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RECENT INCREASE IN MALE HOUSE FINCH PLUMAGE VARIATION AND ITS POSSIBLE RELATIONSHIP TO AVIAN POX DISEASE

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ABSTRACT.—Male House Finches (*Carpodacus mexicanus*) in southern California show a large range of plumage variation, with individuals varying along a continuum from yellow to orange to red. This extreme variation is largely unrelated to age and is likely to have fitness consequences (e.g. Hill 1990, 1991; Belthoff 1994; Thompson et al. 1997). New analyses based on museum specimens, a literature review, and recently captured individuals indicate that the high level of variation is a new phenomenon because most males were red prior to the 1950s, whereas half or more are currently orange or yellow. The change toward orange and yellow plumage may be related to a high incidence of avian pox that was first noted in the early 1970s but probably began earlier. In addition to a temporal link between pox and plumage variation in California, there is also a geographic link. Pox is very common in Hawaii, where most males are orange or yellow, but rare or absent on San Nicolas Island off the coast of southern California and in eastern North America. At least 90% of the males are red in each of these two latter areas. The link between pox and plumage color may occur as an effect of physiological condition, pathogen virulence, or host resistance among populations, or from a combination of these factors. *Received 17 July 1997, accepted 29 April 1998.*

HIGH LEVELS OF INTRASPECIFIC VARIATION in traits such as plumage color are likely to have major fitness consequences, especially if the variation occurs within a class of individuals of the same sex and age. Thus, male House Finches (*Carpodacus mexicanus*) are particularly interesting because they have an extremely high level of variation in plumage color in some populations (perhaps exceeding that of any other North American bird species). Variation in plumage color in male House Finches is related to differences in attractiveness to females (Hill 1990), social dominance (Belthoff et al. 1994), and foraging proficiency (Hill 1991). Therefore, fitness is likely to be affected by plumage color.

Strong phenotypic variation that is correlated with important aspects of fitness raises the question of how such variation is maintained. One possibility is that the variation is an evolutionarily stable trait with different phenotypes reflecting different genetically influenced degrees of resistance to disease (Hamilton and Zuk 1982). House Finches have an unusually high incidence of avian pox, a serious and, for some species, occasionally fatal disease (Karstad 1971). Plumage color may be an indicator of genetic resistance to that disease. Alternatively, it is possible that the high plumage variation is evolutionarily unstable and is due to recent changes in the environment or in the genetic structure of the host or pathogen. We attempted to address the latter alternative using: (1) museum specimens collected as early as 1888 in southern California, (2) data on recently captured birds from throughout much of the species' current range, and (3) a literature review of studies ranging from the early 1900s to the present. Although we could not determine whether the large plumage variation in House Finches currently is stable, we believe that the variation is a new phenomenon related, at least circumstantially, to a high incidence of pox (Power and Human 1976), which itself is a new phenomenon. Thompson et al. (1997) examined high loads of feather mites and visible avian pox lesions in male House Finches captured from 1978 to 1989 and found that parasite infection during molt was correlated with plumage-color changes away from red and toward yellower plumage.

House Finches are sexually dichromatic passerines indigenous to western North America from British Columbia to Baja, California and from the Pacific Ocean to Wyoming and Texas (Bent 1968). They were introduced to Hawaii sometime before 1870 (Grinnell 1911) and to Long Island, New York, around 1940 (Elliott and Arbib 1953). The latter population colo-

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nized much of eastern North America and recently has spread to the Texas panhandle and Oklahoma (Hill 1993a), where it has made contact with the eastern limits of the species' original range. Molt occurs once a year, and male plumage coloration in some regions commonly varies from pale yellow to dark red. The degree of variation varies temporally and spatially at local scales throughout California. Furthermore, the color of an individual may vary from year to year. In these cases, in the absence of pox disease, the hue of a non-red male usually moves closer to the red end of the spectrum (H. E. McClure unpubl. data, S. N. Zahn unpubl. data). However, the correlation between age and plumage color is weak, and males of any age can range from yellow to red (Michener and Michener 1931). Several observers have attempted to quantify the proportions of each color present in males for a number of California and Hawaii populations by classifying males as red, orange, or yellow based on visual surveys, trapping data, or both (Grinnell 1911; Michener and Michener 1926, 1931; Bent 1968; van Riper 1994).

Avian pox is a viral disease that has been reported in many bird species (Musselman 1928; Kossack and Hanson 1954; Kirmse 1967, 1966; Savage and Dick 1969; Dales and Pogo 1981; Forrester 1991; Samour and Cooper 1993; Allwright et al. 1994). It was first identified in House Finches in 1961 in Hawaii (Warner 1969) but was not reported in North America until noted at Santa Barbara, California, in 1972 (Power and Human 1976). Subsequently, pox has been diagnosed in House Finches in four other western states: Idaho in 1983 (Docherty and Long 1986), Washington in 1987, New Mexico in 1990, and Arizona in 1991 (USDI 1991). The highest prevalence of pox in House Finches occurs in the fall, during the prebasic molt, and in early winter (S. N. Zahn unpubl. data, H. E. McClure unpubl. data). This disease is transmitted by mosquitoes and biting flies, and laterally via shared perches and flocking areas (Karstad 1971).

Mortality rates from avian pox are unknown for House Finches. The characteristic tumors are subject to abrasion and bleeding that increase the risk of secondary infection (Hansen 1987). Another source of indirect mortality is occluded vision by head tumors, which may affect the visual field and depth perception. Tumors on the toes may obstruct blood flow to distal portions of the appendages, with subsequent necrosis and impaired perching ability. Missing phalanges in a large proportion of House Finches in some regions are evidence of past episodes of pox, as are deformed mandibles that result from facial tumors (McClure 1989). Because of its diverse detrimental effects, it is clear that pox can have a major influence on fitness in House Finches.

METHODS

We examined 171 study skins of male House Finches collected from Santa Barbara County to San Diego, California, between 1888 and 1995. We concentrated on southern California because avian pox is prevalent there, and a substantial number of specimens is available from the region. These skins are held in The American Museum of Natural History, University of California at Berkeley, University of California at Los Angeles, University of California at Santa Barbara, the Western Foundation of Vertebrate Zoology, and the Santa Barbara Museum of Natural History. Male plumage color of the head, breast, and rump was evaluated by comparison with color chips (Smithe 1975). All specimens were evaluated by daylight and near windows. If a bird had more than one hue, its color was scored as the one that was most abundant. Wing length was measured and feet were examined for evidence of past episodes of pox using criteria suggested by Gillespie and Timoney (1981).

To ensure objectivity in evaluating hue along a continuous scale, the 13 color chips to which the study skins were compared were evaluated by 22 independent observers who assigned the chips to 11 ranked categories. These were, from red to yellow, chip numbers 3, 10, (108A, 108, 11), 12, 13, 210, 14, 15, 16, 17, and 18. The chips were further categorized according to the Munsell color guide (Munsell 1976), thereby reducing subjectivity by comparing colors with a set of specially manufactured color standards. Each bird's plumage was then assigned to one of three general color groups according to the Munsell designations R (red), YR (orange), or Y (yellow).

Information on the color and pox status of House Finches in Hawaii and the eastern United States was evaluated for comparison with that from southern California. Eastern House Finch data were acquired in two ways. One was by examining all eastern males from two museums and evaluating them as previously described. Study skins obtained from the Carnegie Museum of Natural History (n = 39) were collected between 1976 and 1992 and included male House Finches from six counties in Pennsylvania, two counties in Massachusetts, and one county each in Maryland, Ohio, Virginia, and New York. Skins from the American Museum of Natural History (n =

13) were collected between 1948 and 1988 and included male House Finches from three counties on or near Long Island, New York, and two counties in New Jersey.

The other sources of eastern data were two New Jersey banders who captured House Finches in mist nets from 1979 to 1987 in Sussex County (P. Angus unpubl. data) and in both mist nets and Potter traps in 1985 and 1986 in Morris County (C. Kelly unpubl. data). Detailed records of each bird included hue descriptions and feather samples, so plumage could be evaluated according to our established color evaluation criteria.

House Finches captured at four sites in Santa Barbara and Goleta, Santa Barbara County, between May 1993 and March 1996 also are considered in this study. All sites were at least 1 km apart, and the two most distant sites were 6 km apart. All birds were caught in Potter traps and given United States Fish and Wildlife Service leg bands and unique combinations of colored leg bands. Birds were weighed and measured for a suite of standard parameters (i.e. wing length, tarsus length, bill length, bill depth). Male plumage color was evaluated the same way as museum specimens. Evidence of pox disease (e.g. missing toes and active tumors) was recorded.

Pox and color observations also are included for House Finches captured in mist nets, Potter traps, and decoy traps in Pasadena, California, from November 1991 to November 1995 (W. L. Principe unpubl. data) and by mist nets on San Nicolas Island, one of the California Channel Islands, from March 1996 to May 1997 (W. Wehtje unpubl. data).

RESULTS

Temporal variation in color.—The museums we surveyed had relatively few southern California specimens from the 1920s to the 1960s, and none at all for the 1950s (Fig. 1). Therefore, we classed all birds as pre-1950 or post-1960. Although pox was not documented in Santa Barbara County until 1972, it was likely to have existed for at least several years before that because it was present in many finches in 1972, the year Power and Human (1976) began to study House Finches in Santa Barbara. This makes the period between 1950 and 1960 a fortuitous cutoff point. Data were first analyzed by using the red-orange-yellow categories obtained from the comparison of hues to the Munsell scale and contrasting the percentage of birds that were red before 1951 (n = 94; 76.6% red) with the percentage that were red after 1960 (n = 78; 51.3% red). The results show a significant difference (χ^2 = 12.03, df = 3, $P <$ 0.001).

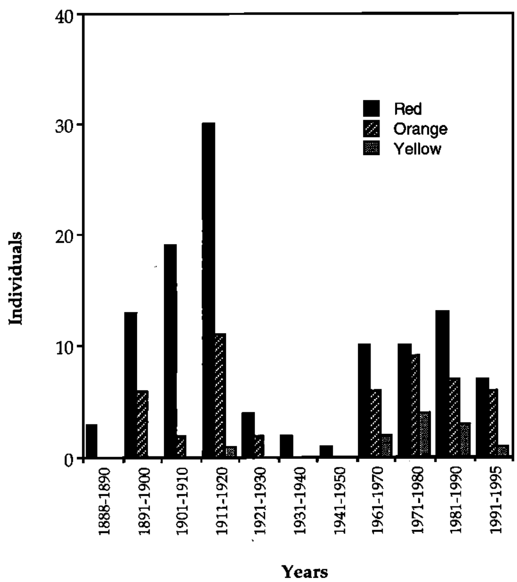

FIG. 1. Temporal changes in the proportions of red, orange, and yellow individuals in museum specimens of male House Finches from southern California.

Besides the shift away from red plumage after 1960, there was a significant shift toward yellow among birds that were not red (Fig.1). Before 1951, 22 of 23 non-red birds were orange, whereas only one (4.3%) was yellow. After 1960, 10 (26.3%) of 38 non-red birds were yellow (Fisher exact test, P = 0.01).

A significant correlation (r_s = 0.258, n = 172, $P <$ 0.0005) exists between time and the 11 categories of the hue continuum determined by 22 independent observers. This analysis has treated color variation as the true continuum that actually occurs, rather than categorizing birds as red, orange, or yellow.

A 1910 survey of study skins for the coastal area from Santa Barbara to San Diego counties (Grinnell 1911) and a study of 1,563 male House Finches banded in Pasadena in the 1920s (Michener and Michener 1926, 1931) also show very high proportions of red males (Table 1). Taken together, all three sources of pre-1951 data show a predominance of red males, ranging from 76 to 92.5%.

In contrast to the high incidence of red males reported by the Micheners (85%) in the 1920s, a recent banding study from November 1991

TABLE 1. Color variation in male House Finches from the eastern United States and California.

Source (range of years)	% Red	% Orange	% Yellow	% Red and gold	*n*
		Recent eastern birds			
AMNH (1948 to 1988)[a,b]	100.0	—	—	—	13
Carnegie Museum (1976 to 1992)[b]	84.5	13.0	2.5	—	39
New Jersey (1985 to 1986)[c]	93.0	3.8	0.7	2.6	157
New Jersey (1979 to 1987)[d]	87.5	9.8	—	2.7	112
Eastern average for all sources	91.3	6.7	0.8	1.3	321
		Recent California Birds			
Pasadena (1991 to 1995)[e,h]	12.2	71.7	16.1	—	459
Santa Barbara Co. (1994 to 1995)[f,h]	29.4	56.0	14.6	—	323
San Nicolas Is. (1996 to 1997)[g]	95.3	4.7	—	—	86
		Historic California birds			
J. Grinnell (pre-1910)	92.5	4.3	3.2	—	94
H. and J. R. Michener (1920s)	85.0	?	?	?	1,563
California average in absence of pox	90.9	—	—	—	2,318

[a] American Museum of Natural History (museum skins).
[b] Museum skins.
[c] Banding data; C. Kelly unpubl. data.
[d] Banding data; P. Angus unpubl. data.
[e] Banding data; W. L. Principe unpubl. data.
[f] Banding data; S. N. Zahn unpubl. data.
[g] Banding data; W. Wehtje unpubl. data.
[h] Populations with avian pox.

and November 1995 by W. L. Principe found only 12.2% to be red at a location only 8 km from the Michener site (Table 1). The proportion of red males present between the months of January through July (i.e. during nonmolting periods) varied among banding sites in Santa Barbara County. Overall, 27.3 and 34.4% of birds in 1994 and 1995 were red, and no site exceeded 52.8% (Table 2). These recently captured birds provide further evidence of a shift away from red plumage that predominated earlier in this century.

Spatial variation in color.—House Finches were introduced to an unspecified site in the Hawaiian islands probably before 1870, and by 1910 males were closer to the yellow end of the continuum than was the original mainland population (Grinnell 1911). Although this Hawaiian phenomenon persists at low elevations, color proportions vary from island to island

TABLE 2. Color variation in male House Finches by banding site in Santa Barbara County, California. UCSB Marine Science Institute is on the Pacific Ocean and is surrounded by coastal habitat. UCSB Police Station is directly between a salt marsh slough and chaparral. The other sites are in suburban areas. NF = no bird feeder present at banding site; F = bird feeder present.

Location	% Red	% Orange	% Yellow	*n*
		January through July 1994		
UCSB Marine Science Institute (NF)	52.8	36.1	11.1	36
UCSB Police Station (NF)	43.1	41.5	15.4	65
Zahn home (F)	14.7	67.4	17.9	95
Endler home (F)	3.2	87.1	9.7	31
Overall	27.3	57.7	15.0	227
		January through July 1995		
UCSB Marine Science Institute (NF)	42.1	42.1	15.8	38
UCSB Police Station (NF)	33.3	66.6	0.0	9
Zahn home (F)	30.5	52.8	16.7	36
Endler home (F)	23.1	69.2	7.7	13
Overall	34.4	52.1	13.5	96

(Dunmire 1961, van Riper 1994). Recent data reveal that on the xeric southwestern slopes of Mauna Kea and the Hawaii Volcanoes National Park, 43% of the male House Finches are red, whereas at the University of Hawaii campus on Oahu, only 5% are red (van Riper 1994). Red males are common at higher elevations, where mosquitoes are rare or absent (L. A. Freed pers. comm.).

A second introduction occurred in Long Island, New York, around 1940. The eastern mainland population descended from the New York introduction appears to have developed or maintained a more consistent dark-red phenotype than have birds from southern California, because 87% or more were red in two recent samples of trapped birds (Table 1).

House Finches are present on the Channel Islands off the coast of Santa Barbara and Ventura counties. A banding study (W. Wehtje unpubl. data) from March 1996 to May 1997 on San Nicolas Island, 100 km from the nearest point of the mainland, found that 95.3% of the males were red and 4.7% were orange (Table 1).

Temporal and spatial variation in avian pox disease.—Pox was first confirmed in mainland House Finches in 1972 at Santa Barbara, California, where 5 of 24 males captured and maintained in captivity had pox lesions and died within a few weeks of capture (Power and Human 1976). Santa Barbara is 161 km from Pasadena, where no cases of pox were noted in a study of 1,563 male House Finches in the late 1920s (Michener and Michener 1931), but where W. L. Principe (pers. comm.) estimated that in the fall approximately 25% of House Finches had tumors between 1991 and 1995. There was no indication of the disease on the pre-1951 study skins we examined ($n = 94$), nor in the accounts by Grinnell (1911). Among post-1960 male museum specimens, 12 of 78 (20%) were missing toes. Evidence of pox based on missing toes of museum specimens was significantly higher after 1960 than before 1950 (Fisher exact test, $n = 172$, $P < 0.0001$). Six of the 12 specimens with missing toes were red and six were orange. The correlation between missing toes and plumage color cannot be meaningfully evaluated for the post-1960 specimens owing to the small sample size and to the fact that plumage can become redder with each molt, and therefore may have been altered considerably since the time of infection.

Banding data from Santa Barbara County between May 1993 and March 1996 reveal that at least 251 of 667 males (37.6%) were infected by pox disease at some time. Banding data from Ventura County, immediately south of Santa Barbara County and north of Los Angeles County, indicate that about one-third of the House Finches from 1977 to 1987 exhibited pox tumors at least once in their lifetime (McClure 1989). In both Santa Barbara and Ventura counties, Zahn and McClure (unpubl. data) have observed tumors as previously described, and also on the cloaca. Data collected at the Ventura site reveal that male House Finches that are moderately to heavily infected with feather mites and avian pox during their annual fall molt grow significantly shorter primaries and have less red (i.e. are oranger and yellower) in their plumage than do males less infected or uninfected (Thompson et al. 1997). On San Nicolas Island, 100 km off the coast of Ventura County, 95.3% of males are red, and no cases of pox have been observed (W. Wehtje unpubl. data).

Twelve banders in coastal states between Maine and South Carolina, whose total sample size of House Finches was >20,841, were contacted for data on pox. Eight did not identify House Finches as having been observed with pox disease, although other species were observed to have had it. Four banders, three in upstate New York and one in Maryland, reported what they believed to be cases of pox in House Finches, although all thought it to be very rare (the only specific figure given was less than 1%). There are no published accounts of pox disease in the eastern population of House Finches.

Although color proportions have been shown to vary among nearby Santa Barbara sites and by year (Table 2), it is noteworthy that sites with the lowest proportions of red males are those that contain bird-feeding stations. Bird feeders result in unnaturally high densities of individuals, thereby promoting lateral transmission of disease. This pattern is supported by the finding that during October and November, the peak months of pox prevalence, a higher percentage of diseased birds was captured at a site with permanently provisioned bird feeders in Ventura County, California, than at a nearby park without a feeding station (McClure 1989).

DISCUSSION

Both temporal and spatial correlations exist among high levels of avian pox, low incidences of male House Finches with red plumage, and high incidences of males that are orange or yellow. Most importantly, the recent change in plumage color of House Finches in southern California (Fig. 1) coincides with the first known observation of pox tumors (Power and Human 1976). 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. 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.

Effects of diet vs. condition.—Differential dietary intake has been proposed as an explanation for color differences in male House Finch plumage (Brush and Power 1976; Hill 1990, 1992, 1993a; Hill and Montgomerie 1994). This hypothesis requires that carotenoids are limited in the wild and that some individuals have greater access to them than others. However, carotenoids may not be limiting in the wild (Hudon 1994) and may be abundant and varied in most habitats (Goodwin 1984, 1992; Gross 1987, 1991; Straub 1987; Goodwin and Britton 1988; Ong and Tee 1992). Furthermore, House Finches feed in flocks, and there is no direct evidence that some males have access to certain dietary resources from which others are excluded. Nor does the diet hypothesis account for the sudden shift in the proportion of red males in south-coastal California in the mid-1900s, which would require a major perturbation of plant species eaten by finches.

The red-orange-yellow coloration of male House Finches results from intake of carotenoid pigments that cannot be synthesized de novo (Brush and Power 1976, Brush 1990, Hill 1993b) but which can be ingested and used directly or converted metabolically into other carotenoids (Thommen 1971, 1975; Needham 1974; Brush 1981, 1990; Britton and Goodwin 1982; Goodwin 1984; Hencken 1992). Birds may be able to convert ingested yellow pigments to red ones (Davies 1985, Schiedt et al. 1985, Matsuno et al. 1986, Hencken 1992). Recent studies indicate that the predominant red pigment in House Finch plumage is 3-hydroxy-echinenone (C. Inouye, J. Hudon, and R. Stradi unpubl. data), which also is the predominant red pigment in the plumage of most cardueline finches (Stradi et al. 1995). This carotenoid is rare in nature and has been reported in a few species of *Euglena,* copepods and mites, and in the Eurasian flower *Adonis annua,* all of which produce various acidogenic carotenoids (Goodwin 1984). None of these is a known food source of House Finches (Beal 1907, Hill 1993a). Isolation and identification of carotenoids from food items contained in the stomachs of male House Finches during molt revealed that they ingest mostly yellow and orange carotenoids; no trace of 3-hydroxy-echinenone was found in the diet (C. Inouye unpubl. data).

Although no conclusive evidence exists that diet plays a major role in plumage coloration of wild House Finches, considerable evidence suggests that physiological condition has such an effect. Male House Finches that are moderately to heavily infected with feather mites and avian pox during molt grow significantly shorter primaries and are likely to become less red than are less-infected or uninfected males (Thompson et al. 1997). Common Redpolls (*Carduelis flammea*) maintained on the same diets in large, medium, and small enclosures (21.5 × 17 m, 16.3 × 8.7 m, and 11.5 × 6.5 m, respectively) molted to red, orange, and yellow, respectively, with the exception of one individual in the largest enclosure that molted to yellow. That individual had lost a foot (probably from a predation attempt) while in captivity, a likely source of a physiological stress (Weber 1961). Similarly, Red Crossbills (*Loxia curvirostra*) may molt to yellow when maintained in small aviaries (Volker 1957). Thus, there appears to be a strong relationship between stress (induced by disease, confinement, or trauma) and the ability to produce red plumage in some species of finches. The precise physiological mechanisms that would result in such a relationship are not known.

Possible relationships between disease and plumage color.—In addition to the finding that parasites influence plumage color in House Finches (Thompson et al. 1997), chickens inoculated with coccidia (a parasitic protozoan) or aflatoxin (fungus toxin) had significantly reduced levels of plasma carotenoids (Ruff et al. 1974, Tyczkowski et al. 1991). Much of what is known about the mechanisms of absorption and deposition of carotenoids in birds result from research on chickens. "Pale bird syndrome" describes the failure of chickens to realize their full color potentials despite the appropriate precursors being supplied in their diets. Absorption sites of different carotenoids are physically separated in the chicken intestine, which may account for differential effects of various parasites on pigmentation, because pathogens may attack localized sites specific to the absorption of a particular carotenoid (Tyczkowski and Hamilton 1986). Such a possibility in molting House Finches is consistent with their failure to produce red plumage when severely infected with pox (Thompson et al. 1997). It is also possible that the disease interferes with the production of red carotenoids from ingested precursors.

Further evidence for a relationship between disease and plumage color exists in the Hawaiian Islands. It is extremely likely that pox virus was introduced soon after Europeans first visited the archipelago in the 1770s. The disease is known to be transmitted by mosquitoes (Warner 1969), and its long-standing association with domestic poultry provided an opportunity for House Finches, a commensal of man, to have been exposed soon after they were introduced to Hawaii. Nearly half of the House Finches trapped in Hawaii in August 1961 exhibited pox lesions, and others lacked one or more toes, indicating previous infection (Warner 1969). The highest densities of mosquitoes are associated with moist habitats and with human habitation, which are the areas of fewest red House Finches in the Hawaiian Islands (van Riper 1994).

The response of Common Canaries (*Serinus canaria*) to pox has been well studied, and because House Finches and Canaries are in the same subfamily (Carduelinae), they are likely to respond similarly. Two forms of canary pox (Kikuth's Disease) are recognized: cutaneous and viremic. The cutaneous form, which may be generally survivable unless secondary bacterial infections occur, results in lesions in the same locations as observed on House Finches and also may occur in the mouth and esophagus (Fowler 1986). This indication that the digestive tract is involved is consistent with observations of cloacal tumors on House Finches (S. N. Zahn unpubl. data, H. E. McClure unpubl. data), and with pale bird syndrome of chickens.

Viremic birds exhibit dyspnea, diarrhea, ruffling, and depression. Death may occur before the development of cutaneous lesions, and mortality may reach 100% within five to six days. Therefore, a viremic infection may result in rapid death of susceptible individuals (i.e. those not protected by either intrinsic or acquired immunity) without external manifestation of disease. If individuals of certain morphs were more susceptible to this form of pox than others, differential mortality might have resulted in a decline in their proportions relative to other morphs.

Possible factors responsible for spatial and temporal variation in pox.—Assuming that anecdotal accounts of avian pox affecting eastern House Finches are accurate, why hasn't this disease spread throughout the eastern population the way it has in the western United States and Hawaii? The answer may lie in epidemiological theory, which supports a direct relationship between high population density of the host, and thus ease of transmission, and high virulence of a pathogen (May 1991, Ewald 1994). The rate of transmission is directly proportional to the frequency of encounters between susceptible individuals and infected hosts and / or vectors. Thus, a higher population density of a host increases both the number of potential infected hosts and the number of new susceptible individuals via births (Cox 1982, Esch and Fernandez 1993). The fact that western House Finches have maintained high densities, whereas the eastern population has experienced only a recent trend toward high density (Veit and Lewis 1996, Sauer et al. 1997), as well as pockets of greatly fluctuating population densities (Yunick 1995), is consistent with the possibility that the opportunity for infection and the evolution of higher pathogen virulence are higher in western populations. Genetic changes in mosquito vectors, House Finches, or in the virus itself also may be factors influencing the incidence of pox.

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