Commentary

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Pox and Plumage Coloration in the House Finch: A Critique of Zahn and Rothstein

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Documenting effects and then establishing their causes lie at the heart of scientific investigation. In a recent study, Zahn and Rothstein (1999) presented evidence that the mean plumage redness of male House Finches (*Carpodacus mexicanus*) in coastal California has decreased over the last 100 years. They then argued that the sole cause of that change in plumage redness was an increased incidence of infection with avian pox. Finally, they looked at current geographic variation in mean male plumage redness and argued that the observed patterns were the result of differential exposure to a pox virus. Unfortunately, the authors did a poor job of documenting the effects that are the focus of their study, and then they proposed an overly simplistic cause for the purported effects.

The House Finch has become a model species for studies of the function and evolution of ornamental plumage coloration (e.g. Olson and Owens 1998, Hill 1999). Male House Finches have carotenoid-based ornamental coloration on the crown, breast, and rump that varies in coloration from dull yellow to bright red. If degree of infection with pox explained most of the variation in expression of male plumage coloration in House Finches as proposed by Zahn and Rothstein (1999), that finding would have important implications for our understanding of carotenoid-based ornamental plumage coloration in the House Finch, in particular, and in birds in general. I believe, however, that the methods employed by Zahn and Rothstein (1999) were sufficiently flawed that the conclusions from their study are questionable.

Careful quantification of plumage hue was central to Zahn and Rothstein's (1999) study, but their method of scoring plumage coloration was somewhat baffling. The coloration of male crown, breast, and rump was first scored by comparison with color chips in Smithe (1975), which is essentially a haphazard collection of color chips (i.e. it is not organized along tri-stimulus color axes). The numbers obtained from Smithe (1975) were then matched to chips in the Munsell color system (Munsell 1976), which is far superior to Smithe (1975) as a standard color reference because it has many more intermediate colors that are arranged along tri-stimulus axes. However, the greater number of color chips and superior arrangement of chips for assessing color variation are pointless when all color observations are first filtered through Smithe (1975). As a last step, color scores were divided into three broad categories: yellow, orange, and red. That method of color quantification is analogous to recording the wing length of a bird using finger widths, measuring the finger widths with a ruler, then calling the bird large, medium, or small. No one would accept that as a suitable way to measure size in a study. Why should an equally bad approach be accepted for measuring color, particularly when much better methods are available (Burley and Coopersmith 1987, Zuk and Decruyenaere 1994, Hill 1998)?

Even if we accept the coarse color-scoring methods of the authors as a suitable means of detecting differences in plumage coloration among populations, the authors' approach to documenting temporal and geographic variation in mean male coloration and then linking the purported change to pox was unconvincing. First, consider whether the mean plumage redness of male House Finches has decreased over time in coastal California. The authors test for an increase in pox over time by dividing birds into those collected before 1960 and those collected after 1960 and looking at the proportion of red males in each group. The rationale for that cutoff is the discovery of the pox virus infecting House Finches in California in 1972. Thus, instead of establishing an effect (change in plumage coloration over time) and then searching for a cause, the authors used their preconceived notions about the purported cause (pox) in how they defined the effect. That approach makes for poor science. Moreover, the 1960 cutoff that was used for including birds in the pox group is not justifiable, even if the lack of specimens from the 1950s makes that a convenient cutoff. As the authors acknowledged, pox was not detected in California until 1972. They argued that it was probably there before that first detection date, so they pushed the date back to 1960. However, one could just as easily argue that pox went undetected for decades or that it appeared very suddenly around 1970. The only objec-

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tive way to group birds is to use the date when pox was first detected in coastal California.

The best evidence for a change in plumage redness over time that is presented by the authors was a weak but significant correlation between plumage hue of study skins and collection year. However, results of that analysis have to be viewed with caution. The authors examined skins in six museums. Anyone who has examined study skins in a collection is aware that the specimens are not collected uniformly over time and space. During any decade or set of decades, most specimens are likely to come from one active collector and from a single location. That can be a problem because, in coastal California, there can be large differences among local populations in mean male coloration (Hill 1993a). Zahn and Rothstein (1999) also documented substantial variation in mean male coloration among years and among local collecting sites in Santa Barbara, California. Thus, it is possible that birds collected early in the century happened to be collected mostly from local populations in which male coloration was bright on average, and that males were collected later in the century mainly from populations that averaged more drab in coloration. Such a collecting bias could have generated artificial time-related variation, regardless of any population-wide change in mean plumage redness over time. The possibility of sampling error could have been reduced by using only one specimen per collection site and collector per year, but then sample size would be greatly reduced. Furthermore, in that correlation analysis, year of collection was only weakly related to variation in plumage coloration ($r_s = 0.26$), so a small sampling bias could have accounted for the pattern.

So, we have weak evidence for a change in plumage color over time and only the most indirect link between a purported change in plumage coloration and exposure to pox. What about geographic variation in plumage coloration and pox? House Finches show substantial geographic variation in the mean plumage redness of males across North America, and the degree to which House Finches are exposed to pox also varies across their range. Zahn and Rothstein (1999) hypothesized that there is concordance between areas of high pox and areas where males average less red in plumage coloration. Unfortunately, poor methods were again employed. To quantify regional variation in plumage coloration, five different subjective descriptions of plumage coloration were used (the authors' own, two eastern banders', and two western banders'). No attempt was made to standardize among those independently derived systems and there was no way to know how various biases may have altered the data. That is equivalent to having five biologists describe the size of birds without any measuring device or without any standardization and then after the fact trying to decide how one observer's ''pretty big'' description compares to another's ''above average'' description.

The use of vague color descriptions for the analysis of geographic variation in coloration was unnecessary. In 1993, I published a detailed account of male plumage coloration based on hundreds of birds sampled in two populations in coastal California, at a high-elevation site on Hawaii Island, at a low-elevation site on Oahu Island, and in two eastern populations (Michigan and New York; Hill 1993a). That is the only study of geographic variation in plumage coloration of male House Finches that used a standardized color scoring method to compare males from different populations. Those would seem to be the ideal data to use in tests of hypotheses related to geographic variation in House Finch plumage coloration. However, the authors did not use those data (although they cite the paper elsewhere) and instead cite various obscure references and unpublished accounts that employ a hodge-podge of vague color descriptions. By ignoring my studies of geographic variation, the authors sidestep several key contradictory observations: a population at a high-elevation site in Hawaii (Pohakuloa, Hawaii Island) with no pox had mostly drab males; males at one feeding station in San Jose, California, where pox infection is common, were as bright as any eastern population; males at another feeding station 12 km away in San Jose, where pox was also common, were drab like males in Hawaii (Hill 1993a; Fig. 1). Even more so than the evidence for a link between pox and temporal change in plumage coloration, the evidence for a relationship between pox and geographic variation in mean male coloration is unconvincing.

One of the claims by Zahn and Rothstein (1999) that I found to be most unfounded was that ''the high level of variation [in plumage coloration of male House Finches] is a new phenomenon . . . '' First, it is not clear what the authors mean by ''high level of variation.'' If the authors mean that before pox there were few or no yellow or orange males in populations, then all early descriptions of plumage coloration in House Finches contradict that statement. The best early descriptions of variation in the plumage coloration of male House Finches in the coastal California population are by Michener and Michener (1926, 1931), who described a full range of plumage variation, from pale yellow to bright red, among male House Finches banded during the 1910s and 1920s. In a series of House Finch specimens from California examined at the turn of century by Grinnell (1911), the full range of color variation from dull yellow to bright red was present. Moreover, Grinnell (1911) cites the collection of 18 male House Finches from the California–Arizona border, and again the full range of plumage variation from drab yellow to bright red was present. In 1939, Moore commented on the increased incidence of yellow and orange male House Finches on islands and stated that 73%

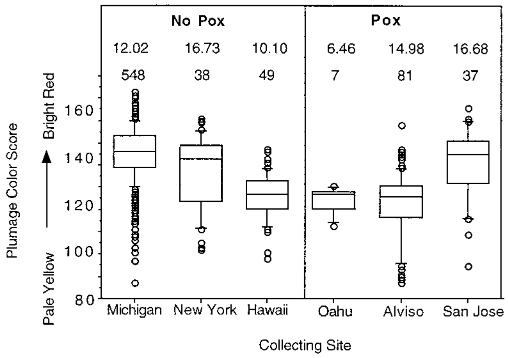

FIG. 1. Variation in the plumage coloration of male House Finches from single capture locations in Ann Abor, Michigan; Long Island, New York; Pohakuloa, Hawaii; Honolulu, Hawaii; Alviso, California; and San Jose, California. The three populations on the right were sampled in areas where avian pox infects House Finches. The three populations to the left were sampled in areas where House Finches are rarely exposed to pox. See Hill 1993 for details of samples locations, capture techniques, and methods for scoring plumage coloration. Plotted are the median, 25th and 75th percentiles, 90th and 10th percentiles, and outlying data points. Samples size and standard deviations for each population are given above the plots.

of males on San Clemente Island were orange or yellow. Moore (1939) also indicated that all populations have some yellow or orange males. All of those accounts came from years that predated the proposed occurrence of pox in House Finches in the western U.S. There is no doubt that male House Finches displayed a highly variable plumage before the date at which Zahn and Rothstein (1999) state that House Finches became exposed to pox.

Perhaps, though, the authors are not referring to the range of plumage variation (i.e. presence of some yellow and orange males) but rather specifically to the statistical parameter ''variance.'' The authors, however, provide no test for difference in variance between pre- and postpox populations. The poor plumage scoring methods of Zahn and Rothstein (1999) in which all color variation is collapsed into three categories makes assessment of variance more difficult than it would be with a more detailed description of color. By comparing populations for which I recorded detailed plumage color data (Fig. 1), I was able to directly test the hypothesis that populations subjected to pox infection have higher variance than populations not subjected to pox infection. The hypothesis is rejected; among the populations that I sampled, males in Michigan, Hawaii, and Oahu had relatively low variance in plumage coloration whereas males in New York, and the two California populations had higher variance. The net result was that there was no consistent relationship between exposure to pox and variance in expression of plumage coloration (Fig. 1): the New York population (no pox) did not have significantly different variance than the two California populations (with pox) ($F = 0.0004$, df = 1 and 73, $P = 0.98$; $F = 0.63$, df = 1 and 117, $P = 0.43$; Bartlett's test) and the Michigan and Hawaiian populations (no pox) did not have significantly different variance than the Oahu population (pox) ($F = 3.01$, df = 1 and 553, $P = 0.08$; $F = 1.89$, df = 1 and 54, $P = 0.17$; Bartlett's test). I conclude that variance in plumage coloration among populations that are exposed to pox is not consistently greater than variance in plumage coloration among populations that are not exposed to pox.

The above criticisms concern problems with documenting temporal and spatial change in coloration. Perhaps the weakest part of the paper, however, is the discussion, where the authors argued that pox is the singular cause for variation in plumage coloration among male House Finches. The authors adopted what is, in my opinion, an unacceptable approach to hypothesis testing. Instead of subjecting the hypothesis that pox is the basis for plumage variation in male House Finches to rigorous attempts at falsification, the authors supported that favored hypothesis by dispensing with what they saw as the only alternatives. Basically, the authors set up a straw man (the idea that diet alone determines coloration), dispensed with it, and concluded that pox must be the explanation for drab House Finch plumage.

The authors dismissed the role of diet in expression of plumage coloration in male House Finches by citing poorly controlled aviary experiments conducted 40 years ago on other cardueline finch species (see Hill [1994] and Hudon [1994] for a previous discussion of this same issue). They never mentioned the extensive aviary feeding experiments with male House Finches that I have conducted and published (Hill 1992, 1993a, 1993b). The authors stated that carotenoids ''may be abundant and varied in most habitats,'' but none of the studies that they cited present any data on that point. To the contrary, the only published study that directly measured abundance of carotenoids in natural environments found that carotenoids were limiting (Slagsvold and Lifjeld 1985), which was not mentioned by the authors. The authors stated that ''there is no evidence that some males have access to certain dietary resources from which others are excluded.'' Again, that is contrary to published evidence. Hill and Montgomerie (1994) provided evidence that there are differences among males in access to nutritional resources during molt. The authors then stated ''Nor does the diet hypothesis account for the sudden shift in the proportion of red south-coastal California males in the mid-1900's, which would require evidence of a major perturbation of plant species.'' I think that any botanist who has lived in southern California over the last several decades would attest to rather massive changes in the biota of the region starting around the turn of the century.

Throughout their discussion, the authors give simple answers based on little or no data to very complex questions. That overly simplistic approach is most obviously absurd when the authors begrudgingly admit that perhaps factors other than pox can also affect plumage coloration: ''Non-red variants existed historically and continue to do so today in populations where male plumage is predominantly red, which may indicate that color change can also result from other sources of weakened body condition in addition to pox.'' However, in the next sentence, they retreat to the idea that pox is the final explanation: ''It could also be that the disease, which has been present in other species for a longer time than in House Finches, may have been present in House Finches but was not detected because of low virulence and an absence of tumors.''

Why does it really matter if the poor methods and faulty logic of Zahn and Rothstein (1999) lead to erroneous conclusions regarding plumage coloration in the House Finch? Over the last decade, behavioral and evolutionary biologists have become increasingly interested in carotenoid pigmentation as an honest signal of male quality (Andersson 1994, Olson and Owens 1998). Central to that issue is the proximate basis for variation in expression of carotenoid-based integumentary coloration. On the basis of the growing number of experimental studies in that field (summarized in Hill [1999] and Olson and Owens [1998]), evidence strongly suggests that a variety of factors combine to determine expression of carotenoid-based plumage coloration. For male House Finches, those factors include dietary access to carotenoids (Hill 1992, 1993a, b), access to nutrition during molt (Hill and Montgomerie 1994, Hill 2000), and degree of parasitism (Brawner 2000, Hill and Brawner 1998, Thompson et al. 1997). Coccidians, protozoan parasites of the gut, have a direct negative effect on carotenoid absorption across the gut lining (Allen 1986, 1987, 1992; Ruff et al. 1974) and hence carotenoid pigmentation in the House Finch (Brawner 2000). Other diseases such as mycoplasmosis (a bacterial infection) also have a negative effect on expression of plumage coloration in this species (Brawner 2000). And yes, evidence also suggests that avian pox has a significant negative effect on House Finch plumage coloration (Thompson et al. 1997). But, the assertions made by Zahn and Rothstein (1999) that temporal or geographic variation in incidence of avian pox among House Finches is the primary or sole source of temporal or geographic variation in male plumage coloration, and that variation in male plumage coloration is a recent phenomenon in male House Finches, are not only unjustified, they contradict the careful research in this field showing the true complexity of control of ornamental plumage coloration.

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LITERATURE CITED

ALLEN, P. C. 1986. Biochemical changes in the intestinal mucosa associated with coccidiosis. Pages 194–202 *in* Research in Avian Coccidiosis (L. R. McDougald, L. P. Joyner, and P. L. Long, Eds.). Proceedings of the Georgia Coccidiosis Conference, 1985. University of Georgia, Athens.

ALLEN, P. C. 1987. Physiological responses of chicken gut tissue to coccidial infection: Comparative effects of *Eimeria acervulina* and *Eimeria mitis* on mucosal mass, carotenoid content, and brush border enzyme activity. Poultry Science 66: 1306–1315.

ALLEN, P. C. 1992. Effect of coccidiosis on the distribution of dietary lutein in the chick. Poultry Science 71:1457–1463.

ANDERSSON, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

BRAWNER, W. R. III., G. E. HILL, AND C. A. SUNDERMANN. 2000. Effects of coccidial and mycoplasmal infections on carotenoid-based plumage pigmentation in male House Finches. Auk 117: 952–963.

BURLEY, N., AND C. B. COOPERSMITH. 1987. Bill color preferences of Zebra Finches. Ethology 76:133–151.

GRINNELL, J. 1911. The Linnet of the Hawaiian Islands: A problem in speciation. University of California Publications in Zoology 7:179–195.

HILL, G. E. 1990. Female House Finches prefer colourful males: Sexual selection for a condition-dependent trait. Animal Behaviour 40:563–572.

HILL, G. E. 1992. Proximate basis of variation in carotenoid pigmentation in male House Finches. Auk 109:1–12.

HILL, G. E. 1993a. Geographic variation in the carotenoid plumage pigmentation of male House Finches (*Carpodacus mexicanus*). Biological Journal of the Linnean Society 49:63–86.

HILL, G. E. 1993b. The proximate basis of inter- and intra-population variation in female plumage coloration in the House Finch. Canadian Journal of Zoology 71:619–627.

HILL, G. E. 1994. House Finches are what they eat: A reply to Hudon. Auk 111:221–225.

HILL, G. E. 1998. An easy, inexpensive means to quantify plumage coloration. Journal of Field Ornithology 69:353–363.

HILL, G. E. 1999. Mate choice, male quality, and carotenoid-based plumage coloration. Pages 1654–1668 *in* Proceedings XXII International Ornithological Congress (N. Adams and R. Slotow, Eds.). University of Natal, Durban, South Africa.

HILL, G. E. 2000. Energetic constraints on expression of carotenoid-based plumage coloration. Journal of Avian Biology 31:559–566.

HILL, G. E., AND W. R. BRAWNER. 1998. Melanin-based plumage coloration in the House Finch is unaffected by coccidial infection. Proceedings of the Royal Society of London Series B 265:1105–1109.

HILL, G. E., AND R. MONTGOMERIE. 1994. Plumage colour signals nutritional condition in the House Finch. Proceedings of the Royal Society of London Series B 258:47–52.

HUDON, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). Auk 111:218–221.

MICHENER, H., AND J. R. MICHENER. 1926. Studies on 1,170 banded House Finches. Condor 28:254–257.

MICHENER, H., AND J. R. MICHENER. 1931. Variation in color of male House Finches. Condor 33:12–19.

MOORE, R. T. 1939. A review of the House Finches of the subgenus *Burrica.* Condor 41:177–205.

MUNSELL. 1976. Munsell Book of Color: Glossy Finish Collection. Munsell/MacBeth/Kollmorgen Corp., Baltimore, Maryland.

OLSON, V. A., AND I. P. F. OWENS. 1998. Costly sexual signals: Are carotenoids rare, risky or required? Trends in Ecology and Evolution 13:510–514.

RUFF, M. D., W. M. REID, AND J. K. JOHNSON. 1974. Lowered blood carotenoid levels in chickens infected with coccidia. Poultry Science 53:1801–1809.

SLAGSVOLD, T., AND J. T. LIFJELD. 1985. Variation in plumage coloration in the Great Tit *Parus major* in relation to habitat, season, and food. Journal of Zoology (London) 206:321–328.

SMITHE, F. B. 1975. Naturalist's Color Guide. American Museum of Natural History, New York.

THOMPSON, C. W., N. HILLGARTH, M. LEU, AND H. E. MCCLURE. 1997. High parasite load in House Finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. American Naturalist 149:270–294.

ZAHN, S. N., AND S. I. ROTHSTEIN. 1999. Recent increase in male House Finch plumage variation and its possible relationship to avian pox disease. Auk 116:35–44.

ZUK, M., AND J. G. DECRUYENAERE. 1994. Measuring individual variation in colour: A comparison of two techniques. Biological Journal of the Linnean Society 53:165–173.

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House Finches Are Not Just What They Eat: A Reply To Hill

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The coevolutionary interactions of pathogens and their hosts are likely to be a widespread mechanism that results in the maintenance of genetic variation. Alternatively, highly variable species may be in a transient state, with their variation reflecting directional selection and new selection pressures. With those insights in mind, we set about to study the House Finch (*Carpodacus mexicanus*), some of whose populations are arguably the most variable among North American birds with regard to plumage coloration in males of the same age. In addition, we were also attracted to House Finches by our observations and those of others (McClure 1989, Power and Human 1976) that this species is highly unusual not only for its color variation, but for its remarkably high incidence of disease, particularly avian pox, which of course raised the question of whether pathogens and plumage color might be related. Lastly, the possibility of recent changes in disease incidence was raised by the first published report (Power and Human 1976) of pox disease in mainland populations of this common species, which reported a severe outbreak in 1972. Accordingly we set out to determine whether there is any evidence of a link between plumage color variation and pox and whether extreme variation in color and high pox-incidence might be new conditions.

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To address our goals, we collected new data through our own field efforts, studied specimens in museums, reviewed available literature, and amassed data from bird banders over a wide part of the species' current range. Although they do not establish causation, our straightforward data and analyses show strong temporal and spatial links between pox and plumage coloration and add potential new insights to work on this interesting species. We found the following major results: birds in southern mainland California had a much lower incidence of pox disease in the first half of the twentieth century than in the second half; over the same period, red coloration has gone from being characteristic of more than three-fourths of southern California males to a much lower incidence today, with orange and yellow males having become much more common. At present, there are strong macrogeographic associations between high pox incidence and high plumage color variation (Zahn and Rothstein 1999).

Hill's (1990, 1991, 1992, 1993a, b, 1994a, b, c) past work has produced much of what was previously known about plumage color variation and its consequences in this species. Unfortunately Hill's critique of our paper adds confusion, but no new insights, to this interesting system. His frenetic attempt to discredit virtually every aspect of our paper is totally unconvincing, contradicts itself, and highlights serious weaknesses in his own work. The putative major problems that Hill alleges deal with the following: our methodology of representing plumage coloration; our temporal criteria for separating samples in analyzing possible historical changes in pox incidence and plumage coloration; our criteria for analyzing possible patterns in present day macrogeographic variation in plumage color and pox. In addition, Hill misrepresents our paper by alleging that we made statements and conclusions that in fact do not appear in our paper.

We address the misrepresentations first. Hill (2001) repeatedly argues that we concluded that pox disease is the ''singular cause'' for plumage variation or ''the primary or sole source of temporal or geographic variation in male plumage coloration.'' In fact, we were careful to never state our conclusions in such absolute terms. For example, our abstract states that high incidences of yellow and orange males ''may be related to a high incidence of avian pox'' (Zahn and Rothstein 1999). No where does our paper state that pox is the only or major determinant of color variation. We would suggest that Hill did nothing further than read the title to our paper were it not for the fact that even it states there is a ''possible relationship'' between pox and plumage variation.

Another misrepresentation is Hill's supposed confusion over our suggestion that ''the high level of variation [in plumage coloration of male House Finches] is a new phenomenon''. Hill suggests that maybe we meant that ''there were few or no yellow or orange males'' (Hill 2001) in the early part of the last century, a suggestion that he then rebuts. This is a pointless discussion by Hill because we never stated that ''there were few or no yellow or orange males.'' Instead, we clearly stressed that early workers, such as Michener and Michener (1931), described the yellow to red range of colors that exists today. Furthermore, our Figure 1 and associated text (Zahn and Rothstein 1999) show that 23.3% of males in a museum sample from the early 1900s were yellow or orange. To further confuse matters, Hill later acknowledges that we recognized that there have always been reports of yellow and orange males and even quotes us as stating ''Non-red variants existed historically . . . '' So it is unclear why Hill raised that red herring in the first place.

Hill's claimed confusion over our use of the phrase ''high variation'' is similarly hard to understand. Given the data we presented, certainly Hill could understand that ''high variation'' referred not to the total range of hues but the proportional representation of hues. It should have been clear to Hill that what we meant by higher variation was a switch from populations in which the majority of males were of one color (red) to ones in which there was a much more even representation of three colors. For example, our museum data showed the following color percentages in the early versus the late twentieth century: 76.6% red, 23.4% orange, and 1.1% yellow, versus 51.3% red, 35.9% orange, and 12.8% yellow (Zahn and Rothstein 1999). Clearly, the second sample shows more variation by any use of the word.

Despite Hill's misrepresentations of our conclusions, he would have valid points to make if our results were unreliable because of faulty methodology. We first address Hill's criticisms of our color scoring methodology. One of us (Zahn) did all color scoring by matching male colors to one of 13 color chips that ranged from red to yellow and that are from a widely available source (Smithe 1975). We had a good rationale for using those particular 13 colors because they represented all of the hues we found among several hundred museum specimens as well as all males captured at our Santa Barbara County field sites. Had other hues been present, we would have used additional chips. Furthermore, Smithe's (1975) color chips were appropriate because they represent colors prevalent in birds and are not a ''haphazard collection'' as Hill incorrectly states. To categorize the 13 Smithe chips, we had 22 people classify each one as red, orange, or yellow. Those people also ranked the chips on a continuum from red to yellow. All 22 people categorized 10 of the 13 chips the same way (i.e. red, orange, or yellow). Amongst the remaining three chips, 21 called one chip orange whereas only one person called it red, 21 called one chip red whereas one called it orange, and 21 called the last chip yellow whereas one called it orange. Clearly our results are replicable. As a final check, we matched the 13 Smithe chips to chips in the Munsell color system (Munsell Color Company 1976). The designations of our 22 judges as red, orange, or yellow agreed in each case with the Munsell system.

Hill lambastes us for using the Smithe chips first and for not using Munsell chips directly and for collapsing our color categorizations into red, orange, and yellow, instead of the true continuum represented by those descriptors. There are two reasons why we chose our color system, historical comparisons were a key goal of ours and those had to rely on studies in which early workers categorized birds as red, orange, and yellow, and the Munsell chips were not available for all of our work. Addressing the latter reason first, the Munsell chips are part of an expensive set that we were allowed to use only in a single indoor location. Because we wanted to use a common rating system in a number of museums and at a range of field sites, we opted for Smithe's chips. Given the consistency of the ratings by our 22 judges, it is clear that our system is highly replicable and that it introduced no problems. Hill's sarcasm that our method was akin to measuring wing lengths with ''finger widths'', reflects poorly on his intentions, which should have been an objective attempt to elucidate the truth, not an attempt at ridicule.

Secondly, we conducted most of our analyses in terms of red, orange, or yellow categorizations because we were interested in historical comparisons and in contemporary comparisons involving a large part of the species' range. So we had to rely on other people. Grinnell (1911) and Michener and Michener (1926, 1931) reported their historical data in terms of red, orange, or yellow categorizations and we had to do the same for meaningful comparisons. The former author reported that red males made up 92.5% of 94 male specimens collected before 1911 in coastal areas of southern California counties from Santa Barbara to San Diego. The Micheners reported that 85% of males were red among 1,563 specimens banded at Pasadena, in the 1920s. Our assessment of pre-1950 museum specimens found that 76.6% of 94 were red. Those three sets of historical data are in stark contrast to available mainland southern California data for recent decades (Zahn and Rothstein 1999): W. L. Principe reported that 12.2% of males were red among 459 banded at Pasadena from 1991–1995. Our 1994–1995 banding at four sites in Santa Barbara County found that 29.4% of 323 males were red. Lastly, 51.3% of 78 museum specimens collected after 1959 were red. Although there is currently considerable spatial heterogeneity in coastal regions of southern California, it is clear from those diverse sources of data that there was a large decline in the proportion of red male House Finches during the 1900s.

We applied statistical testing to our own data from museum specimens in two ways. A chi-squared test showed a significant difference in the proportions of red males before 1951 versus after 1960 ($\chi^2 = 12.03$, df = 1, not 3 as mistakenly cited in our paper, $P < 0.001$). Hill (2001) never mentions the chi-squared test but criticizes a correlation analysis we presented as showing only a weak relation ($r_s = 0.26$, although the P value was <0.0005). The correlation coefficient was indeed low because the test was inherently conservative. A correlation analysis would be best suited to detecting a progressive color change over the entire time period covered by our data. By contrast, the true relationship indicated by our data and the hypothesis that pox is implicated in the temporal color shift is that color changed over a short period roughly coinciding with appearance of pox. Although it was not well suited to our data, we carried out the correlation analysis for two reasons. First, it did not involve any temporal cut-offs chosen by us, so it eliminated any issues concerning arbitrariness. Secondly, we wanted to reflect the fact that there is a continuum of colors, and the correlation analysis allowed us to use the red to yellow ranking of our 13 color chips, not just the three color designations.

Hill further criticizes our museum analyses by raising the issue of collecting biases, but fails to note that collecting biases were minimized because the specimens we assessed were housed in six museums and were therefore collected by a considerable assortment of individuals over many decades. There is no reason why collecting biases would shift from inflating the proportion of red individuals in the early 1900s to deflating that proportion in the late 1900s. Furthermore, the most likely collecting bias in a common species that is a commensal of man, as is the case for House Finches, would have been a preference for uncommon individuals, which may mean that old museum specimens have a disproportionate representation of yellow and orange birds.

Hill's second major criticism is that our choice of temporally partitioning the museum data as pre-1951 versus post-1959 in our analysis of color changes reflects our ''preconceived notions'' about pox, which is simply false. We explicitly stated that we chose those cut-offs because there were no museum specimens from the 1950s. So our cut-offs were dictated by the independent variable (year) not by the dependent variable or by any preconceived notions. We next pointed out that the lack of specimens from 1950s provided a fortuitous link with the first published report of pox in California, in which Power and Human (1976) documented a severe outbreak at Santa Barbara in 1972. However, Power and Human's account makes it clear that pox was noted at Santa Barbara in years prior to 1972 and that it occurred over at least a 340 km span of coastal California in the winter of 1972–1973. Three of our 19 museum specimens collected from 1961–1970 had missing toes, providing further evidence for the onset of pox sometime before 1972. Therefore, we decided it was most objective to simply let the data partition themselves, that is, pre-

1951 versus post-1959 given the absence of specimens from the 1950s. If Hill objects to that, the solution is to delete our 1961–1970 data, which means that 51.7% or 30 of 58 birds were red in years after the severe outbreak of pox in 1972, which still results in a significant comparison with the pre-1951 period ($\chi^2 = 10.05$, df $= 1$, $P < 0.01$).

We also note that Hill's multi-pronged but ineffective criticism of our museum data ignores the fact that those data are consistent with all other sources of plumage color data, as noted above. In addition, neither the Micheners nor Grinnell noted pox lesions or a common sign of past pox infection—missing toes—in any of the birds from the early 1900s they examined. We found pox indicators in 37.6% of 663 males we banded in Santa Barbara County between 1993 and 1996. Similarly, McClure (1989) found that about one-third of thousands of House Finches he banded in Ventura County from 1977–1987 had pox at some time in their lives (see also Thompson et al. 1997). Principe, who worked only 8 km from the Michener's 1920s Pasadena site found active pox tumors in 1991–1995 on approximately 25% of males during fall, which is when pox infections peak (Harrison and Harrison 1986, Zahn 1999). Among our museum specimens, none of 94 males collected before 1950 had missing toes compared to 12 of 78 collected after 1959 ($P < 0.0001$, Fisher exact test). As with our color information, diverse types of data on pox collected by different people all point to the same result: a temporal shift. Hill can focus on the uncertainty concerning the exact timing of the shifts, which our data indicate occurred sometime between 1950–1970, but that does not support his attacks on the issue of whether those shifts occurred at all.

Because data indicated historical shifts in both color and pox incidence in southern California, we explored the possibility of a relationship between color and pox by considering the potential physiological links between pox and carotenoids and by determining whether there are currently spatial links between pox and color. The latter approach brings us to Hill's third major criticism, which is that we used unjustifiably subjective criteria to assess current macrogeographic patterns of variation in plumage color. Our macrogeographic analyses employed recent data from four areas, mainland southern California (as described above), the eastern United States, Hawaii, and San Nicolas Island (110 km off the coast of southern California). The eastern data on color come from specimens in two museums and from two banders who sent us feather samples from males they banded. Colors were scored with the same methodology as described above, either at those museums or in Santa Barbara using the banders' feather samples (not by the banders as Hill mistakenly states). As we reported above, that methodology is replicable and objective. We find it odd that Hill attacks the reliability of our new data that show that red coloration predominates in eastern House Finches, because he criticizes us for not citing his data, which he says show the same result! We did not cite his data because of its methodological flaws, which we discuss below.

It is true that some or all of the recent data we cited for three of the areas in our macrogeographic assessments (mainland southern California, Hawaii, and San Nicolas Island) were collected by other people who did not use our methodology. Those people simply categorized birds as red, orange, or yellow. However, such data are reliable as shown by the nearly 100% uniformity in our panel of 22 color judges. The spatial link between decreased proportions of red males and the occurrence of pox is clear from our data. Color categorizations of House Finches have also been acceptable to other researchers (van Riper 1994, Thompson et al. 1997), so our work is not unique in that respect. As with our data on temporal shifts, our data on macrogeographic patterns come from diverse sources, not just our own work. Hill can belittle such evidence as a ''hodgepodge'' of information, but our methodology shows that red, orange, and yellow categorizations are reliable across different people. Furthermore, all evidence we amassed for both temporal and macrogeographic trends is consistent and its diverse nature is a strength of our paper.

In attacking our paper, Hill not only criticized our methodology, he also touted his methods as superior. Unfortunately, Hill has misrepresented the implications of his scheme for quantification of plumage coloration, and that makes it difficult for others to be certain of the hue of birds he has studied. Hill (1993b) assigns a composite plumage score to each male by summing values based on three characteristics: hue (the red–orange–yellow continuum), chroma (degree of color saturation, such that pink is a low chroma red), and tone (total reflectance). Because those birds vary in all three characteristics (Hill 1998), that method results in one numeric score that represents three distinct variables. Hill equates high composite color scores with increased brightness and redness. Although there may be a correlation here, highly chromatic orange males can have higher scores than low chroma red ones. Furthermore, brightness is a vague term that relates to both chroma, and tone, but not to hue, yet Hill stresses hue when he equates high color scores with red. Hill's (1998) own data on spectrophotometer output show weaknesses in his composite scores based on his visual assessments of hue, chroma and tone (as used in all of his prior papers). Hill (1998) reported that only his hue and chroma values were correlated with readings from the spectrophotometer. Although he pointed out that tone contributes less numerically to his composite color score than do hue and chroma, Hill's (1998) results show that his composite scores have a component—tone—that adds noise and is essentially a random variable. In recognition of that, Hill (1998) stated that ''I find it relatively easy to assign a hue score to patches of feathers, more difficult to assign a saturation [chroma] score, and very tough to assign a tone score.'' Hill's own data and perceptions thus agree with the near unanimity of our 22 judges and because they validate the reliability of color categorizations based on hue, they validate our methodology for categorizing colors.

We chose to focus on only one aspect of coloration—hue—because it is unknown how House Finches integrate hue, chroma, and tone and it is not even clear if those three axes of color variation are completely meaningful to birds given that the Munsell system is based on human perception. In addition, we knew that the historical data on color and recent data collected by other workers, all of which categorized birds as red, orange, or yellow, were based on hue alone. We do not dispute Hill's general findings that female House Finches prefer males with high composite color scores under his scheme, but it is not clear just what is important to females until Hill analyzes the effects of hue, chroma, and tone separately. Thus, conclusions by Hill such as ''it appeared to be the red pigmentation of males and not a correlated character that the female House Finches were choosing'' (1990) may be invalid. Hill's attempts to determine the cues females use for mate choice are further complicated by the fact that humans and birds perceive color differently and only the latter perceive ultraviolet light, as acknowledged by Hill (1998). Yet even Hill's (1998) spectrophotometric methodology does not involve UV reflectance, which may be a problem because yellow bird plumages often show some reflectance in the UV range (J. Endler pers. comm.). Perceptual differences between humans and birds do not affect our paper (Zahn and Rothstein 1999), as we focussed on differences in plumage reflectance with no assertion as to whether those differences are important to birds.

Besides attacking our methodology and advancing the primacy of his own methods, Hill (2001) presented data that he claims are counter to our findings. The data in Hill's Figure 1 have all been presented before. Hill categorizes his study sites as with and without pox, but presents no data on pox. He argues that birds from pox-free sites are not consistently brighter than birds exposed to pox. Because Hill's composite plumage score confounds three variables (whereas we dealt with just one—hue), comparisons between our data and his are difficult to interpret. For similar reasons, Hill's failure to find greater plumage color-score variation at pox sites is not easily interpreted. It is clear that there is a strong association between pox and increased variation when color is represented by hue only, as in our data. We tested for increased variation in recent years in two ways. First, we used a simple hue scoring system with yellow, orange, and red equaling 1, 2, and 3 respectively, which follows the system of Thompson et al. (1997) except that they called the intermediate category ''mixed red and yellow/gold'' instead of orange. With that system, our pre-1951 museum series for southern California had a mean score of 2.725 and a variance of 0.214. The post-1959 sample had a mean of 2.385 and with a variance of 0.499, was significantly more variable as the F ratio is 2.332 ($P < 0.001$). Because our data are not normally distributed, we also quantified plumage-color diversity by eschewing scores and instead calculating Shannon-Wiener diversity indices for the color classes (Zar 1999). Those indices were 0.2605 and 0.4228 for the pre-1951 and post-1959 samples, respectively. The latter had significantly ($P < 0.0001$, $t = 4.487$, df = 167) greater color diversity using Hutcheson's test (Zar 1999).

Even if Hill had quantified plumage color in a more interpretable way relative to our assessment of hue, the data in his Figure 1 would have little value in assessing validity of our results. As shown by our data for Santa Barbara County (Zahn and Rothstein 1999), there is considerable spatial and temporal heterogeneity in plumage color. Among our four sites, one had red males at 52.8% ($n = 36$ males) and another at only 3.2% ($n = 31$) in 1994. At the latter site in 1995, red males were at 23.1% ($n = 13$). The data we used in our temporal and spatial assessments came from numerous sites. All samples were collected over two or more years and many involved hundreds or thousands of birds. By contrast, Hill's data for all samples in his Figure 1 other than Michigan were each collected in a single month at a single site (two nearby sites in the case of New York) and had n values of only 7 to 81 males. The bottom line is that one can not use a single small sample collected over a short time period in one season to categorize the coloration of House Finches within a region. Ironically, the charge that Hill applied to our museum data, namely that our samples have little global validity because they are clumped in time and space, applies instead to his own data.

Lastly, regarding Hill's data, we address his suggestion that because males at San Jose (a purported pox area) were as red as ones from the East (where pox is rare or absent), the link between pox and color is weakened. Other problems aside (such as Hill's color scoring scheme and the lack of global validity), we note that our data on temporal trends deal solely with southern California and none of our macrogeographic comparisons involve northern California, where San Jose is located. Because northern and southern California differ in many ways, we cannot assess Hill's data. We do not know the incidence of pox in northern California nor the degree of color variation and Hill's sparse data are of little help here.

Hill refers to our Discussion section as ''Perhaps the weakest part of the paper . . . '' In that section, we argued that differential diet uptake of carotenoids is unlikely as a complete explanation for plumage color variation in House Finches. Instead, we recognized that carotenoid pigments in birds, or the precursors of those pigments, must come from the diet but suggested that pigments are not likely to be limiting in nature. We argued that variation in color is more likely to be related to ability to use ingested carotenoids. We further suggested that pox, either through direct effects on uptake of carotenoids (such as through pathogenic effects on the intestine), and general factors that reduce a bird's condition (e.g. diseases, ectoparasites) are the primary factors responsible for a bird's failure to become red. Hill strongly attacked our suggestions and in doing so gave insufficient weight to mounting evidence concerning carotenoid metabolism in birds (Olson and Owens 1998) and undue importance to his own feeding experiments with captive birds (Hill 1992).

We need not review the evidence concerning carotenoid metabolism, other than to state that it is widely recognized that carotenoids are naturally abundant in plants and that there are links between an animal's ability to use carotenoids and its condition (Hudon 1994, Olson and Owens 1998). For House Finches in particular, Thompson et al. (1997) showed that birds afflicted with pox during molt are more likely to grow non-red feathers than birds not afflicted. The latter study is clearly applicable to our findings indicating spatial and temporal links between pox and was done in our primary area of focus, southern California. Besides pox, Thompson et al. (1997) found that intense mite infestations during molt were also related to a decreased likelihood of growing red plumage. Hill briefly acknowledges that Thompson et al. (1997) showed that pox affects color, but, instead of admitting that this supports the conclusions in our paper, he argues that that effect does not mean that pox ''is the primary or sole source of temporal or geographic variation'' in plumage coloration. Of course, we never argued that it was. We merely argued that a bird's condition is likely to influence its coloration and that pox is one of a number of things that can depress condition.

In his early work (e.g. Hill 1992), Hill attributed all plumage color variation in House Finches to diet and differential foraging ability. Evidence for that viewpoint seems to come from three sources. As in a previous rebuttal (Hill 1994) to a critique of his differential foraging ability hypothesis by Hudon (1994), Hill (2001) cites the same single study (Slagsvold and Lifjeld 1985) showing that carotenoids are limiting for birds. But the species in that study is mainly a carnivore, whereas the House Finch is primarily herbivorous, and carotenoids are so widespread in plant matter that they may be limiting only for animals that are primarily carnivorous (Hudon 1994, Olson and Owens 1998). In a second line of putative evidence, bright male House Finches (under Hill's composite scoring scheme) provided more food for their offspring and therefore seemed to be better foragers than dull-colored males (Hill 1991). However, that result is consistent with both our condition hypothesis and Hill's foraging-ability hypothesis because birds in the best condition are likely to be the ones best able to feed both themselves and their offspring. In arguing for the importance of diet, Hill (2001) states that Hill and Montgomery (1994) ''provided evidence that there are differences among males in access to nutritional resources during molt.'' The latter paper showed that bright males grow feathers more quickly and begin to molt earlier than dull males. Although that result is consistent with bright males being better foragers for all aspects of food, including carotenoids, it is also consistent with such males simply being in better condition as regards all factors affecting condition, including disease. In that paper, Hill and Montgomery (1994) stated that ''reduced plumage brightness of males in the drab Alviso population is a result either of reduced access to carotenoid pigments or of reduced ability to metabolize carotenoids (e.g. due to parasites or poor health).'' Hill and Montgomery's suggestion that disease may be important in limiting a finch's ability to metabolize carotenoids agrees with our general conclusion yet strangely it is not acknowledged in Hill's (2001) critique.

The third apparent reason for Hill's defense of the importance of diet deals with his feeding experiments, which do indeed demonstrate a clear effect of diet on the coloration of captive House Finches. In those experiments, Hill showed that birds fed a special diet deficient in carotenoids molted into dull plumage. Birds fed the same diet but given a red carotenoid, canthaxanthin, grew bright red plumage. The first of those results was completely predictable, because all workers agree that carotenoid pigments in animals must come from dietary intake (see discussions in Hudon 1994 and Zahn and Rothstein 1999). The second result has no bearing on what occurs in nature as canthaxanthin is not present in the finches' diets nor is it the pigment responsible for their red color. Those results show only that people can control bird coloration by feeding them unnatural diets, a trick long known to zoo keepers. Those results do not show that the range of naturally occurring diets controls or even influences coloration. Even the first workers to use diet to manipulate coloration in captive House Finches, concluded that the dietary intake of carotenoids is necessary but ''not completely sufficient to explain color variation in native birds'' (Brush and Power 1976).

In questioning the primacy of diet, we noted that there were no major plant perturbations in California in the mid-1900s when House Finch coloration apparently shifted. Hill (2001) retorted that there were ''massive changes in the biota starting around the turn of the century.'' In fact, the major changes to California's flora that have displaced native plants that dominate the open habitats used by House Finches took place by the mid-1800s (Mensing 1998). Indeed, changes to open habitats occurred so early after the European colonization that there is even considerable controversy concerning the original nature of those habitats (Hamilton 1997).

Remarkably, after criticizing us for doubting his early diet-as-key-factor hypothesis, Hill's (2001) critique acknowledges ''that a variety of factors combine to determine expression of carotenoid-based coloration'' and that ''degree of parasitism'' is one of these factors. So Hill is free to modify his hypothesis, but without admitting that his initial diet hypothesis was overly simplistic, whereas we are not. Furthermore, the bottom line of Hill's critique is that after all the disparagement of our methods, logic, and data, he comes to the same general conclusion we reached, namely there is a ''possible relationship'' between pox and coloration after all.

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LITERATURE CITED

BRUSH, A. H., AND D. M. POWER. 1976. House Finch pigmentation: Carotenoid metabolism and the effect of diet. Auk 93:725–739.

GRINNELL, J. 1911. The Linnet of the Hawaiian Islands: A problem in speciation. University of California Publications in Zoology 7:179–195.

HAMILTON, J. G. 1997. Changing perceptions of pre-European grasslands in California. Madroño 44: 311–333.

HARRISON, G. J., AND L. R. HARRISON. 1986. Clinical Avian Medicine and Surgery. Saunders, Philadelphia.

HILL, G. E. 1990. Female House Finches prefer colourful males: Sexual selection for a condition-dependent trait. Animal Behaviour 40:563–572.

HILL, G. E. 1991. Plumage colouration is a sexually selected indicator of male quality. Nature 350: 337–339.

HILL, G. E. 1992. Proximate basis of variation in carotenoid pigmentation in male House Finches. Auk 109:1–12.

HILL, G. E. 1993a. Male mate choice and the evolution of plumage coloration in the House Finch. Evolution 47:1515–1525.

HILL, G. E. 1993b. Geographic variation in the carotenoid plumage pigmentation of male House Finches (*Carpodacus mexicanus*). Biological Journal of the Linnean Society 49:63–86.

HILL, G. E. 1994a. Trait elaboration via adaptive mate choice: Sexual conflict in the evolution of signals of male quality. Ethology, Ecology and Evolution 6:351–370.

HILL, G. E. 1994b. House Finches are what they eat: A reply to Hudon. Auk 111:221–224.

HILL, G. E. 1994c. Geographic variation in male ornamentation and female mate preference in the House Finch: A comparative test of models of sexual selection. Behavioral Ecology 5:64–73.

HILL, G. E. 1998. An easy, inexpensive means to quantify plumage coloration. Journal of Field Ornithology 69:353–369.

HILL, G. E. 2001. Pox and plumage coloration in the House Finch: A critique of Zahn and Rothstein. Auk 118:256–260.

HILL, G. E., AND R. MONTGOMERIE. 1994. Plumage colour signals nutritional condition in the House Finch. Proceedings of the Royal Society of London Series B 258:47–52.

HUDON, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). Auk 111:218–221.

MCCLURE, H. E. 1989. Epizootic lesions of House Finches in Ventura Co., California. Journal of Field Ornithology 60:421–430.

MENSING, S. A. 1998. 560 years of vegetational change in the region of Santa Barbara, California. Madroño 45:1–11.

MICHENER, H., AND J. R. MICHENER. 1926. Studies on 1170 banded House Finches. Condor 28:254–257.

MICHENER, H., AND J. R. MICHENER. 1931. Variation in color of male House Finches. Condor 33:12–19.

MUNSELL COLOR COMPANY. 1976. Munsell Book of Color, Glossy Finish Collection. Munsell/Macbeth/Kollmorgen Corporation, Baltimore, Maryland.

OLSON, V. A., AND I. P. F. OWENS. 1998. Costly sexual signals: Are carotenoids rare, risky or required? Trends in Ecology and Evolution 13:510–514.

POWER, D. M., AND G. HUMAN. 1976. A local occurrence of avian pox in the House Finch. Condor 78:262–263.

SLAGSVOLD, T., AND J. T. LIJELD. 1985. Variation in plumage coloration in the Great Tit *Parus major* in relation to habitat, season, and food. Journal of Zoology (London) 206:321–328.

SMITHE, F. B. 1975. Naturalist's Color Guide. American Museum of Natural History, New York.

THOMPSON, C. W., N. HILLGARTH, M. LEU, AND H. E. MCCLURE. 1997. High parasite load in House Finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. American Naturalist 149:270–294.

VAN RIPER, C. III. 1994. Coloration frequencies of male House Finches in Hawaii. Western Birds 25: 163–165.

ZAHN, S. N., AND S. I. ROTHSTEIN. 1999. Recent increase in male House Finch plumage variation and its possible relationship to avian pox disease. Auk 116:35–44.

ZAR, J. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

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