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ORIGINAL PAPER

Do feather-degrading bacteria affect sexually selected plumage color?

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Abstract Models of parasite-mediated sexual selection propose that males with more elaborate sexual traits will have fewer parasites. These models have generally been tested using metazoan or protozoan parasites of the blood, gut, or integument. Fewer studies have examined sexual ornaments in relation to bacterial infections. While most surface bacteria are harmless or beneficial, feather-degrading bacteria may have detrimental effects. In this study, we examined the relationships between overall bacterial load, feather-degrading bacterial load, and sexually selected carotenoid-based plumage color in a wild population of house finches (*Carpodacus mexicanus*). We found that males with the redder plumage preferred by females had similar overall bacterial loads, but lower feather-degrading bacterial loads, than males with less red plumage. These data suggest that plumage color can signal abundance of feather-degrading bacteria to potential mates. It remains unclear whether feather-degrading bacteria directly or indirectly affect plumage color, but the observed correlations suggest that feather-degrading bacteria may play some role in sexual selection.

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Indicator models of sexual selection propose that ornamental traits signal some aspect of male quality (Andersson 1994). One important aspect of quality for virtually all animals is the degree to which an individual is parasitized. If rates of parasitism vary within a population, high-quality males should have fewer parasites than low-quality males. If ornaments are signals of quality, it follows that males with few parasites should be more highly ornamented than males with many parasites. Females should prefer to mate with males with low parasite loads to avoid parasite transfer (Freeland 1983; Borgia 1986; Hillgarth 1996), to gain greater parental care (Hamliton 1990; Milinski and Bakker 1990; Møller 1990), or to pass on genes for parasite resistance (Hamilton and Zuk 1982).

Most studies testing parasite-mediated sexual selection have focused on protozoan or metazoan parasites of the blood, gut, or integument (Møller et al. 1999), while fewer studies (Nolan et al. 1998; Brawner et al. 2000) have documented associations between internal bacterial infection and sexually selected traits. Clearly, more studies that include bacteria are needed because bacteria are ubiquitous symbionts of animals, and they frequently have deleterious effects on organisms. Bacterial colonization can cause acute diseases, or they can have more subtle deleterious effects.

Degradation of feathers is a consequence of bacterial infection that can have non-lethal but important consequences for birds (Burtt and Ichida 1999; Clayton 1999; Shawkey and Hill 2004; Shawkey et al. 2007). Feather-degrading bacteria could negatively affect birds by decreasing the thermoregulatory or aerodynamic efficiency of plumage as well as by lessening protection from other bacterial infections (Muza et al. 2000) provided by feathers (Burtt and Ichida 1999; Clayton 1999; Shawkey and Hill

2004). Based on models of parasite-mediated sexual selection, we predicted that birds with lower abundances of feather-degrading bacteria during the breeding season would have more elaborate expression of plumage coloration. Only a small subset of the bacteria on feathers degrades the feathers and cause damage to the birds. The theory of parasite-mediated sexual selection proposes that prevalence of parasitic microbes—microbes that are detrimental to their hosts—rather than all microbes, will be negatively correlated to ornament expression. Thus, we would expect a stronger negative association between ornamentation and feather-degrading, parasitic bacteria than between ornamentation and all bacterial taxa.

We tested these predictions by studying plumage coloration and feather bacteria in the house finch (*Carpodacus mexicanus*). Carotenoid-based coloration of house finches is a classic example of a sexually selected trait driven by female choice; females prefer brighter males and these males have lower parasite loads, better body condition, and bring more food to the nest than duller males (Hill 2002). Thus, indicator models of sexual selection predict that bright red males should have fewer feather-degrading bacteria than dull males. We tested this prediction by trapping adult male house finches during the breeding season and measuring the total abundance of bacteria and the abundance of feather-degrading bacteria on their feathers. We then compared measures of bacterial abundance on these feathers to their plumage color and an index of overall condition. We then isolated and identified the feather-degrading subset of bacteria found on these birds.

Methods

Sampling

During the breeding season, from April 1–July 1, 2002 we captured 29 adult male house finches in mist nets and feeder traps on the campus of Auburn University in Lee County, Alabama (32°35′ N, 82°28′ W). Wearing latex gloves, we gently rubbed a BBL™ CultureSwab™ (Becton–Dickinson, Sparks, MD, USA) dipped in sterile phosphate-buffered saline (PBS) for 3 s on the carotenoid-colored breast, rump, and crown of the birds. A separate swab was used for each area. The swabs were immediately refrigerated and then washed in 1 ml sterile PBS within 4 h of collection.

Media

We used two types of media for quantification of bacteria. Tryptic soy agar (TSA; Difco, Detroit, MI, USA) is a rich medium that supports a wide variety of microorganisms, and its use enabled us to quantify overall bacterial load, including most feather-degrading and other bacterial biota. We sampled for the feather-degrading subset of these bacteria by using feather meal agar (FMA; Sangali and Brandelli 2000) containing 15 g l^{-1} feather meal, 0.5 g l^{-1} NaCl, 0.30 g l^{-1} K_2HPO_4, 0.40 g l^{-1} KH_2PO_4, and 15 g l^{-1} agar. FMA was used specifically to estimate feather degrading bacterial load, as it contains feather keratin as its sole source of carbon (Sangali and Brandelli 2000). Therefore, any bacteria growing on it should be able to digest keratin and could be considered "feather degrading."

We spread-plated 100 μl of our inoculated PBS samples in duplicate on TSA and FMA and incubated the plates at 37°C. TSA plates were removed after 2 days, while FMA plates were removed after 14 days. The faster growth of microorganisms on TSA than on FMA necessitated this difference in incubation time, as colonies began to merge and, hence, became uncountable after 48 h on TSA. FMA plates were incubated longer as colonies could be clearly distinguished only after 2 weeks. The numbers of visible colony forming units on each plate from each location (breast, rump, and crown) were counted and added together for each media type as estimates of total and feather degrading bacterial load. All counts were performed by one of us (M.D.S.) without knowledge of the bird's color scores.

Color scoring

Following bacterial sampling, the color of the breast, rump, and crown of these house finches was measured using a Colortron™ reflectance spectrophotometer (Hill 1998). The Colortron™ provides hue, saturation, and brightness scores in the wavelengths from 400–700 nm for each area of color measured. Although it does not measure into the bird-visible ultraviolet wavelengths (Bennett et al. 1994), the Colortron™ measures variables that are known to be important in house finch color signaling (Hill 2002) and, thus, is a valid tool for this study. We used hue in our comparisons of plumage color and bacterial load because hue has been shown to be the most important color variable in house finch color signaling (Hill 2002). By arbitrary convention, the Colortron™ scores hue as a position on a circular 0° to 360° scale, in which red hues have lower values than yellow hues. Each bird was measured three different times on each body region. These three measurements were averaged together to provide a single score for each body region, and these scores were averaged together to provide an overall measure of color for each bird.

We measured the left tarsus of all birds using calipers accurate to 0.1 mm and weighed them using a digital scale readable to 0.01 g. We used the residuals from the linear

(ordinary least squares) regression of mass on tarsus as our index of condition (Jakob et al. 1996).

Identification of bacteria

We isolated all bacterial strains with distinctive colony morphology from FMA and streaked them on TSA. We incubated them for 48–72 h until we could determine the purity of our cultures as evidenced by unique colony morphology characteristics. Pure cultures were (a) restreaked on TSA and incubated at 28°C for 48 h in preparation for identification and (b) grown overnight in tryptic soy broth and then mixed 1:1 with glycerol for storage at −80°C.

A loopful of cell material of late-log phase cells was harvested from the restreaked cultures, and fatty acids were extracted and methylated according to the procedure described by the manufacturer (Microbial ID, Inc., Newark, DE, USA). Samples were analyzed using a Hewlett 137 Packard (Palo Alto, CA, USA) 5890 series II gas chromatograph with a 7673 autosampler, a 3396 series II integrator, and a 7673 controller. Using the Sherlock (Microbial ID, Inc.) program on a Hewlett–Packard Vectra QS/20 computer, the chromatograms were compared to a database of reference cultures previously grown on TSA. This identification method is widely used and accurate (Smit et al. 2001; Shawkey et al. 2005; Krejci and Kroppenstedt 2006).

Although FMA contains feather keratin as its sole source of carbon, some bacterial taxa may utilize the byproducts of other bacteria rather than the keratin itself. To control for this possibility, we restreaked each unique identified FMA taxon from cold storage back on FMA and incubated them at 37°C for up to 2 weeks. We considered any growth of the isolated bacterial strains on FMA as evidence of keratinolytic capabilities.

Analyses

All analyses were performed on SPSS v.10. Total and feather-degrading bacterial load was not significantly different between months ($F_{2,26}$=1.63, P=0.23; $F_{2,26}$=1.83, P=0.19), so we pooled the data. We correlated TSA and FMA plate counts with overall hue and condition using Spearman's rank correlation test because abundance data were not normal. All tests were two-tailed.

Results

We calculated repeatability from duplicate data for TSA and FMA plate counts and from triplicate data for hue scores using the method of Lessells and Boag (1987). TSA (repeatability=0.85) and FMA (repeatability=0.81) plate counts as well as hue scores (repeatability=0.93) were all highly repeatable.

Total bacterial counts were almost three times higher on TSA than on FMA (t_{29}=−3.126, P=0.004), showing that FMA was a more restrictive growth medium. Of taxa isolated from FMA, 100% (22 of 22; see Table 1) grew on FMA in pure culture. Thus, no bacterial strains growing on FMA were utilizing the metabolic byproducts of other bacteria rather than keratin.

It is also unlikely that these bacteria were utilizing carbon dioxide rather than keratin as a carbon source because every isolate from FMA was identified as a heterotrophic taxon (see Table 1). If a significant portion of bacteria on FMA were autotrophs, we would expect to find at least one among our isolates, but we did not. We did not misidentify these isolates as fatty acid similarity indices were all greater than 0.500, which is considered robust for this type of analysis (Smit et al. 2001). Furthermore, in another study, 100% of

Table 1 Taxa of bacteria

Bacteria	Gram ±	Previously reported keratinolytic activity?	Reference
Arthrobacter agilis	+	N	
Arthrobacter ilicis	+	Y	(Lucas et al. 2003)
Bacillus sp.	+	?	
Bacillus cereus	+	N	
Bacillus megaterium	+	Y	(El-Shora et al. 1993)
Bacillus pumilus	+	Y	(Burtt and Ichida 1999)
Bacillus thuringiensis	+	Y	(Lucas et al. 2003)
Brevibacterium epidermidis	+	N	
Brevibacterium iodinum	+	N	
Brevibacterium sp.	+	N	
Dermacoccus nishinomiyaensis	+	N	
Flavimonas oryzihabitans	+	N	
Kocuria kristinae	+	N	
Micrococcus lylae	+	N	
Paenibacillus apiarius	+	N	
Pseudomonas pseudoalcaligenes	–	N	
Pseudomonas putida	-	N	
Staphylococcus arlettae	+	N	
Staphylococcus hominis	+	Y	(Shawkey et al. 2003b)
Staphylococcus kloosii	+	N	
Staphylococcus warneri	+	N	
Streptomyces halstedii	+	N	

bacteria on feathers of a bird species (eastern bluebirds *Sialia sialis*) from the same geographic location were identified as heterotrophs using both fatty acid analysis of isolates and culture-free cloning techniques (Shawkey et al. 2005). Some of these heterotrophic taxa may have as-yet undiscovered autotrophic capabilities; but, since most bacteria we identified are common soil bacteria, and most facultative and obligate autotrophs are found in either extremely harsh environments such as acid mine drainages (chemoautotrophs) or in marine environments (photoautotrophs), this seems unlikely. Thus, although it is possible that autotrophs could grow on FMA (as is true for any minimal media), the evidence suggests that in this study, they did not.

Total bacterial load was not significantly correlated with hue (Fig. 1a; ρ_{29}=0.210, P=0.273), but feather-degrading bacterial load was significantly correlated with hue (Fig. 1b; ρ_{29}=0.460, P=0.012). Males with redder plumage had fewer feather-degrading bacteria than males with less red plumage. Total bacterial load was not correlated with condition (ρ_{29}=−0.139, P=0.473), and feather-degrading bacterial load was not significantly correlated with condition (ρ_{29}=−0.328, P=0.082). Condition was not correlated with hue (ρ_{29}=0.039, P=0.840).

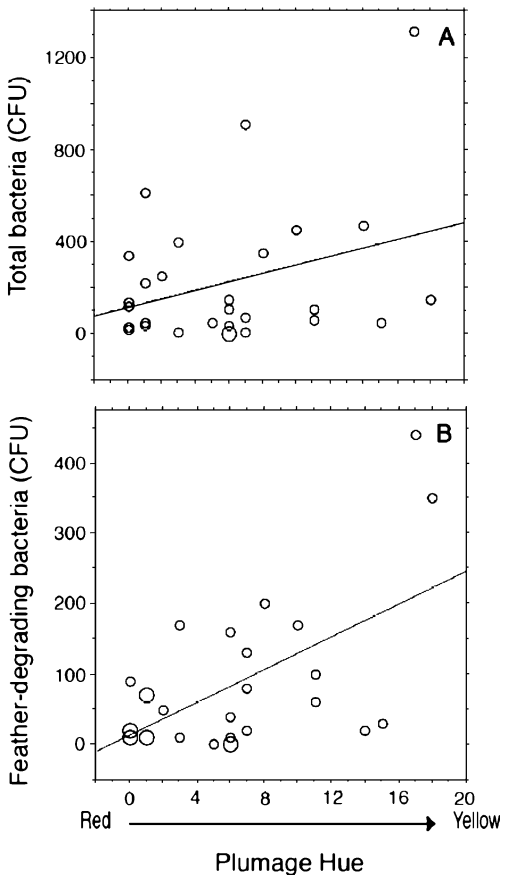

Fig. 1 Overall **a** and feather-degrading **b** bacterial abundance relative to hue in a population of house finches in Auburn, AL, USA. *Small circles* represent one point, and *large circles* represent two points. *Higher hue values* indicate less red colors. N=29 birds

We isolated 22 taxa of bacteria, representing ten genera from FMA (Table 1). Two taxa of bacteria isolated from FMA were gram-negative (*Pseudomonas pseudoalcaligenes*, *Pseudomonas putida*), and the remainder was gram-positive. Of the genera isolated, keratinolytic activity has previously been reported in *Bacillus* (El-Shora et al. 1993; Burtt and Ichida 1999; Shawkey et al. 2003b), *Streptomyces* (Noval and Nickerson 1959; Bockle et al. 1995; Ichida et al. 2001), *Arthrobacter* (Lucas et al. 2003), and *Pseudomonas* (Lucas et al. 2003; Shawkey et al. 2003b).

Discussion

As predicted by models of parasite-mediated sexual selection, we found a negative correlation between the prevalence of feather degrading bacteria and carotenoid-based feather coloration in male house finches. As far as we are aware, this is the first study to test and to find a negative the relationship between abundance of bacteria on feathers and pigment-based feather color.

Our observations of feather-degrading bacteria and carotenoid-based feather coloration in house finches stand in contrast to a previous study conducted on the eastern bluebird (*Sialia sialis*; Shawkey et al. 2007) in which we found positive correlations between blue structural color and abundance of both total bacteria and feather-degrading bacteria on feathers.

Blue structural coloration, however, is created by entirely different mechanisms than pigment-based coloration (Prum et al. 1999; Shawkey et al. 2003a), and the evolution of blue structural coloration is likely driven by different selective pressures; for example, there is little evidence that females choose mates based on structural coloration (Ballentine and Hill 2003; Liu et al. 2006) though it may be used in male–male competition (Siefferman and Hill 2005).

Other studies have shown correlations between plumage color and abundance of parasites (Hill 2006). Like many of these studies, particularly those involving mites (Proctor and Owens 2000), the cause of the observed correlations is unclear at this point. Feather-degrading bacteria may directly affect the color of the bird by destroying colored barbs between molt and the breeding season. Feather-degrading bacteria appear to increase brightness of structural blue feathers by wearing away the outer keratin cortex, allowing the light-scattering blue structures to reflect more light (Shawkey et al. 2007). The seasonal shift in structural color of blue tits (Örnborg et al. 2002) may be caused by a similar mechanism.

How bacteria could change hue of pigment-based feather colors is less clear. Natural loss of melanized tips after feather

growth appears to brighten lesser goldfinch (*Carduelis lawrencei*) feathers (Willoughby et al. 2002). By contrast, feather wear, perhaps partially caused by feather-degrading bacteria, may cause house finch feathers to become duller (less red) over the breeding season (McGraw and Hill 2004). However, no clear mechanism for this shift in colors by bacteria has been proposed. Hue in house finches is determined by the ratios of pigments deposited in the feathers (Inouye et al. 2001); thus, it seems unlikely that feather wear directly caused the observed correlation. Bacteria may also interfere with the deposition of carotenoids during molt, although there is no obvious mechanism by which such ectoparasites could disrupt internal pigmentation processes. We are not aware of any examples of bacteria using carotenoids as a nutritional source.

Alternatively, and more likely, abundance of feather-degrading bacteria may be a correlate of overall quality or parasite load and may not directly cause changes in feather color. High quality males may have fewer parasites in general (Thompson et al. 1997), of which only one or a few directly affects plumage color. This is particularly likely to be true in house finches, where color is directly affected by other parasites such as coccidial and *Mycoplasma gallisepticum* infections (Brawner et al., 2000). House finch preen oil is a potent antimicrobial (Shawkey et al. 2003b), and experimental removal of preen oil shifts hue of carotenoid-colored great tit (*Parus major*) feathers towards shorter (more yellow) wavelengths (Surmacki and Nowakowski 2007), so perhaps higher quality, redder birds have more effective preen oil or preen more frequently. Similarly, European starlings (*Sturnus vulgaris*) with experimentally increased brood sizes had more abundant bacterial assemblages on their feathers than starlings with reduced workloads (Lucas et al. 2003), perhaps because they devoted less time to sanitation behavior. Body condition and bacterial load were not correlated in the present study, however. Future studies should directly examine whether redder birds preen more or have more highly antimicrobial preen oil.

Our findings, unlike those of Shawkey et al. (2007) are consistent with hypotheses of parasite-mediated sexual selection, but whether the feather degrading bacteria in this study are true parasites or simply commensals remains to be determined (Shawkey and Hill 2004; Cristol et al. 2005). This study and others (Lucas et al. 2003; Shawkey et al. 2005) have shown that diverse groups of bacteria are capable of degrading keratin, and others have shown they can disintegrate entire feathers in liquid culture (Burtt and Ichida 1999; Grande et al. 2004).

However, one study (Cristol et al. 2005) showed no effect of experimentally applied feather-degrading bacteria on captive birds, perhaps because the birds were able to control their activity through chemical and behavioral mechanisms. Examining the effects of bacteria when preening is experimentally limited or prevented will enable us to determine whether they exert any selective pressure. Much work remains to determine the role of feather microbes in sexual selection as well as all the other functions that plumage performs.

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