

11-1-2003

Wing Shape in House Finches Differs Relative to Migratory Habit in Eastern and Western North America

Jeremy R. Egbert
Boise State University

James R. Belthoff
Boise State University

ulation to changes in rainfall, which could amount to several breeding seasons.

It has previously been shown that Bananaquits on another Caribbean island, Puerto Rico, suffered a large population decline during a drought there in the mid-1970s, and that there was a lag in the response to rainfall (Faaborg et al. 1984). The size of the Bananaquit population was most closely related to rainfall two years previously. This provides strong support for our suggestion that drought could have perturbed the Bananaquit population in Grenada. If black birds are more strongly affected by drought than yellow birds, as is suggested by their relative rarity in the driest areas of Grenada, then it seems likely that drought could result in movement of the cline. If movement in the cline is caused by variation in rainfall acting with a lag, then the cline should have moved to the southwest during the late 1950s, following a wet period in the mid-1950s. We have been unable to find data to test this prediction.

In summary, the Bananaquit morph-ratio cline has not experienced any net movement in 20 years, which is approximately 20 generations. This suggests that the cline is in equilibrium. Previous movements of the cline may have been the result of long-term variation in rainfall.

We thank the Ministry of Agriculture, Forestry, Lands and Fisheries, Grenada, for permission to carry out the work. We also thank C. Macpherson, M. Phillip, D. Ramsier, and M. Sousa for assistance in Grenada; Blue Horizons Hotel and Mr. Ross for permission to mist net on their land, and B. Hatchwell and J. Wunderle for comments on a previous version of the manuscript. The work was funded by the British Ecological Society.

LITERATURE CITED

- BARTON, N. H., AND G. M. HEWITT. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113–148.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, N.J.
- FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest—a nine year study. *Wilson Bulletin* 96:575–593.
- FISHER, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355–369.
- HULME, M. [ONLINE]. 2000. Datasets/global precipitation: global land precipitation. (<http://www.cru.uea.ac.uk/~mikeh/datasets/global>) (5 June 2003).
- HULME, M., T. J. OSBORN, AND T. C. JOHNS. 1998. Precipitation sensitivity to global warming: comparison of observations with HadCM2 simulations. *Geophysical Research Letters* 25:3379–3382.
- ORDNANCE SURVEY INTERNATIONAL. 1988. Grenada south. Ordnance Survey International, Southampton, UK.
- SAS INSTITUTE INC. 1999. OnlineDoc. Version 8.0. SAS Institute Inc., Cary, NC.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, New York.
- THERON, E., K. HAWKINS, E. BIRMINGHAM, R. E. RICKLEFS, AND N. I. MUNDY. 2001. The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the Bananaquit, *Coereba flaveola*. *Current Biology* 11:550–557.
- WUNDERLE, J. M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution* 35:333–344.
- WUNDERLE, J. M. 1983. A shift in the morph ratio cline in the Bananaquit on Grenada, West Indies. *Condor* 85:365–367.

The Condor 105:825–829
© The Cooper Ornithological Society 2003

WING SHAPE IN HOUSE FINCHES DIFFERS RELATIVE TO MIGRATORY HABIT IN EASTERN AND WESTERN NORTH AMERICA

JEREMY R. EGBERT AND JAMES R. BELTHOFF¹

Department of Biology, Boise State University, Boise, ID 83725

Abstract. We investigated whether wing morphology differed between the sedentary House Finches

(*Carpodacus mexicanus*) of western North America and the introduced population of eastern North America, as the latter has developed migratory behavior since its inception. Wing morphology differed between eastern and western House Finches. Eastern House Finches had shorter proximal primaries and a longer outer primary, perhaps reflecting a thinner and more pointed wing, although no disparity in wing length was

Manuscript received 24 December 2002; accepted 4 June 2003.

¹ Corresponding author. E-mail: jbeltho@boisestate.edu

detected. Since we interpret these differences in wing shape as modifications for flight capability, we believe that initial evidence for morphological divergence relative to migratory habit between eastern and western House Finches has been established here. Confirmatory studies to determine if wing morphology varies according to the gradient in expression of migratory behavior throughout the range of eastern House Finches are now warranted.

Key words: *Carpodacus mexicanus*, House Finch, intraspecific variation, morphology, partial migration, wing shape.

La Forma Alar en *Carpodacus mexicanus* Difiere en Relación a los Hábitos Migratorios entre el Este y Oeste de Norte América

Resumen. Investigamos si la morfología del ala difiere entre individuos sedentarios de *Carpodacus mexicanus* del oeste de Norte América y la población introducida en el este de Norte América, la cual ha desarrollado un comportamiento migratorio desde su inserción. La morfología del ala difirió entre las poblaciones de *C. mexicanus* del este y del oeste. Los individuos del este tuvieron primarias proximales más cortas y primarias externas más largas, lo que quizás refleja un ala más fina y más puntiaguda, aunque no se detectó una diferencia en el largo del ala. Ya que interpretamos estas diferencias en la forma del ala como modificaciones para la capacidad del vuelo, creemos que se ha establecido una evidencia inicial de divergencia morfológica en relación con el hábito migratorio entre las poblaciones de *C. mexicanus* del este y del oeste de Norte América. Actualmente, son necesarios estudios que confirmen y determinen si la morfología del ala varía de acuerdo al gradiente de expresión del comportamiento migratorio a través del rango de distribución de la población de *C. mexicanus* del este.

One of the most notable ornithological events of the twentieth century in North America was the introduction of House Finches (*Carpodacus mexicanus*) into the eastern United States from native western populations and their subsequent spread (Hill 1993). The eastern population is believed to have originated from the release of a small but unknown number of captive birds on Long Island, New York, around 1940 (Elliot and Arbib 1953), and the source of the birds is presumed to be the Los Angeles area of southern California (Mundinger 1975). After a decade or so of local increases in the vicinity of western Long Island, the introduced population grew exponentially and rapidly expanded its range across the continent (Veit and Lewis 1996). House Finches are now naturalized and common throughout most of the eastern and midwestern United States, and in southern Canada.

As House Finches in the native range are essentially sedentary, one striking outcome of the introduction has been the appearance and increased frequency of migratory behavior in the eastern population of House Finches (Belthoff and Gauthreaux 1991, Able and Belthoff 1998). In fact, the eastern House Finch pro-

vides one of the very few cases in which the establishment of a large-scale pattern of migratory behavior has been documented under natural conditions in our lifetime. Over the 60 or so generations since their introduction, a complex system of seasonal migration has evolved in House Finches (Able and Belthoff 1998) in a remarkably brief and perhaps unprecedented period of time, something that studies on captive birds suggest can occur under strong selection (Berthold et al. 1990, Berthold 1996).

Wings of migrant species often are characterized by long distal primaries and short proximal primaries, resulting in relatively long and thin wings (compared with nonmigratory species; Rayner 1988, Winkler and Leisler 1992, Alerstam 1993, Lockwood et al. 1998), and a wing tip close to the leading edge. A pointed tip may reduce drag associated with the wing tip vortex (Lockwood et al. 1998). Even within species, comparisons between sedentary and migratory individuals or populations show that the migratory representatives indeed have wing features more characteristic of migration (Senar et al. 1994, Copete et al. 1999, Perez-Tris and Telleria 2001).

Wilson (1975) pointed out that behavior is the part of the phenotype that is most likely to change in response to long-term environmental change, such that behavior will usually be altered first and physical structure second. Thus, given that selection has apparently favored migratory behavior in eastern House Finches since their introduction, we investigated whether corresponding changes in wing morphology have arisen as well.

METHODS

We captured a sample of western House Finches ($n = 60$) with mist nets and baited traps at several suburban locations in Boise, Idaho (43°34'N, 116°13'W) from May to November 2002 (most were captured September–November 2002). Eastern House Finches ($n = 92$) were trapped at several locations near Ithaca, New York (42°27'N, 6°29'W) in mist nets and baited traps in October–November 2002. All captured finches received U.S. Geological Survey aluminum leg bands for individual identification. At the time of capture, sex and age were determined where possible. However, because we could not age many birds, we pooled individuals of all ages for analyses. Birds showing signs of wing molt (primaries or secondaries) were excluded from our study. JRE measured the wings of all captured House Finches with a ruler and digital calipers to determine wing length (to nearest 0.25 mm) and the differences between the tip of the longest primary and the tips of each of the other eight primaries (to nearest 0.01 mm). This was done with the wing in a consistent, folded position such that the primaries were partially stacked on top of each other as in Senar et al. (1994). We refer to these measurements for the nine primaries as primary distances. We then calculated the length of each primary (P1 through P9, where P1 is the most proximal primary) by subtracting each primary distance from the maximum wing length according to the formula $P_i \text{ length} = (\text{wing length}) - (\text{primary distance of } P_i)$ (see Evered 1990). As Senar et al. (1994) suggest, we then corrected these primary lengths for body

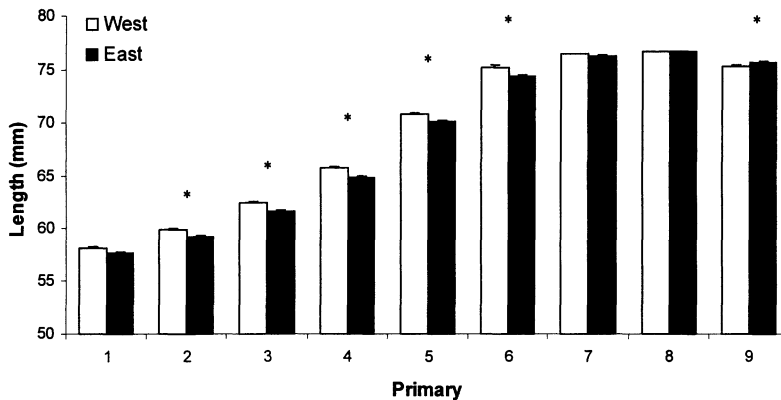


FIGURE 1. Standardized primary lengths of House Finches in two populations in the eastern and western United States (Ithaca, New York, $n = 92$ birds, and Boise, Idaho, $n = 60$ birds). Asterisks above bars indicate primaries for which the two samples differed significantly using one-way ANOVA and sequential Bonferroni corrections following a significant MANOVA.

size by taking into account allometric relationships using the SIZESTD program (Leonart et al. 2000), which produced a standardized length for each primary. Briefly, this program transformed feather length as follows:

$$P'_{ji} = P_{ji}(l_0/l_i)^{b_j}$$

where P_{ji} is the original measurement of the primary j in individual i , l_i is the wing length (an indication of body size) of individual i , l_0 is a standard wing length (taken as 76.81 mm, the mean wing length of the House Finches in our study) to which all individuals are reduced (or increased), and b_j is the allometry coefficient of primary j according to the growth model of Senar et al. (1994). These corrected measurements formed the basis of a multivariate analysis of wing-shape variation using principal components analysis (PCA), which was shown to be an accurate analysis of wing shape by Chandler and Mulvihill (1988).

STATISTICAL ANALYSIS

Wing length in eastern and western House Finches was compared using ANOVA. We compared transformed primary lengths (P1' through P9') between sexes and populations using two-way multivariate analysis of variance (MANOVA) followed by inspection of univariate tests to determine which transformed primary lengths contributed to overall range differences. Because sex did not affect P1' through P9', and sex did not interact with range in either multivariate or univariate analyses, we pooled sexes for all subsequent analyses and used all 152 captured individuals. To help control for inflated Type I errors following the initial MANOVA, follow-up univariate ANOVAs were evaluated using sequential Bonferroni corrections (Rice 1989), in which alpha was $0.05/9 (= 0.0055)$ for the first comparison and sequentially adjusted. We conducted PCA on the standardized primary lengths and compared PC scores between House Finches in the eastern and western populations using ANOVA with sequential Bonferroni corrections. Analyses were con-

ducted using SAS (Version 8.2, SAS Institute Inc. 2000), and all results are reported as means \pm SE.

RESULTS

Despite the prediction relative to migratory habit, there was no difference in mean wing length between the eastern (76.7 ± 0.2 mm) and western (76.9 ± 0.3 mm) House Finches in our sample ($F_{1,150} = 0.2$, $P = 0.68$). However, there was a significant difference in standardized primary lengths between populations (MANOVA: Wilks' lambda = 0.79, $F_{9,142} = 4.1$, $P < 0.001$). Follow-up univariate ANOVAs revealed that mean P2' through P6' were greater in western House Finches, whereas average P9' was greater in eastern House Finches (Fig. 1).

The first three principal components (PCs) explained 73% of the variation in transformed primary lengths (Table 1). The first axis, PC1, represented increasing proximal primary (P2'–P6') lengths. PC2 represented increasing distal primary length (P8' and P9'), and P6' loaded most highly on PC3 (Table 1). Eastern and western House Finches differed significantly along PC1 ($F_{1,150} = 25.9$, $P < 0.001$). Eastern House Finches (PC1 = -0.64 ± 0.20) had shorter proximal primary lengths than western House Finches (PC1 = 0.98 ± 0.25), and this contributed to wings of eastern House Finches being thinner and somewhat more pointed (Fig. 2, 3). Eastern and western House Finches did not differ along PC2 (0.08 ± 0.12 and -0.12 ± 0.14 , respectively; $F_{1,150} = 1.1$, $P = 0.29$) or along PC3 (-0.10 ± 0.10 and 0.16 ± 0.12 , respectively; $F_{1,150} = 2.6$, $P = 0.11$).

DISCUSSION

Results of our study indicate that the wings of the more migratory eastern House Finches tended to be more pointed than those of western House Finches. The shorter proximal primaries of eastern House Finches perhaps reflected a thinner wing proximally. In accordance with another prediction of morphology based on migration, the transformed length of P9 also was

TABLE 1. Results of a principal components (PC) analysis on standardized primary lengths (P1' through P9') of House Finches from eastern and western North American populations ($n = 152$). P1' represents standardized length of the most proximal primary.

Variable	Factor loadings		
	PC1	PC2	PC3
P1'	0.353	0.058	-0.383
P2'	0.430	0.116	-0.216
P3'	0.451	0.140	-0.088
P4'	0.436	0.093	0.118
P5'	0.398	0.100	0.278
P6'	0.186	-0.165	0.666
P7'	0.292	-0.253	-0.121
P8'	-0.051	0.707	0.397
P9'	-0.124	0.595	-0.303
Eigenvalue	4.29	1.27	1.01
% Variance explained	48	14	11
Cumulative variance explained (%)	48	62	73

significantly longer in eastern House Finches, which may represent the wing point being closer to the leading edge.

While we observed wing-shape differences consistent with each population's migratory habit, the predicted increase in the overall wing length of the more migratory (eastern) population was not observed. It is possible that this is related to the short amount of time that selection has had to operate on wing morphology. Longitudinal studies of wing morphology in House Finches could help document these changes over time. Alternatively, decreased wing lengths in at least one population of eastern House Finches have been documented after the recent mycoplasmal conjunctivitis outbreak (Nolan et al. 1998), so differences in wing lengths may have been more apparent before the outbreak. Finally, we were uncertain if the eastern House Finches we sampled were actually migratory or sedentary, as House Finches in the East are partial migrants (Belthoff and Gauthreaux 1991, Able and Belthoff 1998). A future study in which the migration distance of individuals is known might uncover a significant difference in wing length between the two populations. Nevertheless, the patterns of wing-shape

differences between regions (east and west) that we observed despite the lack of differences in overall wing length indicate potential changes in wing morphology consistent with a more migratory habit in eastern House Finches.

An alternative hypothesis for the pattern of wing-shape differences we observed between eastern and western House Finches is that the measured morphological features of eastern House Finches also may be characteristic of the southern California source population from which the eastern population presumably arose. That is, southern California House Finches could have shorter proximal primaries and longer distal primaries than the sample of western House Finches we measured from Idaho for the current study, and these differences carried over via their introduction to the East.

In conclusion, we interpret the differences that were detected in wing shape between eastern and western House Finches as initial evidence for morphological divergence as a result of migratory habit. However, our study was limited to single populations in the East and the West. Confirmatory tests should include measurements of wing morphology in populations throughout both the sedentary and migratory ranges of House Finches. For instance, Able and Belthoff (1998) showed that populations colonized most recently, and farther from the origin of the eastern population, had the greatest propensity to migrate. Considering this gradient in the expression of migratory behavior, we hypothesize that wing morphology will vary accordingly within the eastern population of House Finches.

We thank the Cornell Laboratory of Ornithology's House Finch Project personnel, C. Moulton, and J. Soules for assistance in the field. We especially thank A. Dhondt for his assistance, hospitality, and many stimulating and interesting discussions. We also thank J. C. Senar and J. Leonart for providing the SIZESTD program for use in this study, and J. C. Senar and two anonymous referees for helpful comments on our manuscript. Finally we thank Sigma Xi, The Scientific Research Society, and Boise State University for provid-

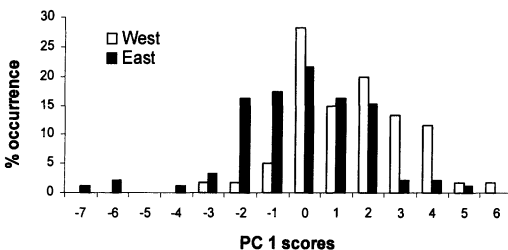


FIGURE 2. Frequency distribution (% occurrence) of eastern-U.S. ($n = 92$) and western-U.S. ($n = 60$) House Finches along the first axis generated by a principal components analysis of standardized primary lengths (Table 1). Increasing PC1 score corresponds to increasing lengths of proximal primaries.

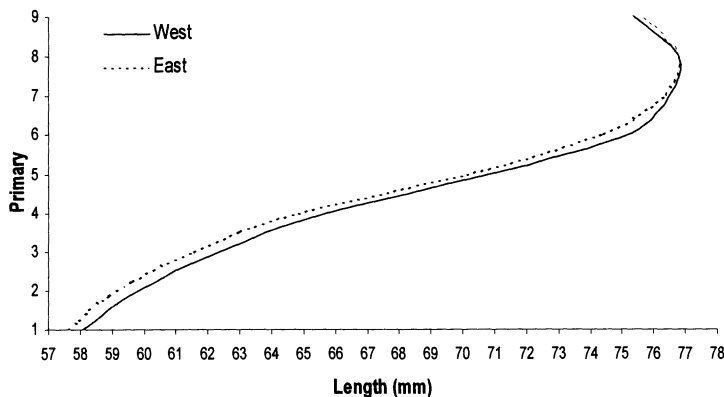


FIGURE 3. Graphical representation of distal wing segments produced using mean standardized primary lengths to visualize differences in wing morphology between eastern and western House Finches (note that these are not wing tracings). Wings are less rounded proximally (thinner) and more pointed distally in eastern House Finches, which appears to correlate with their more migratory habit.

ing financial or logistical support. This research was completed in partial fulfillment of requirements for undergraduate research credit at Boise State University for JRE.

LITERATURE CITED

- ABLE, K. P., AND J. R. BELTHOFF. 1998. Rapid 'evolution' of migratory behaviour in the introduced House Finch of eastern North America. *Proceedings of the Royal Society of London Series B* 265:2063–2071.
- ALERSTAM, T. 1993. *Bird migration*. Cambridge University Press, Cambridge, UK.
- BELTHOFF, J. R., AND S. A. GAUTHREAUX JR. 1991. Partial migration and differential winter distribution of House Finches in eastern United States. *Condor* 93:374–382.
- BERTHOLD, P. 1996. *Control of bird migration*. Chapman & Hall, London.
- BERTHOLD, P., G. MOHR, AND U. QUERNER. 1990. Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilziehverhaltens: Ergebnisse eines Zweiweg-Selections experiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). *Journal für Ornithologie* 131:33–45.
- CHANDLER, C. R., AND R. S. MULVIHILL. 1988. The use of wing shape indices: an evaluation. *Ornis Scandinavica* 19:212–216.
- COPETE, J. C., R. MARINE, D. BIGAS, AND A. MARTINEZ-VILALTA. 1999. Differences in wing shape between sedentary and migratory Reed Buntings *Emberiza schoeniclus*. *Bird Study* 46:100–103.
- ELLIOT, J. J., AND R. S. ARBIB JR. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31–37.
- EVERED, D. S. 1990. Measures of wing area and wing span from wing formula data. *Auk* 107:784–787.
- HILL, G. E. 1993. House Finch (*Carpodacus mexicanus*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 46. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- LLEONART, J., J. SALAT, AND G. J. TORRES. 2000. Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology* 205:85–93.
- LOCKWOOD, R., J. P. SWADDLE, AND M. V. RAYNER. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29:273–292.
- MUNDINGER, P. M. 1975. Song dialects and colonization of the House Finch *Carpodacus mexicanus* on the East Coast. *Condor* 77:407–422.
- NOLAN, R. M., G. E. HILL, AND A. M. STOEHR. 1998. Sex, size, and plumage redness predict House Finch survival in an epidemic. *Proceedings of the Royal Society of London Series B* 265:961–965.
- PEREZ-TRIS, J., AND J. L. TELLERIA. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* 32:207–213.
- RAYNER, J. M. V. 1988. Form and function in avian flight. *Current Ornithology* 5:1–66.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SAS INSTITUTE INC. 2000. *SAS/STAT user's guide*. Version 8. SAS Institute Inc., Cary, NC.
- SENAR, J. C., J. LLEONART, AND N. B. METCALFE. 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *Journal of Avian Biology* 25:50–54.
- VEIT, R. R., AND M. S. LEWIS. 1996. Dispersal, population growth, and the Allee effect: dynamics of the House Finch invasion of eastern North America. *American Naturalist* 148:255–274.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, MA.
- WINKLER, H., AND B. LEISLER. 1992. On the ecomorphology of migrants. *Ibis* 134:21–28.