at 11.77% in the eastern region of the USA from 1990 to 1994. From 1994 to 1995, a period coinciding with the first, limited outbreak of *Mycoplasma gallisepticum*,

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Figure 1. A house finch showing moderate mycoplasmal conjunctivitis. Additional symptoms include sinusitis, rhinitis and respiratory diseases (Luttrell *et al.* 1996). A broth culture and PCR confirmed the presence of *Mycoplasma gallisepticum* in a similarly infected bird. (Photograph: G. Mullen, Auburn University.)

population growth was estimated at 4.5%. During the period from 1995 to 1996, when principal outbreaks were occurring in east coast population centres (Fischer *et al.* 1997), the house finch population across the eastern United States was estimated to have declined 20.73% (Sauer *et al.* 1997). These observations support our assumption of widespread mortality associated with the *Mycoplasma gallisepticum* outbreak. Also, we observed 100% mortality of untreated captive house finches ($n=10$) infected with *Mycoplasma gallisepticum*, and numerous blind or near-blind birds in the wild population that were highly likely to starve or be depredated.

Estimates of the size of the house finch population in the USA range from 250 million to 1.5 billion, with about half of those in the eastern states affected by the epidemic (Hill 1993a). Therefore, if only half of the birds that were infected died as a result, the epidemic may have killed as many as 225 million birds in the USA. By October 1996, the proportion of sick birds at our study site had declined to less than 2%, indicating an end to the epidemic-level phase of the outbreak.

2. METHODS

Birds were caught at feeders using wire-mesh traps. We weighed each individual, fitted them with a unique colour combination of leg bands, then measured the lengths of the tarsus, beak, tail, and wing chord. All birds were scored subjectively for the presence and abundance of feather mites and pox lesions, and

for the presence of *M. gallisepticum* infection as shown by conjunctivitis (see figure 1).

A cell culture and polymerase chain reaction (PCR) performed by the Diagnostics Laboratory of the Veterinary School at Auburn University confirmed the presence of *M. gallisepticum* in both a house finch and an American goldfinch (*Carduelis tristis*) from our study site, validating our use of visual inspection for swelling around birds' eyes as an assay of the presence of *M. gallisepticum*.

We used a hand-held Colortron[®] spectrophotometer to measure the plumage hue on each male's crown, rump and breast regions (Hill 1998). We measured three different spots within each region, for a total of nine measurements that we averaged to give a total score of colour.

We determined the sex of individual birds using the species' plumage dimorphism. House finches complete their basic moult by October, with males showing ornamental coloration on the head, breast and rump that ranges from pale yellow to bright red. Whereas some females express a wash of carotenoid-based coloration, the plumage coloration of the sexes is distinct and the sex of the birds can be determined with relative certainty using plumage coloration (Hill 1993a,c, 1996).

Because the sex of all individuals cannot be determined accurately before completion of the autumn moult, and to account for seasonal differences between the sexes in their susceptibility to trapping (i.e. when females are incubating eggs), we calculated sex ratios in each year by examining only data gathered from November through to February (i.e. from 1 November 1993 through to 28 February 1994). We report data from the summer of 1995 only for individuals that had already completed the

moult, because no trapping was done in the autumn of that year. Data for comparison of pre- and post-epidemic morphological characteristics were gathered between 23 January and 16 May in both 1996 and 1997.

Pre-epidemic versus post-epidemic comparisons were made by Student's two-sample *t*-tests (two-tailed) after testing for equality of variances, all using Microsoft Excel[®] software. χ^2 analysis of differences in the sex ratios between years was also done using Microsoft Excel[®] software. The χ^2 statistic was calculated by comparing the observed values for November 1996 to February 1997 ($n=441$ birds; 182 males and 259 females) against the expected values as derived from observations during the period from November 1993 to February 1994 ($n=108$ birds; 56 males and 52 females). We used the values from 1993 to 1994 for comparison because they were the most similar to those from 1996 to 1997, and so represented a conservative test for a shift in the sex ratio.

3. RESULTS

A total of three traits predicted individual survival of the epidemic: ornamental plumage colour, sex and body size. In birds like the house finch that undergo a single moult each year, plumage develops in the late summer and the carotenoid-based ornamental coloration of new feathers is dependent on nutritional condition at that time (Hill 1992; Hill & Montgomerie 1994). Following the epidemic, we captured very few males with drab yellow plumage and the mean plumage score of males was significantly lower (i.e. colours were brighter) than it had been before the epidemic. These observations suggest that the individuals that died in the epidemic were those that were in poor nutritional condition in the summer of 1996 and which would have been drably pigmented after the moult. Before the epidemic, the sex ratio ranged from 1.08 to 1.44 males per female, but declined to 0.72 males per female following the epidemic (see figure 2). This suggests that a higher proportion of females than of males survived exposure to *M. gallisepticum*.

The means of all body size measurements taken of males after the epidemic declined significantly relative to measurements taken before the epidemic, with one exception. Tail length showed a significant increase (see table 1). Females also showed significant decreases in wing chord, bill length, tarsus length and weight, but did not show a significant increase in tail length (table 2).

4. DISCUSSION

Sexual selection favours those traits that increase performance in either male–male competition or in female mate choice (Darwin 1871), and some models predict that traits will be favoured if they honestly advertise the individual's genetic or physical quality (Andersson 1982; Kodric-Brown & Brown 1984). Sexual selection in house finches acts predominantly by female mate choice rather than by male–male competition, with females preferring as mates those males with the reddest and most intensely pigmented plumage (Hill 1990, 1991, 1994). The observation that brightly plumaged males survived the epidemic better than drably plumaged males suggests that plumage colour serves as an honest signal of male condition.

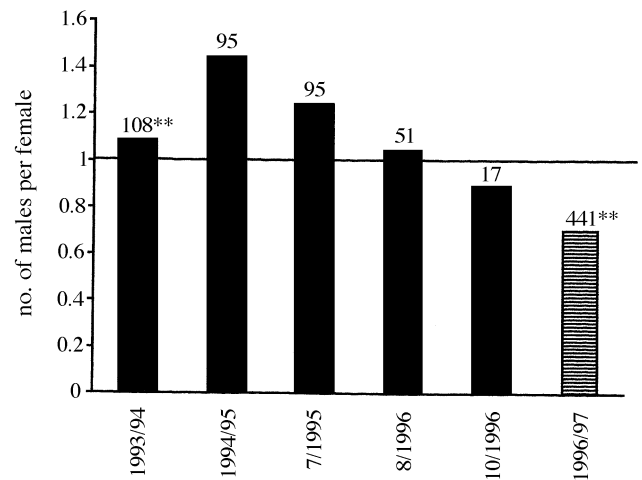


Figure 2. Temporal changes in sex ratio at Auburn, Alabama. The horizontal line represents a sex ratio of one male per female. Numbers above the bars are the combined sample size of males and females from which the sex ratio was calculated. Data for 1993 to 1994, 1994 to 1995, and 1996 to 1997 were collected from 1 November to 28 February of each winter. Data for July 1995 are included because no banding was done in the winter of 1995–1996. Data from August 1996 and October 1996 are presented to show the timing of the decline in sex ratio, but are not included in the calculation of the 1996–1997 sex ratio. **Post-epidemic sex ratio was significantly different than the most similar of the pre-epidemic sex ratios, that observed from November 1993 to February 1994 ($\chi^2=20.07$, d.f.=1, $p<0.001$). The χ^2 -statistic was calculated by comparing the observed values for November 1996 to February 1997 ($n=441$ birds; 182 males and 259 females) against the expected values from 1993 to 1994 ($n=108$ birds; 56 males and 52 females).

One mechanism by which signal honesty may be maintained is if the ornament is testosterone-dependent and elevated testosterone levels carry a mortality cost owing to immunosuppression. This mechanism is a critical prediction of another model of female mate choice, the immunocompetence handicap hypothesis (Folstad & Karter 1992). Males are typically more susceptible than females to pathogens or parasites (Alexander & Stimson 1988; Zuk 1992; Zuk & McKean 1996), and show depressed levels of response when their immune system is challenged with novel antigens (Grossman 1985). These differences have been shown experimentally to correlate with an individual's circulating level of testosterone (Alexander & Stimson 1988), which in most avian species is higher in males than in females. However, it is important to note that because we have no information on the hormone status of the birds exposed to the epidemic, or on the role of testosterone in expression of carotenoid-based plumage coloration, our data represent a necessary—but not a sufficient—test of the immunocompetence handicap hypothesis.

Given that house finches of both sexes do not defend territories (Hill 1993a) and should, therefore, have access to similar food resources, mortality owing solely to poor nutrition should strike the sexes equally and leave the population sex ratio unchanged. However, after the epidemic, we observed a female-biased sex ratio of 0.72:1 (male:female; figure 2). This differs significantly from past observations of male-biased sex ratios in five other

Table 1. *Male morphological and plumage characteristics pre- and post-epidemic*

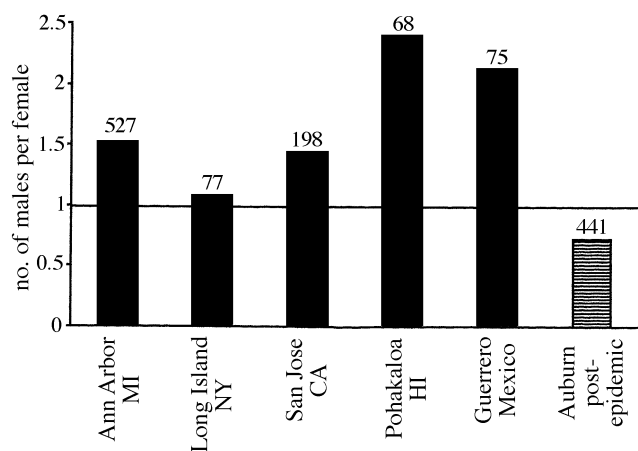
(No significant differences were found in levels of infestation with pox or mites.)

	pre-epidemic mean (s.d.)	post-epidemic mean (s.d.)	<i>t</i>	d.f.	<i>p</i>
plumage colour ^a	5.53 (4.33)	3.74 (5.19)	2.94	302	0.004
wing chord (mm)	77.98 (2.00)	77.27 (1.89)	3.03	307	0.003
bill length (mm)	9.33 (0.84)	8.75 (0.38)	8.34	309	≤0.001
tarsus length (mm)	18.83 (1.44)	16.88 (0.55)	12.94	109	≤0.001
tail length (mm)	58.11 (2.57)	59.85 (2.34)	-5.88	307	≤0.001
weight (g)	20.70 (1.09)	20.22 (1.27)	3.14	309	0.002

^aColour hues are expressed as angles on a 360° colour wheel; lower values are more red (Hill 1998).Table 2. *Female morphological characteristics pre- and post-epidemic*

(No significant differences were found in tail length or levels of infestation with pox or mites.)

	pre-epidemic mean (s.d.)	post-epidemic mean (s.d.)	<i>t</i>	d.f.	<i>p</i>
wing chord (mm)	76.39 (2.00)	74.65 (2.05)	8.13	422	≤0.001
bill length (mm)	9.13 (0.53)	8.81 (0.40)	6.24	195	≤0.001
tarsus length (mm)	17.69 (1.10)	16.87 (0.72)	9.37	199	≤0.001
weight (g)	20.78 (1.32)	20.24 (1.37)	3.63	405	≤0.001

Figure 3. Sex ratios of six house finch populations. All populations of house finches studied in the past have shown sex ratios of greater than one male per female (represented by the horizontal line) (Hill *et al.* 1994). Numbers above the bars are the combined sample size of males and females from which the sex ratio was calculated.

populations in the USA and Mexico (Hill *et al.* 1994; figure 3), and also from three years of previous observations at our site. Because males and females frequently associate, we attribute this shift in the sex ratio to greater male susceptibility to *M. gallisepticum* and not to increased male exposure to the organism. Thus, the poor nutritional condition of some birds, as reflected in their plumage colour at the time of the epidemic, may have made an additive or even synergistic contribution to testosterone-influenced mortality. The resultant higher mortality of

male house finches in the *M. gallisepticum* epidemic is consistent with key predictions of both the immunocompetence handicap hypothesis and the honest advertisement model of sexual selection.

More puzzling was our finding that small body size predicted survival (see tables 1 and 2). A similar survival advantage for small-bodied birds was observed for sand martins (*Riparia riparia*) following a severe drought (Jones 1987). However, Bumpus's classic study (1899) of house sparrows documented stabilizing rather than directional selection, with decreased survival of the largest and smallest individuals enduring a severe winter storm. Darwin's finches (*Geospiza* sp.) feed more efficiently when their beak size is closely fitted to the size of seeds available during periods of strong natural selection (Grant & Grant 1996). Large beaks, and therefore large individuals, were favoured by selection when a drought left only large seeds (Boag & Grant 1981). A second drought left predominantly small seeds, shifting the advantage in feeding efficiency to small-beaked individuals (Gibbs & Grant 1987). Nutrition is an important determinant of immunocompetence (Glick *et al.* 1981, 1983), so perhaps smaller house finches found it easier to gather the resources necessary to resist infection by *M. gallisepticum* than the larger individuals.

Explanations other than selection for favoured characteristics certainly exist for the shifts we observed in body size and plumage colour, and can only partly be discounted given the available data. For example, house finches typically show at least a slight increase in plumage colour as they age and pass through successive moults (Hill 1992). If the epidemic primarily struck hatch-year birds, then the resulting age structure in the following year would be skewed towards birds that were older and redder. However, the high rate of infection we observed, and the gregarious nature of house finches, should have

ensured that all birds were exposed to the pathogen, and we observed infection in both sexes and all age classes except nestlings. Furthermore, adult body size is reached soon after fledging, so body size would not have been affected by a shift in age structure.

The shortage of breeding males in the 1997 population decreased the ability of females to be 'choosy' when judging potential mates, and may have temporarily decreased the value of mate choice because all males in the area were proven survivors. In past years, and at other study sites, brighter males were more successful than drabber males at acquiring mates (Hill 1990, 1991; also G. E. Hill, unpublished data). In other populations of house finches as many as 40–50% of males failed to attract mates (Hill 1993a; Hill *et al.* 1994), whereas at our study site in 1997 nearly all males were paired, regardless of their plumage coloration. We predicted that some females would form polygynous relationships with the most desirable males, because there were insufficient males for all females to be simultaneously in monogamous pairs. However, careful observation and periodic video-taped monitoring of nests in our study site revealed no evidence of polygyny in the 1997 field season.

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