ORIGIN AND EVOLUTION OF THE EASTERN HOUSE FINCH POPULATION

JOHN W. ALDRICH AND JOHN S. WESKE

National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA and National Fish and Wildlife Laboratory, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560 USA

ABSTRACT.—The House Finch (*Carpodacus mexicanus*) became established in the eastern United States after liberation in the New York City area, spreading from there along the Atlantic seaboard. It has been assumed that the liberated birds were from California. Specimens of the new eastern population resemble most closely those from western California in size but differ from them in having relatively smaller legs and feet. In color, eastern birds resemble House Finches from northeastern Colorado and southeastern Wyoming, as well as those from eastern Washington and northern Idaho. On the basis of historical and size evidence we conclude that the eastern House Finch population is descended from California stock but has differentiated from it in color and size after liberation in the east. The change took place rapidly, as two specimens taken 9 and 11 yr after introduction showed the differences from California birds that now characterize the eastern population. The case of the House Finch parallels that of the House Sparrow (*Passer domesticus*) in its rapid evolutionary change after introduction and spread into new environments.

Several climatic and associated vegetational differences from California were encountered by eastern House Finch pioneers. The lower temperatures have not selected for larger size in the new eastern population as was the case in House Sparrows that moved into colder climates, and no other environmental factor or combination of factors including substrate aspect is the obvious cause of differentiation of eastern birds from their California ancestors. *Received 7 February 1977, accepted 20 September 1977.*

THE unexpected appearance in 1941 and rapid spread of the House Finch (*Carpodacus mexicanus*) as a breeding species in the eastern United States has been documented by Elliott and Arbib (1953), Potter (1964), Katholi (1967), Woods (1968), Paxton (1974), and Bull (1974). The extension of its range as far south as North Carolina was discussed by Quay (1967), and further by Cohen and Cohen (1971) who had banded a House Finch at Atlantic Beach, New York that was later recovered in North Carolina. Bock and Lepthien (1976) computed population growth and winter range expansion from 1962 to 1971 from data contained in the Christmas Bird Counts published in *American Birds*. The consensus is that the founder individuals of the new eastern population were liberated by cage bird dealers on western Long Island, New York in 1940 when they were informed that the species was protected by federal law. It seems unlikely that House Finches arrived by natural range extension from western populations since the known natural eastward limits of the breeding range at the time of introduction were in north-central and southeastern Wyoming (McCreary 1939), western Nebraska (Rapp et al. 1958), western Kansas (Johnston 1965), western Oklahoma (Sutton 1967) and central Texas (Oberholser 1974).

It has been assumed that the liberated birds that became established in the east were obtained in California because large numbers of House Finches, called Hollywood Finches or Red-headed Linnets by the trade, were known to have been furnished by a wholesaler in that state to New York cage bird dealers, including a pet store on western Long Island (Elliott and Arbib 1953). Furthermore, two specimens (a male and female) taken on Long Island in 1949 and 1951 were compared with specimens from California by Alden H. Miller, who reported that he could

match them perfectly with individuals taken in spring in the San Joaquin Valley and Los Angeles areas (Elliott and Arbib 1953).

Since specimens of the House Finch taken in the eastern states have been gradually accumulating in museum collections, it seemed to us desirable to reinvestigate the matter of geographic origin of the eastern population, based on more adequate comparisons of morphological characters than had been possible in the past.

Methods

For comparative studies, specimens were grouped by six major ecologically and faunally distinct regions of the United States where House Finches were known to occur commonly at the time of introduction of the eastern population, and also a seventh region where liberated birds have become established in the East (Fig. 1). Those regions are: (1) Western California, (2) Great Basin, (3) Southwestern Desert, (4) Columbia Basin, (5) Great Plains, (6) Chihuahuan Desert, and (7) Eastern Region. Those ecogeographical units conform in general to the following "Biotic Provinces" of Dice (1943): (1) Californian, (2) Artemisian, (3) Mohavian & Sonoran & Navahonian, (4) Palusian, (5) Kansan, (6) Chihuahuan, and (7) Carolinian. They are closely similar also to the following "Provinces" within "Ecoregions" of Bailey (1976): (1) California Grassland & California Chaparral, (2) Intermontane Sagebrush, (3) American Desert & Colorado Plateau, (4) Palouse Grassland, (5) Great Plains Short-grass Prairie (Grama-Buffalo Grass Section), (6) Chihuahuan Desert, and (7) Eastern Deciduous Forest & Southeastern Mixed Forest. Morphological variation in House Finches had been noted previously by Moore (1939) and Aldrich (1949) to be in accordance with geographic areas conforming roughly to those ecogeographic regions. Therefore the units seemed a logical basis for stratification of samples for comparison in the present study. To comprise our Southwestern Desert region the Mohavian, Sonoran, and Navahonian Biotic Provinces of Dice (1943) and the American Desert and Colorado Plateau Ecoregion Provinces of Bailey (1976) were combined because our preliminary analysis of size and color in House Finches indicated no differences within those combined areas. For the same reason the California Grassland and California Chaparral provinces of Bailey were combined into our Western California region, which is the same as Dice's Californian Biotic Province minus the Sierra Nevadas, where few if any House Finches occur.

As pointed out by Moore (1939), it is particularly important with House Finches to compare only specimens taken at the same time of the year. This is because of the extraordinarily great seasonal variation, described in detail by Michener and Michener (1931), as well as age variation, noted by Gill and Lanyon (1965). In the present study only specimens taken in equivalent months were compared with each other for color differences to avoid confusing seasonal change with actual individual differences and geographic variation. We found no evidence of color change because of museum age.

The significance of yellow coloration in place of red in male House Finches was elucidated by Michener and Michener (1931) and subjected to experimentation by Brush and Power (1976). This abnormal condition existed in only a very few of the specimens of any mainland population that we examined. These were excluded from our color comparisons, as were all males in the brown female plumage, a condition discussed by van Rossem (1936) and Moore (1939). Also excluded from the samples for study of color were specimens that showed any indication of soiled plumage. The soiled and yellow colored specimens eliminated for study of color were, however, used for measurements presented in Table 1, but the males in brown female plumage were not. Observations of color differences were made under a Macbeth Examolite Fixture, Type TC440, a combination of artificial lights designed to simulate daylight quality. Series of specimens were arranged in parallel lines for comparison on a background of neutral gray. Measurements were made with a dial caliper to the nearest 0.1 mm. Measurement of the wing was the chord of the unflattened wing. The t-test was used to make statistical comparisons of mean measurements.

Observations

The series of eastern United States House Finches could be separated easily from all examples of Mexican populations on the basis of color. Of all Mexican populations, that of the Chihuahuan Desert most closely approximates eastern United States birds in color. Its characters are exhibited by individuals ranging from northeastern Mexico northward to the Rio Grande Valley of western Texas and central southern New Mexico (Fig. 1). Eastern United States House Finches resemble that

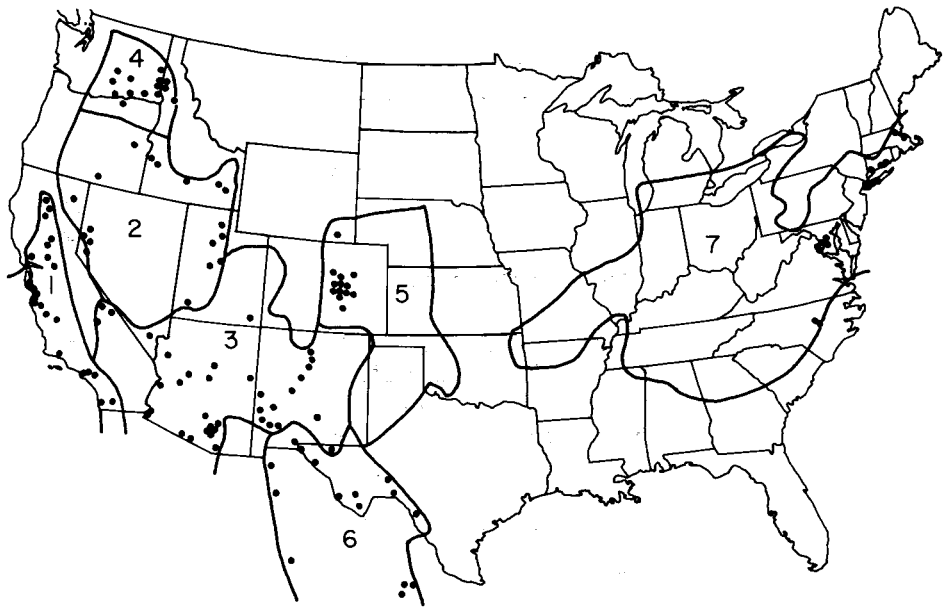

Fig. 1. *Carpodacus mexicanus* specimen localities by ecogeographical region: 1 = Western California [=Californian (Dice) or California Grassland & California Chaparral (Bailey)], 2 = Great Basin [=Artemisian (Dice) or Intermontane Sagebrush (Bailey)], 3 = Southwestern Desert [=Mohavian & Sonoran & Navahoan (Dice) or American Desert & Colorado Plateau (Bailey)], 4 = Columbia Basin [=Palusian (Dice) or Palouse Grassland (Bailey)], 5 = Great Plains [=Kansan (Dice) or Great Plains Short-grass Prairie (Bailey)], 6 = Chihuahuan Desert [=Chihuahuan (Dice) or Chihuahuan Desert (Bailey)], 7 = Eastern Region [=Carolinean (Dice) or Eastern Deciduous Forest & Southeastern Mixed Forest (Bailey)].

population in the darkness of plumage coloration but are more grayish (less olivaceous) brown in both sexes and the red of the head and underparts of males is more dusky (less bright) red; they are also significantly smaller in wing, tail, tarsus, mid toe, and bill than the Chihuahuan Desert specimens.

Eastern birds are quite different, as well, from the large-billed, extremely dark reddish-brown, and buffy birds of the Channel Islands off the southern California coast and are not compared further with that population.

From all other United States populations (Fig. 1), except that of the Great Plains and Columbia Basin, Atlantic coastal House Finches differ in having more dusky (less bright) red coloration of the heads, rumps, and underparts of the males. However, both the eastern and Great Plains series differ very slightly from Columbia Basin birds in averaging darker dorsally, particularly in females, and in having underparts more heavily streaked. Eastern House Finches are significantly smaller than Great Plains birds in all measurements except (male) tarsus, and significantly smaller than Columbia Basin examples in all measurements except (female) bill (Table 1). In color, eastern birds are unlike those from the Southwestern Desert and Great Basin by being much darker and more grayish, by having broader and more dense ventral streaks, more grayish (less buffy) white ground color of underparts, and more dusky red coloration in males. In size Eastern birds are smaller than those of the Southwestern Desert, and significantly smaller in wing, (male) tail, tarsus,

(male) middle toe, and (male) bill. Eastern birds resemble the Great Basin population closely in size, although they are somewhat smaller and significantly so in (female) wing, (female) tarsus, and (male) middle toe. Southwestern Desert examples differ from the Great Basin sample in color only in averaging slightly darker in males, with practically no difference in color of females. They also average significantly larger in (male) wing, (male) tail, and (male) bill. Eastern House Finches differ from those of Western California in having more dusky, less pure red heads and breasts in males, less buffy white underparts and more grayish brown backs and ventral streaks in both sexes. Those two populations resemble each other closely in size, Western California birds averaging only slightly larger in all measurements except exposed culmen. In (male) tarsus and (male) middle toe California birds are significantly larger than Eastern House Finches. Western California birds differ from Southwestern Desert and Great Basin examples primarily in being darker and in having more pure (less orange) red coloration in males and darker and more olivaceous (less grayish) brown coloration in females. Females of those three populations differ very little in color, but Western California birds are smaller in both sexes and significantly smaller than Southwestern Desert birds in (male) wing, (male) tail, (female) middle toe, and bill. The series of Western California House Finches differs from Great Plains, Columbia Basin, and Eastern examples in having more pure (less dusky) red heads and underparts of males, more olivaceous (less grayish) brown backs and ventral streaking, and more buffy (less grayish) white ground color of underparts of both males and females. Western California birds are also significantly smaller than Great Plains specimens in wing, tail, (female) tarsus, (male) middle toe, and bill. They are significantly smaller than Columbia Basin birds in tail, middle toe, and (male) bill.

Moore (1939) commented that House Finch populations of desert regions are the smallest, lightest colored, and least heavily streaked. He was incorrect that they are the smallest, as that characteristic belongs to the Pacific coast birds and their presumed descendants on the Atlantic coast. He was correct that desert birds of the Southwestern and the Great Basin deserts are the lightest but Chihuahuan Desert birds are dark and heavily streaked. Moore also noted a high degree of yellowish coloration in Pacific coastal males (18.4%) as compared with 3.3% of desert and plateau birds. If that is the case, Atlantic coast birds are unlike their presumed ancestors in that respect. In our series of specimens from the East only 2 out of 26 (7%) showed a trace of yellowish coloration. By far the highest incidence of yellow-colored individuals is among the introduced population of the Hawaiian Islands that became established at an undetermined date, presumably descended from California stock (Grinnell 1911). The Hawaiian birds have differentiated from those on the mainland not only in the incidence of yellow-colored males but in other morphological characters to the extent that they have been considered a distinct species (*Carpodacus mutans*) by Grinnell (1912) and Moore (1939). Brush and Power (1976) found that yellow coloration in House Finches can be due to nutrition or physiological deficiencies.

The conclusion that may be drawn from color comparisons of the eastern United States population of *C. mexicanus* is that it is different in color from all others of that species except the population of the Great Plains. Those two resemble each other very closely in their relatively dark and grayish brown coloration in both sexes and dusky red coloration (predominantly "Brick Red" of Ridgway [1912] or 7.5 R 4/6 of Munsell [1929–1942]) in males. This combination of shade, hue, and value of

TABLE 1. Measurements (mm) of House Finches

Population	Males N	Mean ± 2 SE	Range	SD	Females N	Mean ± 2 SE	Range	SD
WING LENGTH								
Western California	48	77.49 ± 0.58	74.6–80.3	2.04	35	74.78 ± 0.60	71.7–78.2	1.77
Great Basin	29	77.29 ± 0.62	71.1–79.9	1.65	26	75.35 ± 0.78	71.1–79.6	1.98
Southwestern Desert	45	78.46 ± 0.48	74.2–82.4	1.59	24	75.10 ± 0.54	73.2–78.2	1.33
Columbia Basin	44	77.80 ± 0.56	72.2–81.6	1.83	35	75.46 ± 0.50	72.6–78.4	1.49
Great Plains	34	78.67 ± 0.58	74.5–82.7	1.71	31	75.99 ± 0.60	73.0–79.8	1.68
Chihuahuan Desert	26	77.96 ± 0.96	73.7–81.6	2.45	18	75.68 ± 0.88	72.2–77.9	1.87
Eastern	26	76.70 ± 0.66	73.4–80.2	1.66	14	73.75 ± 0.74	71.9–75.9	1.37
TAIL LENGTH								
Western California	47	59.75 ± 0.54	53.8–63.8	1.83	35	57.58 ± 0.60	53.5–63.8	1.76
Great Basin	30	59.96 ± 0.74	55.0–64.0	2.04	23	57.95 ± 0.80	55.0–63.0	1.93
Southwestern Desert	45	61.49 ± 0.60	58.1–65.6	1.99	24	58.07 ± 1.02	53.5–63.3	2.49
Columbia Basin	44	61.12 ± 0.48	57.5–66.0	1.83	35	58.48 ± 0.50	56.1–62.8	1.48
Great Plains	34	62.23 ± 0.70	58.0–66.2	2.04	31	59.78 ± 0.72	54.7–64.3	2.02
Chihuahuan Desert	26	61.46 ± 1.00	57.4–66.4	2.55	19	59.75 ± 0.96	57.4–66.4	2.10
Eastern	26	59.58 ± 0.88	56.0–66.3	2.26	14	56.91 ± 1.28	54.2–60.7	2.38
TARSUS								
Western California	48	17.49 ± 0.16	16.3–18.7	0.59	35	17.39 ± 0.20	16.5–17.9	0.58
Great Basin	30	17.55 ± 0.22	16.0–18.6	0.62	26	17.64 ± 0.18	16.9–18.8	0.48
Southwestern Desert	45	17.63 ± 0.18	16.0–18.7	0.63	24	17.65 ± 0.30	15.8–19.1	0.72
Columbia Basin	44	17.64 ± 0.14	16.8–18.7	0.44	35	17.47 ± 0.18	16.4–18.3	0.52
Great Plains	34	17.50 ± 0.24	16.2–18.6	0.68	29	17.80 ± 0.24	16.5–18.6	0.62
Chihuahuan Desert	26	17.65 ± 0.22	16.4–18.7	0.58	19	17.46 ± 0.22	16.4–18.3	0.50
Eastern	26	17.18 ± 0.24	15.8–18.1	0.61	14	17.04 ± 0.32	15.7–17.8	0.59
MIDDLE TOE								
Western California	48	13.20 ± 0.19	12.0–14.2	0.54	35	12.96 ± 0.18	12.1–14.2	0.54
Great Basin	29	13.55 ± 0.22	12.4–14.4	0.58	26	13.41 ± 0.24	12.2–14.4	0.59
Southwestern Desert	45	13.34 ± 0.18	12.0–14.2	0.58	24	13.29 ± 0.26	12.3–14.4	0.63
Columbia Basin	44	13.46 ± 0.16	12.3–14.6	0.56	35	13.55 ± 0.16	12.2–14.5	0.49
Great Plains	34	13.48 ± 0.24	12.4–14.8	0.55	30	13.12 ± 0.22	12.0–14.2	0.58
Chihuahuan Desert	26	13.40 ± 0.24	12.1–14.7	0.62	19	13.12 ± 0.26	12.0–13.8	0.55
Eastern	26	12.87 ± 0.18	12.0–13.6	0.47	14	12.60 ± 0.38	11.2–13.8	0.72
EXPOSED CULMEN								
Western California	48	9.41 ± 0.12	8.5–10.1	0.38	34	9.21 ± 0.14	8.6–10.0	0.43
Great Basin	28	9.39 ± 0.16	8.3–10.6	0.43	26	9.32 ± 0.18	8.3–10.6	0.44
Southwestern Desert	46	9.61 ± 0.12	8.7–10.6	0.40	46	9.61 ± 0.12	9.0–10.0	0.40
Columbia Basin	44	9.62 ± 0.10	8.8–10.4	0.35	35	9.40 ± 0.14	8.6–10.1	0.42
Great Plains	32	9.73 ± 0.16	8.9–10.5	0.47	31	9.60 ± 0.14	8.8–10.3	0.38
Chihuahuan Desert	26	9.84 ± 0.16	9.2–10.8	0.40	19	9.83 ± 0.26	8.6–10.6	0.55
Eastern	26	9.55 ± 0.16	8.7–10.3	0.43	14	9.31 ± 0.16	8.8–9.9	0.31

coloration distinguishes House Finches of the new Eastern and Great Plains populations from all others. The duskiness of eastern specimens and their resemblance to Great Plains birds was first noted by Elliott and Arbib (1953) who attributed it to soiling or "sooting." Most of the specimens they examined, now in the American Museum of Natural History, are indeed soiled. But two were washed when prepared, and even those clean specimens show the color characteristic of the larger series of eastern birds now available to us.

In size characteristics a different picture emerges. Table 1 indicates that the eastern population of House Finches is very similar to that of Western California in measurements, averaging only slightly smaller, but compared with all other populations, its smaller size is more pronounced.

DISCUSSION

We are faced with the contradictory situation that Eastern birds resemble more closely in size the Western California population, tending to corroborate the histor-

ical evidence that they originated from that stock, but they are different from that population in color. At the same time, Eastern birds are indistinguishable in color from a population with larger measurements in the Great Plains of northeastern Colorado and southeastern Wyoming, for which there is no historical evidence of relationship with the Eastern group. Thus, despite the color and slight size differences, the preponderance of evidence favors a California origin.

A characteristic the three dusky populations of House Finches have in common is their recent occurrence in geographic areas beyond the ranges of their presumed ancestral populations, from which they differ in color. Assuming that Eastern House Finches are in fact descendants of California stock, the color differences must have developed very rapidly after establishment of the Eastern population. The two washed specimens collected on Long Island by Robert Arbib in 1949 and 1951, presumably only 9 and 11 yr after introduction from California, already showed the color that characterizes Eastern birds. Documentation of relatively recent occurrence in the Columbia Basin of eastern Washington of House Finches that have been characterized as dusky-colored is supplied by Jewett et al. (1953); and appearance of that type of coloration on the east side of the Continental Divide in northeastern Colorado was documented by Figgins (1930). The morphological characteristics of the new breeding populations in southern British Columbia (Brooks 1942, Cowan 1937) and west of the Cascade Mountains in western Washington and northwestern Oregon (Christmas Bird Counts published in *Audubon Field Notes*) remain undetermined.

Rapid morphological changes have been noted in the introduced House Sparrow (*Passer domesticus*) after establishment in new and environmentally different situations (Calhoun 1947, Johnston and Selander 1964, Packard 1967). Possibly the changes in both the House Finch and the House Sparrow began to occur coincident with range extension, through selection of pioneers possessing adaptive characters (Mayr 1951: 118). Environmental differences from ancestral regions that confront the three newly established dusky-colored House Finch populations are less sunshine, higher humidity, lower evaporation rate, higher total precipitation, higher snowfall, lower winter minimum temperature, and lower summer maximum temperature (Environmental Data Service 1974). At least for the Eastern population, the background aspect of the natural vegetation is also quite different.

Acceleration of natural selection through elimination of poorly adapted individuals by a severe snowstorm was noted for the House Sparrow (Bumpus 1899, Calhoun 1947, Johnston et al. 1972). The disappearance of House Finches from the initial Long Island population after heavy snow in the winter of 1947 and 1948, mentioned by Elliott and Arbib (1953) and Katholi (1967), demonstrated the possibility of rigorous winter climate as a selective influence on the pioneering Eastern population of that species as well. Other northern House Finch populations have been observed partially to disappear in winter, a situation that has been presumed to result from migration (Salt 1952, Burleigh 1972). However, the consensus of a number of observers that the species is essentially sedentary and that movement of individuals for substantial distance is exceptional is borne out by our analysis of recoveries of House Finches banded in British Columbia, Washington, Idaho, and Oregon (only 4% moved as much as 200 km), and by observation of movements of birds banded and color-marked at Manomet, Massachusetts (Betty Smyth, pers. comm.). Thus, Eastern birds do seem to encounter colder and more snowy weather than their California relatives, but the reason that such climatic factors might select for more

grayish-brown and dusky red characteristics is not apparent, although its possible relationship to thermoregulation or other physiological adaptations to different climatic factors should be investigated. There has been no increase in size of Eastern House Finches compared to those of California, unlike the situation in the House Sparrow, for which Calhoun (1947) noted an increase in wing length correlated with range extension into regions of lower temperature. In fact the reverse seems indicated.

Another environmental factor that might contribute to evolutionary change in eastern House Finches is atmospheric moisture. The physiological effect of evaporation rate (vapor pressure) related to high temperatures was considered by Salt (1952) as a primary factor limiting distribution of House Finches, although his methods were challenged by Kendeigh (1953). Based on experiments on birds trapped in the Berkeley, California area, Salt theorized that (assuming suitable habitat) the species is limited in its distribution primarily by high vapor pressure, and that where it does occur in relatively humid areas, such as southwestern California, it is able to do so because of compensation provided by an exceptionally favorable food supply.

Actually one of the highest House Finch population densities in the United States (31 to over 100 per 25-mi census route) is in southwestern California (Robbins and Van Velzen 1969, Danny Bystrak, pers. comm.). Evidently that area is optimal for House Finches, and it seems unlikely to us that its population is poorly adapted to it. We agree with the suggestion of Bock and Lepthien (1976) that southwestern California birds, and the new Eastern population as well, may have evolved a tolerance for high vapor pressure. Salt himself allowed for the possibility of geographic variation in physiological characteristics of the species. On the basis of his experiments, he theorized that the lack of close correspondence between the physiological optimum of his Berkeley birds and climatic conditions in other portions of the species' range suggests that more northerly populations may possess slightly lower physiologically optimum temperatures.

Although Eastern House Finches have become adapted to temperatures and atmospheric moisture conditions different from those in California, it is not apparent how those factors could be directly responsible for the color or leg and foot changes that have occurred. It would appear equally likely that the very different climatic factors experienced by the Eastern birds have been responsible indirectly for the color difference through selection of colors of cryptic value, as postulated by various authors for a number of species, and particularly convincingly in the case of the Wrentits (*Chamaea fasciata*) studied by Bowers (1960). The environment of lush, green deciduous woods and fields in the east certainly presents a different substrate or background aspect from that of the drier California chaparral, oak woodland, and grassland. Plant growth types producing background characteristics of shade and color, which, as noted by Bowers (1960), are involved in the selection for cryptic coloration in birds, are controlled by combinations of climatic factors such as amount of sunshine, relative humidity (particularly in summer), total precipitation, snowfall, maximum temperature, minimum temperature, and evaporation rate. But the manner in which the dusky pigmentation of eastern birds may enhance cryptic coloration in their eastern habitat remains to be demonstrated. At present, the factor or combination of factors underlying the rapidly evolved color change in Eastern birds is not apparent although cryptic value and possible relationship to physiological adaptations cannot be ruled out without further investigation. The seemingly shorter

wings and tails, larger bills, and significantly shorter legs and toes of Eastern House Finches compared with California specimens are difficult to explain in terms of adaptation to a different environment. Possibly dependence on different kinds of food and sources of food supply may be responsible. It is quite possible that Eastern birds are more dependent on artificial feeding than are their western relatives.

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The International Commission on Zoological Nomenclature, to avoid uncertainty and preserve general usage, has validated *Geositta peruviana* Lafresnaye, 1847, and the subspecific name *paytae* Ménégaux and Hellmayr, 1906, and has suppressed *Anthus paytensis* Lesson, 1837, (usually considered a *nomen dubium*), which Zimmer had revived believing it a senior synonym of *Geositta peruviana paytae*, but as to which Vaurie was dubious (see Bull. Zool. Nomencl. 34 (pt. 4): 205–212, February 1978).