Carotenoid-based plumage colouration predicts resistance to a novel parasite in the House Finch

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Geoffrey E. Hill
Auburn University

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SHORT COMMUNICATION

Geoffrey E. Hill · Kristy L. Farmer

Carotenoid-based plumage coloration predicts resistance to a novel parasite in the house finch

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Abstract The Hamilton-Zuk hypothesis proposes that the bright colours displayed by many species of birds serve as signals of individual resistance to parasites. Despite the popularity of this hypothesis, only one previous study has tested whether plumage coloration predicts how individuals respond to a disease challenge. We inoculated 24 male house finches (*Carpodacus mexicanus*) of variable plumage hue with a novel bacterial pathogen, *Mycoplasma gallicepticum* (MG). We found no relationship between plumage hue and time to first symptoms following inoculation, but we found a significant negative relationship between plumage hue and clearance of disease: males with redder plumage cleared MG infection significantly better than did males with yellower plumage. The hue of carotenoid-based plumage coloration has been shown to be a primary criterion in female mate choice in the house finch. These observations suggest that one benefit to females for choosing redder males is obtaining mates with better resistance to parasites.

Introduction

A basic tenet of honest signalling theory is that expression of ornamental traits provides reliable information about the signaller to a receiver (Zahavi 1975; Andersson 1994). For ornamental traits that are used by females to assess potential mates, disease resistance has been proposed to be one of the key types of information that is signalled (Hamilton and Zuk 1982). By pairing with disease-resistant males, females would reduce their risk of losing resource investment if a mate became infected during breeding or would gain good genes for disease resistance for offspring if disease resistance were heritable.

G. E. Hill (✉) · K. L. Farmer
Department of Biological Sciences,
Auburn University,
331 Funchess Hall, Auburn, Alabama, 36849, USA
e-mail: ghill@acesag.auburn.edu
Tel.: +01-334-8449269
Fax: +01-334-8449234

Plumage coloration in particular has been proposed to serve as an honest signal of disease resistance (Hamilton and Zuk 1982). It has now been shown experimentally that parasites can have a direct negative effect on expression of structural (Hill et al. 2004b) and carotenoid-based (Brawner et al. 2000; McGraw and Hill 2000; Hill et al. 2004a) plumage coloration, so there is direct evidence that plumage coloration can serve as a signal of exposure to parasites during the previous moult. However, the evidence that plumage coloration honestly signals the potential to resist future infections is scant. A number of correlative field studies have shown that males with brighter plumage coloration have fewer parasites (reviewed in: Hamilton and Poulin 1997; Lindström and Lundström 2000), but in these sorts of correlative studies it is not possible to distinguish cause and effect. In addition, studies have shown a relationship between plumage coloration and immune function (Roulin et al. 2000; Saks et al. 2003), which has been interpreted as evidence that plumage colour signals disease resistance, but others have argued that the relationship between immune responsiveness, parasite resistance, and ornamentation can be complex (Folstad and Karter 1992; Gonzalez et al. 1999; Poiani et al. 2000). Only in one experimental study has it been clearly demonstrated that males with more elaborate display of plumage coloration are more resistant to infection by a pathogen. Lindström and Lundström (2000) infected a group of male greenfinches (*Carduelis chloris*) with Sindbis virus and found a significant negative relationship between the size of the patch of yellow carotenoid coloration on the tail and time to clear the virus. This study is the only direct test of the hypothesis that plumage coloration signals disease resistance.

Here, we experimentally infected adult male house finches (*Carpodacus mexicanus*) with a novel bacterial pathogen *Mycoplasma gallicepticum* (MG) and tested the hypothesis that expression of plumage coloration predicts parasite resistance. The house finch is the best-studied bird in the world with respect to the control and function of carotenoid-based plumage coloration. Male house finches have carotenoid-based plumage coloration on their heads, undersides, and rumps that varies in expression from pale yellow to bright red (Hill 2002). Female house finches use expression of male plumage coloration as a primary criterion in mate choice, preferring as mates males with redder and more saturated coloration and larger patches of coloration (Hill 1990, 1991, 1994, 2002). Expression of carotenoid coloration by males is dependent on their condition during moult. Infection by coccidia, pox virus, and *Mycoplasma* during moult have been shown to decrease expression of plumage coloration (Thompson et al. 1997; Brawner et al. 2000; Hill et al. 2004a). General nutrition and access to carotenoid pigments during moult can also affect expression of plumage coloration (Hill 1992, 1993, 2000).

MG is a bacterium that is a well-known pathogen of domestic chickens and turkeys (Yoder 1991). It was essentially unknown as a songbird disease until 1994 when it was confirmed in house finches in Maryland (Ley et al. 1996). The disease subsequently spread as an epidemic across the eastern portion of North America in the house finch population (Dhondt et al. 1998; Roberts et al. 2001b). In poultry, MG is primarily a respiratory disease (Yoder 1991), but in the house finch in addition to causing a respiratory infection it infects the conjunctiva of the eye causing conspicuous swelling (Ley et al. 1996; Roberts et al. 2001a). MG has not been confirmed from the Pacific coast of North America nor anywhere outside of North America (Duckworth et al. 2003), so no songbirds in the Hawaiian Islands have been exposed to the pathogenic strain of MG that has spread through the eastern North American house finch population.

In this study, we captured adult house finches representing a full range of colour variation from the island of Hawaii. These birds lived outside the known range of house finch MG and are presumed to have never been exposed to this pathogen. We inoculated them with house finch MG, and then monitored the onset and clearance of disease in each individual over an 8-week period. Following honest-signalling theory, we predicted that there would a negative relationship between resistance to and clearance of disease caused by MG and expression of carotenoid-based plumage coloration.

Methods

We captured 24 adult (after hatch year) house finches at Pohakuloa Training Area between Mauna Loa and Mauna Kea on the island of Hawaii on 10–12 June 2003. All birds were free of pox infection based on visual inspection. These birds were shipped to Auburn, Alabama, on 13 June 2003 where they were held in pairs in cages 0.5 m^3. All birds were given ad libitum water and pellet food.

Within 1 week after transport to Auburn, technicians measured the hue, within the human visible spectrum (400–700 nm), of the crown, breast, and rump of each male using a Colortron II reflectance spectrophotometer (Hill 1998). Hue is a measure of the region of the spectrum that is reflecting the most light; it is the property of reflectance spectra that we typically think of as the colour of an object. The Colortron assigns a value to hue as an angle on a colour wheel, from red (0) to violet (360), which means that redder males are assigned lower hue scores and yellower males higher scores.

Three measurements were taken in each of the three plumage regions by lifting the Colortron and placing it over a different patch of feathers. We used the averaging function of the Colortron II software to calculate a mean hue for crown, rump, and breast. We then calculated an overall mean hue from these crown, breast, and rump scores. Hue was chosen as the colour variable on which to focus in this study because it is the colour descriptor that varied the most among the males that we captured in Hawaii (coefficients of variation: hue =60%, saturation =18%, brightness =23%), it is the most condition-dependent component of colour in the house finch (Hill 2002), and it is the aspect of male coloration that is most important in female mate choice in the house finch (Hill 2002).

Our approach to this study was to use the wealth of information available on house finch carotenoid ornamentation to focus on the single ornamental trait most likely to serve as a signal of disease resistance, instead of measuring many ornaments and using statistics to search for relationships to disease resistance. By focusing exclusively on plumage hue, we increased the power of our tests and greatly reduced the number of finches needed to detect a weak effect in the infection experiment. Because birds used in this experiment had to be killed at the completion of the project and had to endure an infection during the experiment, reducing the number of test subjects was a priority in our experimental design.

In Auburn, the finches were given 3 weeks to adjust to captivity and then were inoculated with 20 μl of SP4 culture containing 1×10^7 colour-changing units/ml of house finch MG in both eyes, as described in detail in Farmer et al. (2002). The MG used in this infection experiment had been cultured from a wild house finch captured in Auburn, Alabama. Colour changing units are calculated using an end-point titration assay based on detection of a colour change in the culture medium that results from acid production during the growth of the bacteria. While not commonly used with other bacteria, this assay is used to quantify mycoplasmas because they are fastidious, do not grow well on solid media, and do not produce turbidity in liquid culture. On Monday, Wednesday, and Friday of each week an observer scored the severity of disease in both eyes of each bird on a 5-point scale, where 0 = no disease and 4 = blindness due to swelling (see Farmer et al. 2002 for details). Technicians who scored eye infection could see the colour of the bird, but were not aware of the hypothesis being tested and thus were unlikely to bias eye scores relative to male plumage coloration.

Males were monitored for 8 weeks after inoculation, and we divided these 8 weeks into four 2-week observation periods. For each period, we took the mean eye-swelling score for each male and used this as a measure of degree of mycoplamsal infection. Males remained free of disease symptoms for different numbers of days during period one (weeks 1 and 2 post exposure), so mean score in period one was not used in analyses of disease clearance. We did, however, look at time to first symptom in relation to plumage hue. We determined clearance of MG infection by subtracting the mean disease scores of period two from period three and the mean disease scores of period three from period four. Negative clearance values indicate a reduction in disease symptoms and positive clearance values indicate an increase in symptoms.

Because disease symptoms were assessed on an ordinal scale, we used non-parametric Spearman rank correlation coefficients to test for relationships between plumage hue and disease onset and clearance. We used the Bonferroni-corrected alpha of 0.025 to test for significance.

Results

Following inoculation, 22 of 24 males developed symptoms of mycoplasmosis at some point during the 58 days of the experiment. The two birds that never developed symptoms of mycoplasmosis were included in the analysis of time-to-infection data, but were not included in the analysis of disease clearance.

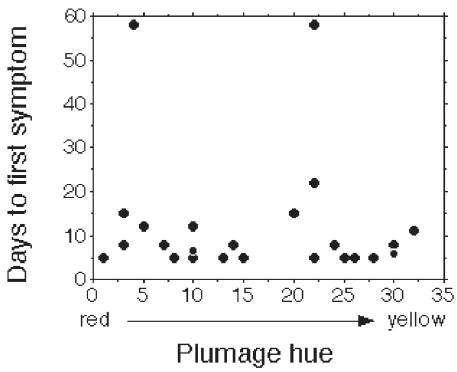

Fig 1 The relationship between the hue of carotenoid-based plumage coloration of male house finches (*Carpodacus mexicanus*) and time to first symptoms of mycoplasmosis following experimental inoculation with *Mycoplasma gallicepticum*. Hue is position on a colour wheel where red =0 and yellow =30, so redder males receive lower scores

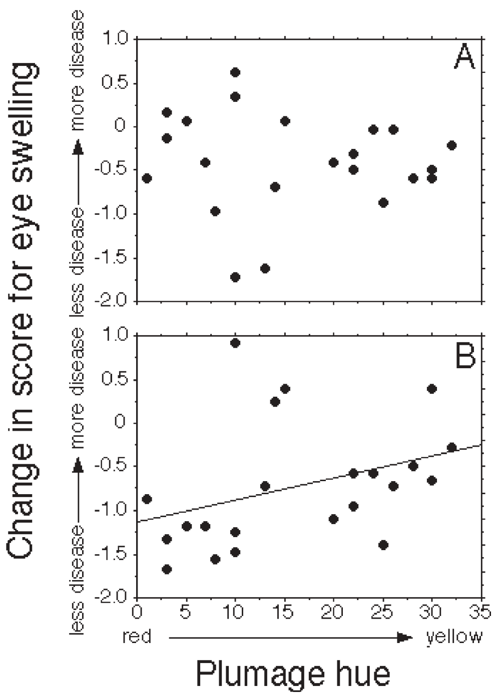

Fig 2a–b The relationship between the hue of carotenoid-based plumage coloration of male house finches and change in infection status between sampling periods. Plotted are the changes in mean eye scores for males between (**A**) periods two and three and (**B**) periods three and four. Positive values indicate an increase in symptoms of mycoplasmosis and negative values indicate a clearance of mycoplasmosis symptoms. See text for an explanation of the scale for eye scores and sampling periods. Hue is position on a colour wheel where red =0 and yellow =30, so redder males receive lower scores

There was no significant relationship between the number of days to reach an eye swelling score of one and the hue of a male's plumage (hue: r_s=–0.09, n=24, P=0.65; Fig. 1). Thus, we found no evidence that plumage coloration signals a male's ability to resist initial infection following exposure to a pathogen.

There was no significant relationship between plumage hue and clearance of disease between periods two and three (n=22, r_s=-–0.15, P=0.49; Fig. 2a), but there was a significant relationship between plumage hue and clearance of disease between periods three and four (n=22, r_s=0.54, P=0.01; Fig. 2b).

Discussion

When we infected adult male house finches of variable plumage coloration with a novel bacterial pathogen, we found a significant relationship between hue of breast coloration and ability to clear the disease. Specifically, redder males showed a greater clearance of MG infection than did yellower males between 6 and 8 weeks after inoculation. It is interesting that the relationship between clearance of infection and plumage coloration only became significant toward the end of the experiment. MG infection is associated with a long progression of illness in house finches (Roberts et al. 2001a). By 7–8 weeks after infection some birds began to clear their infections and these birds tended to be brighter than average.

We designed this study thinking that time to initial clinical symptoms would be our best and most direct measure of disease resistance. However, we found no relationship between time to initial symptoms of mycoplasmosis and plumage coloration. Combined with the significant relationship between disease clearance and colour, this observation suggests that plumage redness in the house finch is a reliable indicator of ability to recover from MG infection, but not ability to resist becoming infected. However, the mode by which male house finches were exposed to MG in this experiment may have masked differences in ability to resist initial infection. We exposed male finches by dropping medium with a high concentration of MG into both eyes; in contrast, in the wild, birds would likely be exposed to much lower doses of MG at feeders or roost sites. Any subtle differences in ability to resist infection could have been overwhelmed by the massive exposure created by inoculation.

To date, most of the numerous studies that have addressed the Hamilton-Zuk hypothesis (Hamilton and Zuk 1982)—that expression of ornamental traits signals resistance to parasites—as it relates to plumage coloration have either shown that exposure to parasites depresses expression of an ornament or that ornament expression is negatively correlated with parasite load (see Hamilton and Poulin 1997; Lindström and Lundström 2000 for reviews). Both of these types of data, however, merely show that ornament expression can reflect past parasite infection. For a female choosing a mate based on expression of an ornamental trait, information about ability to resist future infections should be equally or more important than information on past parasitism. Thus, a key prediction of the Hamilton-Zuk hypothesis, that expression of an ornamental trait predicts ability to resist infection, has rarely been tested.

In the only previous study looking at whether plumage coloration predicts how individuals respond to a disease challenge, Lindström and Lundström (2000) looked at whether the pattern of coloration of greenfinches predicted ability to deal with a viral infection. In their study, they measured the extent of yellow for six plumage patches and used multivariate statistics to compare these patch sizes to the ability of males to resist infection by a virus. Only the size of the yellow tail patch was significantly related to total viremia and virus clearance rates. Eley (1991) reported indirect evidence for mate choice related to plumage coloration in the greenfinch, which could provide a link between colour display, disease resistance, and mate choice. But in her study, Eley (1991) looked at colour quality (the saturation of yellow coloration), not patch size. Thus, the relevance of the link between tail patch size and disease resistance in the greenfinch is not entirely clear.

Saks et al. (2003) also studied carotenoid-based plumage coloration of male greenfinches in relation to disease resistance. Rather than studying response to infection directly, they measured both humoral and cell-mediated immune responsiveness in relation to plumage coloration. They found that males with brighter yellow breast feathers had a stronger humoral immune response, but there was no relationship between cell-mediate response and colour. Roulin (2001) found a positive relationship between amount of melanin pigmentation of female barn owls (*Tyto alba*) and the ability of offspring to resist parasitism, but studies with house sparrows (*Passer domesticus*) have found a complex relationship between measures of immunocompetence and the size of black, melanin-based feather patches (Gonzalez et al. 1999; Poiani et al. 2000).

The strength of the present study is that it fits within an extensive framework of knowledge of carotenoid-based plumage hue in the house finch. Both laboratory and field studies on a number of populations of house finches, including the Hawaiian population, have shown that females prefer to mate with males with redder plumage hue (Hill 1990, 1991, 1994; Hill et al. 1999). Plumage hue is a condition-dependent trait in the house finch that is affected by past exposure to parasites (Thompson et al. 1997; Brawner et al. 2000; Hill et al. 2004a), access to carotenoids (Hill 1992; Hill 1993; Hill et al. 2002), and nutritional condition during moult (Hill and Montgomerie 1994; Hill 2000). The most likely means by which plumage hue relates to ability to recover from MG infection is that redder males are in better phenotypic condition and thus better about to withstand a disease challenge (Hill 2002). Alternatively, plumage coloration might be linked to genes for disease resistance, but this has yet to be shown convincingly for plumage coloration in any species.

Another mechanism that could link plumage coloration to disease resistance is an enhancement of the immune system resulting from the anti-oxidative effects of carotenoid pigments (Lozano 1994; Møller et al. 2000). Carotenoid pigments have been shown to be effective free-radical scavengers that can bolster the immune systems of vertebrates (reviewed in Møller et al. 2000). Recent studies have shown that supplementing zebra finches (*Taeniopygia guttata*) with carotenoids can simultaneously cause bill hue to become redder and improve immune responsiveness to a novel protein (Blount et al. 2003; McGraw and Ardia 2003). Potentially, male house finches with redder plumage could have greater stores of carotenoids that could be used for immune enhancement, but house finches do not store significant amounts of mobilisable carotenoid pigments (Hill 1992; Inouye 1999). Alternatively, male house finches with redder plumage might be more efficient at extracting carotenoids from the diet, and the better clearance of disease by redder male house finches might be a result of higher levels of circulating carotenoid pigments. We cannot directly address this latter hypothesis, but all house finches in this study were held on a diet with low levels of carotenoids. In an experimental study of American goldfinches (*Carduelis tristis*), another finch in the same subfamily with bright carotenoid-based plumage coloration, two orders of magnitude differences in intake of dietary carotenoids had no effect on immune responsiveness or ability to clear MG infection (Navara and Hill 2003).

Regardless of the mechanism linking plumage redness to disease resistance, our observations suggest that a benefit to female house finches of choosing a male with redder plumage is that such males are more likely to withstand future disease challenges.

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