
Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America

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The house finch (*Carpodacus mexicanus*) of eastern North America was introduced onto Long Island, New York, around 1940. The source is presumed to be southern California, where *ca.* 80% of individuals are completely sedentary. The eastern population has become migratory: by the early 1960s, 36% of eastern house finches were performing migratory movements (more than 80 km from their banding site) and that proportion has fluctuated between 28 and 54% in succeeding years. The movements of birds banded during the breeding season and recovered in winter were strongly orientated towards the south-west, and the same pattern was evident in the earliest recoveries (1958–1966); recoveries of birds banded during winter and recovered in the breeding season were orientated toward the north-east. The average distance of migration has continued to increase logarithmically. Areas colonized later, as the range expanded, were characterized by initial long migration distances and high proportions of migrants, suggesting that these traits have evolved in the eastern population. Eastern house finches are partial migrants: not all individuals migrate, and birds that migrate some winters remain in breeding areas in others. Younger birds exhibit a stronger tendency to migrate. A very few western (including southern California) house finches moved long distances, but they did so in directions consistent with seasonal migration, indicating that the machinery subserving migratory behaviour pre-existed in the parent population.

Keywords: migration; evolution; birds; *Carpodacus mexicanus*

1. INTRODUCTION

The population of house finches (*Carpodacus mexicanus*) that now occupies nearly all of temperate eastern North America originated from the release of captive birds on Long Island, NY, around 1940 (Elliott & Arbib 1953). The source of the released birds is presumed to be the Los Angeles area of southern California (Mundinger 1975; Hill 1993). After a decade of local increases, the population grew explosively and expanded its range so that by 1993 the house finch was a common breeder throughout most of eastern North America (Hill 1993; Veit & Lewis 1996). Birds of the eastern population have now made contact with native western house finches in mid-continent (Sauer *et al.* 1997).

The native house finch populations of western North America have generally been reported to be sedentary (Thompson 1960; Hill 1993). In the introduced eastern population, latitudinal migration appeared fairly soon after the establishment of the population. During the winter of 1959–60, round-trip migration between the Long Island area and Philadelphia, PA, was documented in two banded birds (Cant & Geis 1961; Bull 1964). Migratory behaviour developed rapidly, at least in the northern populations, and by the mid-1980s house finches

were migrating to the Gulf Coast and northern Florida (Mundinger & Hope 1982; Hamilton 1992).

Studies using captive breeding and artificial selection in other songbirds have shown that the suite of traits accompanying migratory behaviour (e.g. fat deposition, orientated migratory restlessness) can be established in or eliminated from a population in as few as three to six generations (Berthold *et al.* 1990; Berthold 1996). The eastern house finch provides one of very few cases in which the establishment of a large-scale pattern of migratory behaviour has been documented under natural conditions. The appearance and increased frequency of this behaviour in the introduced eastern population provides a unique opportunity to study the behavioural, physiological and genetic changes that have accompanied the rapid 'evolution' of the migratory syndrome.

We have analysed banding data to examine several questions about the development of migratory behaviour in the eastern house finch: (i) Were the earliest long-distance movements orientated as one would expect of migration, or did they involve dispersal in many directions? (ii) Do the movements show the northward spring and southward autumn directions typical of migration in eastern North America? (iii) What has been the historical pattern of distance moved by migrant individuals? (iv) Are there differences in migratory behaviour associated with the age or sex of individuals? (v) Are

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individual birds obligate or facultative migrants?
(vi) Can any roots of migratory behaviour be found in the presumed southern California source population?

2. MATERIALS AND METHODS

(a) *General*

We obtained from the Bird Banding Laboratory (USGS, Biological Resources Division, Laurel, MD) encounter data on all house finches banded in the United States and Canada and recovered or recaptured up until August 1997. These records provide the band number, date and location where banding occurred, the age and sex of the bird at the time of banding (if determinable), and the date and location of recovery or recapture. From this information we computed the direction and great circle distance between the location of banding and later encounter location. Banding localities are recorded in 10-min blocks of latitude and longitude; thus a bird recaptured anywhere within the same block where banded will appear to have been sedentary. We assumed that any bird banded or encountered between 15 March and 15 October was on its breeding ground, and that records between 1 December and 1 March pertained to birds in the wintering area. It is possible, by these criteria, that some late-autumn and early-spring migrants might be misclassified as birds on the wintering area and that some early-autumn and late-spring migrants might be assumed to be at breeding localities. Such misclassifications should have no effect on the analysis of migration direction, but could produce an underestimation of migration distance.

Because it is impossible to know whether a bird captured in early or even mid-winter has moved as far as it will go, banding data always tend to yield minimal estimates of migration distance. We have included in our analysis both direct recoveries (those in which only one migration season occurred between banding and recovery) and indirect recoveries (those with more than one migration season intervening between banding and recovery) because the number of direct recoveries is small. The patterns revealed by direct recoveries are very similar to those shown by indirect recoveries.

We have considered those areas colonized earliest to constitute the core eastern house finch population: New York and Pennsylvania east of 76°, Maine, Connecticut, Rhode Island, Massachusetts, New Jersey, Delaware and Maryland.

(b) *Natal dispersal*

Except in cases where band recoveries document a round-trip movement by an individual bird, it may be difficult to distinguish migratory movements from natal dispersal, the movement of individuals from their place of birth to the site of first breeding. To examine natal dispersal, we have used banding data from the core eastern population, and analysed the direction and distance between banding and recovery sites for house finches banded as nestlings, fledglings or hatching-year birds (HY) during the months May–August, and recovered in a subsequent breeding season (May–August).

(c) *Propensity to migrate*

It is not a straightforward matter to estimate the proportion of individuals that migrate versus those that are sedentary, by examining band recoveries. Bird banders do not routinely report, nor does the Bird Banding Laboratory store, records of birds retrapped alive at the banding site. Thus any analysis of all band encounters would greatly underestimate the sedentary

population. All banded birds recovered dead are required to be reported, regardless of the location of recovery, so this subset of the encounter data should not be biased against residents. We used the codes indicating how the banded bird was obtained to identify birds recovered dead, and used these data to examine the proportion of individuals that migrated. Operationally, we defined a migrant as an individual recovered more than 80 km from the banding site. The analysis of natal dispersal indicates that this arbitrary definition is a reasonable one (see §3a). Because an individual recovered at the banding site might have migrated and returned in the interim, data from indirect recoveries will tend to overestimate the proportion of the population that appears to be sedentary. Migrants and residents probably do not have equal probabilities of dying or of being recovered once dead. However, these biases should not vary across populations, therefore relative comparisons should be valid.

(d) *Directionality of recoveries*

Directional data were analysed using standard methods of circular statistics (Batschelet 1981). The Rayleigh statistic was used to test the null hypothesis—the population of directions from which the sample was drawn is randomly distributed (i.e. the directions are not orientated). Lengths of mean vectors (\bar{r}) vary between zero (uniform distribution of directions) and one (all points in the same direction).

(e) *Pattern of migration in areas colonized later*

For states and regions beyond the core north-eastern range, we calculated the mean distance moved by birds banded during the breeding season and recovered during winter for the first two to four years in which recoveries were obtained (number of years varies because some years lack recoveries). The states, regions and recovery years were as follows: Pennsylvania west of 76° W, 1978–1980; West Virginia, 1980–1981; New York west of 76° W, 1980–1982; New Hampshire, 1981–1983; Ohio, 1982–1984; Michigan, 1985–1988; Illinois, 1988–1990; Indiana, 1988–1990; Iowa, 1990–1991.

3. RESULTS

(a) *Natal dispersal*

The banding data from the core eastern house finch population contain 95 recoveries of birds banded during their hatching summer and recovered in a subsequent breeding season. Of these, 30 (31.6%) were recovered within the 10-min block of latitude and longitude where they were banded. For those that moved beyond the 10-min block of banding, the median recovery distance was 22.5 km, 90% were below 80 km, and the longest recovery was 225 km. These recoveries were not directional: mean direction = 53°; $r = 0.215$, $p > 0.10$, $n = 65$.

(b) *Propensity to migrate*

Recoveries of banded birds from the core eastern house finch population do not begin until 1956 and are of negligible numbers until after 1960, two decades after the introduction. Therefore, we have no estimate of the proportion of birds that migrated during the earliest years of colonization. Of six recoveries of dead banded birds before 1960, four (66.7%) were recovered at the banding site, the remaining two moved 56 km and 98 km. Over the following years, the proportion of recoveries made more than 80 km from the banding site

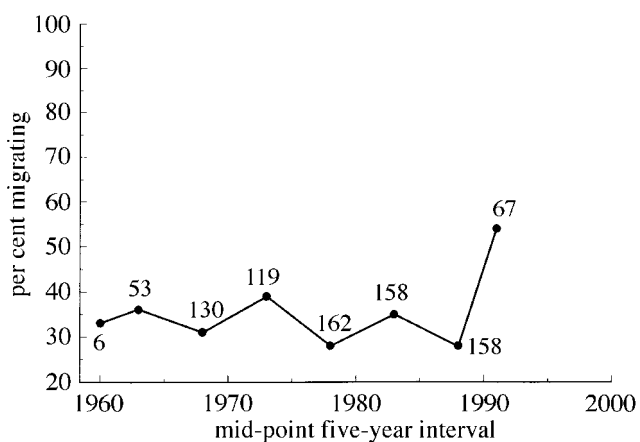


Figure 1. The percentage of birds from the core eastern population (New York and Pennsylvania east of 76°, Maine, Connecticut, Rhode Island, Massachusetts, New Jersey, Delaware and Maryland) that moved more than 80 km from where banded, and were recovered dead. Data were pooled over five-year intervals. Numbers beside points indicate the number of recoveries in each case.

has fluctuated between 28 and 54% (figure 1). At the present time (1994–1997), 46.0% of the eastern population is sedentary by this criterion (30% are recaptured within the same block where banded), compared with 98.8% in southern California (78.6% within the same block where banded).

(c) Directionality of movements

Using the band recovery data from the core eastern house finch population, we examined the directionality of all recoveries made more than 80 km from the site of banding. Birds banded during the breeding season and recovered in winter showed movements strongly orientated towards the south-west (mean direction = 225°; $r = 0.874$, $p < 0.0001$, $n = 266$) (figure 2a). Conversely, recoveries of birds banded during the winter and encountered during the breeding season were highly orientated toward the north-east, almost exactly opposite the autumn migration direction (mean direction = 48°; $r = 0.860$, $p < 0.0001$, $n = 363$) (figure 2b).

(d) Pattern of migration distance

Using the same data, we analysed the distances between banding and recovery points as a function of the year in which the recovery was made. Recovery distance of birds banded during the summer and encountered more than 80 km from the banding site in winter increased logarithmically over the years (figure 3). The linear regression describing this relationship is: $\log(\text{distance (in km)}) = 1.56 + 0.01(\text{year recovered} - 1900)$; $F_{1,264} = 37.9$, $p < 0.001$; $R^2 = 0.13$. This pattern holds both for first-year birds as well as for adults. Not only did migration distance increase over the years after introduction, but also the variance in distance moved increased. Throughout the 30 years of records there continue to be birds that move relatively short distances (80–100 km), whereas the proportion of birds moving long distances and the maximum distances moved have increased dramatically. The pattern of distances moved by birds banded in winter and recovered during the

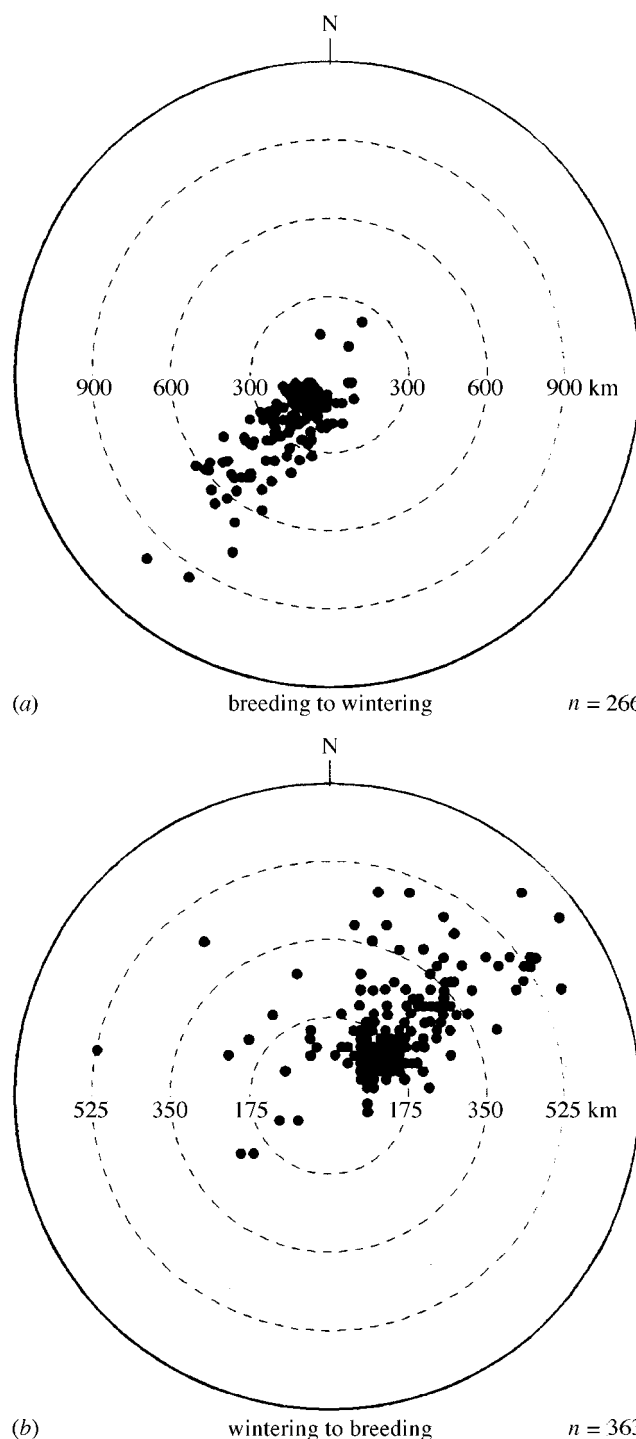


Figure 2. Directions of all recoveries obtained more than 80 km from the site of banding of house finches from the core north-eastern population. (a) All recoveries of birds banded between 15 March and 15 October and recovered between 1 December and 1 March are included. (b) Recoveries plotted here are of birds banded between 1 December and 1 March and recovered between 15 March and 15 October.

breeding season is essentially identical (regression: $\log(\text{distance (in km)}) = 1.58 + 0.01(\text{year recovered} - 1900)$; $F_{1,361} = 67.8$, $p < 0.0001$; $R^2 = 0.16$).

(e) Directionality of the earliest long-distance movements

Figure 4a shows the direction and distance of birds banded during the breeding season in the core north-

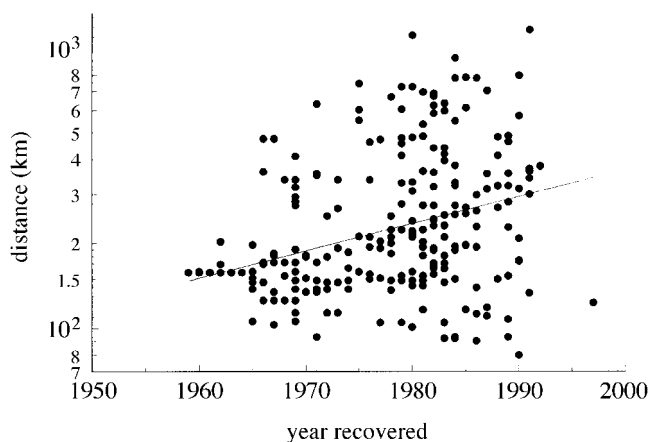


Figure 3. Distance between banding and recovery sites for all north-eastern house finches recovered more than 80 km from the site of banding. Plotted by year of recovery, the data represent birds banded between 15 March and 15 October and recovered between 1 December and 1 March. Note that distance is a log scale.

eastern range and recovered more than 80 km away during the winter before 1967. The movements show strong directionality (mean direction = 235° ; $r=0.993$, $p<0.0001$, $n=38$) towards the south-west, a distribution that does not differ from that of recoveries between breeding and wintering seasons after 1967 (Watson-Williams test). Similarly, recoveries between wintering and breeding seasons are orientated towards the north-east with a distribution that does not differ from that of similar recoveries after 1967 (mean direction = 54° ; $r=0.955$, $p<0.0001$, $n=90$) (figure 4b).

(f) *Pattern of migration in areas colonized later*

From the point of introduction on Long Island, the breeding range of the eastern house finch expanded westward, southward, and to a lesser extent northward (Hill 1993, fig. 2). The dates of arrival in new areas were well-documented. We asked whether newly established breeding populations developed migration *de novo*, beginning with short-distance movements, or alternatively whether migration distance moved as a trait with the dispersers. If the latter were the case regions colonized more recently should have exhibited longer initial migration distances, as predicted by the regression of migration distance on year in the eastern core population (figure 3).

The number of recoveries contributing to each mean is unfortunately small, but the regression (figure 5) indicates that areas colonized later were characterized by longer initial migration distances (regression: $\log(\text{mean recovery distance (in km)}) = -0.87 + 0.04 (\text{year recovered} - 1900)$; $F_{1,7}=12.6$, $p<0.01$; $R^2=0.64$). Figure 5 also shows that the initial recovery distances in newly colonized areas were greater than those predicted by the regression of increasing migration distance over time within the core eastern population from which they came. A reasonable interpretation is that colonizers of new areas are not a random subset of the source population, but are biased toward longer-distance migrants, thus carrying that trait with them to the new locales.

Consistent with this interpretation are the data on the proportion of individuals that moved more than 80 km,

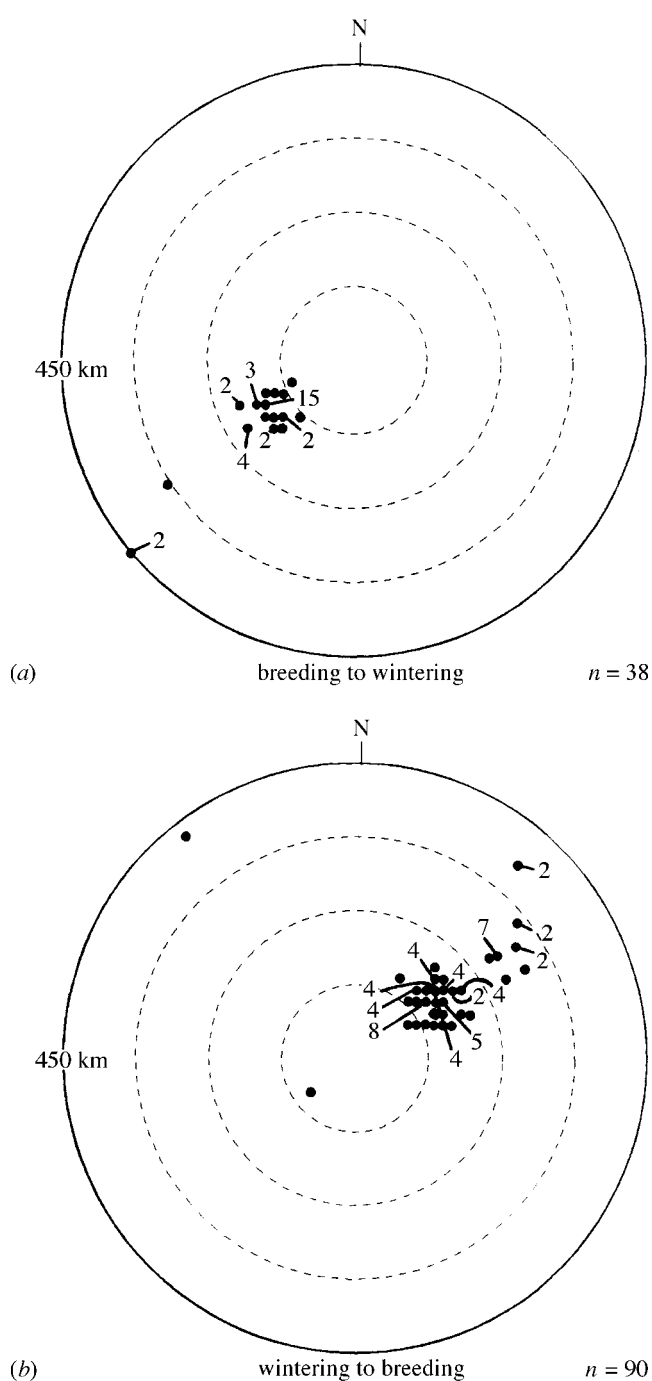


Figure 4. Directions of banding recoveries (made more than 80 km from the banding site) of north-eastern house finches obtained before 1967. (a) Recoveries of birds banded between 15 March and 15 October and recovered between 1 December and 1 March. (b) Recoveries of birds banded between 1 December and 1 March and recovered between 1 December and 1 March. Numerals associated with dots indicate overlapping data points.

based on recoveries of dead birds (table 1). The proportion of birds that migrated during the first years after colonization was significantly greater than that in the eastern core population during the same years (G -test with Yates correction, $p<0.01$, two-tailed). This indicates again that the colonists responsible for the range expansion in this population exhibited, on average, a greater propensity to migrate as well as to migrate longer

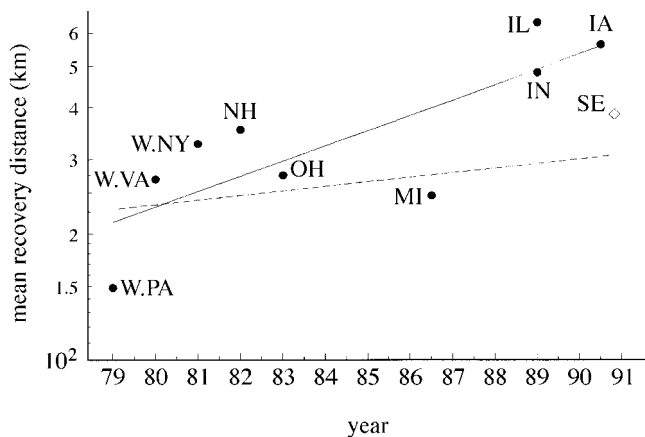


Figure 5. Regression of the mean distance (all recoveries obtained more than 80 km from then banding site) of the earliest band recoveries from more recently colonized states and regions at the middle year of those recoveries (1979–1990). The dashed line is the distance on year regression for the core eastern population (figure 3) for comparison. W. PA, Pennsylvania west of 76° W longitude; W. VA, West Virginia; W. NY, New York west of 76° W longitude; NH, New Hampshire; OH, Ohio; MI, Michigan; IL, Illinois; IN, Indiana; IA, Iowa. The open diamond denoted SE indicates the comparable value for the south-eastern states (Virginia, South Carolina, Georgia, Tennessee and Missouri combined). This value was not included in the regression. Note that mean recovery distance is a log scale.

Table 1. Comparison of the proportion of birds that migrated (moved more than 80 km from the banding site to the point of recovery) among dead birds recovered during the first two to four years after colonization of new areas with the proportion of migrants in the core eastern population during the same time period

state/region	years	n	% migratory	core eastern population % migratory
W. Pennsylvania	1978–1984	52	46.1	31.5
West Virginia	1978–1984	10	60.0	31.5
W. New York	1981–1985	29	44.8	35.0
Ohio	1981–1985	20	50.0	35.0
Michigan	1986–1993	37	46.0	41.0
Indiana	1988–1992	26	76.9	43.0
Illinois	1988–1993	9	66.7	43.0
south-eastern states	1988–1994	19	42.1	45.0

distances than the typical individual in the parent population.

Expansion of the breeding range of eastern house finches has only recently reached the south-eastern United States, so recoveries of birds banded in summer in these areas are few. However, because of the much milder winters at these lower latitudes, knowing the pattern of migration in this area is important in attempting to assess the role of environmental induction in the expression of migratory behaviour. Recoveries of birds banded during summer and recovered dead during winter are available from: Virginia (7); Tennessee (4); South Carolina (6); Georgia (1); Missouri (1). Of these 19 birds, 16 (84.2%) moved some distance between banding and recovery

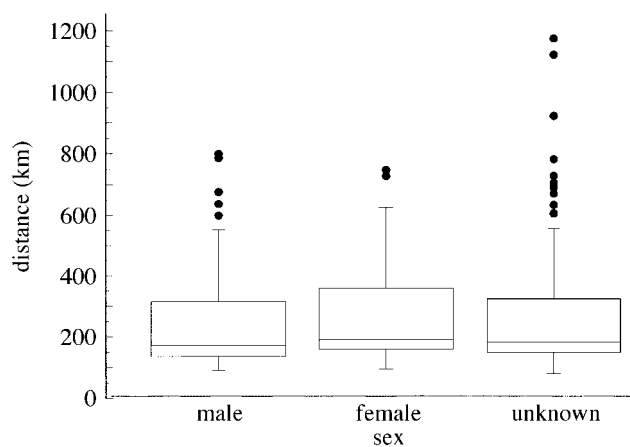


Figure 6. Distance of banding recoveries (more than 80 km from banding site) of eastern house finches by sex. All recoveries are of birds banded between 15 March and 15 October and recovered between 1 December and 1 March. Horizontal lines in the boxes denote the 25th, 50th and 75th percentiles of the data; vertical bars indicate 1.5 times the range between the first and third quartiles. $n=68$ males, 64 females, 134 unknown sex.

(table 1). The median distance moved was 53 km. The proportion of birds that were recovered more than 80 km from the banding site (42.1%) was not statistically different from the comparable proportion in the core eastern population at the same time (45.0%) (table 1). The mean recovery distance of these birds was 370 km ($n=8$), somewhat greater than predicted by the core eastern population.

(g) **Patterns of migration in relation to sex and age**

Based on recoveries of dead birds banded in the core eastern range, there was no sex-based difference in the propensity to migrate (G -test, $p=0.45$). Sedentary individuals (recovered within the 10-min block where banded) accounted for 51.9% of males, 50.0% of females, and 29.7% of birds of unknown sex. Of those birds that moved, 10.0% of males, 9.1% of females, and 24.3% of unknown-sex birds were recovered more than 80 km from the point of banding. Figure 6 shows that there is also no significant difference in the distances moved by males and females.

Again, based on recoveries of dead birds, young birds were more likely to move than older ones (G -test with Yates correction, $p<0.05$, two-tailed). Although a larger proportion of young birds than adults (33.3% versus 9.3%) was recovered more than 80 km from the banding site, there was no overall difference in the distances moved by birds recovered as adults and those recovered before their first breeding season (figure 7).

(h) **Patterns of movement in house finches from the western population**

The southern California population from which eastern house finch populations were reportedly derived is strongly, but not completely, sedentary. Of birds banded south of 35° N latitude in California (slightly north of Los Angeles), 81.5% of those recovered dead between 1922 and 1997 ($n=460$) were found within the 10-min block where they were banded; 97.9% were recovered within

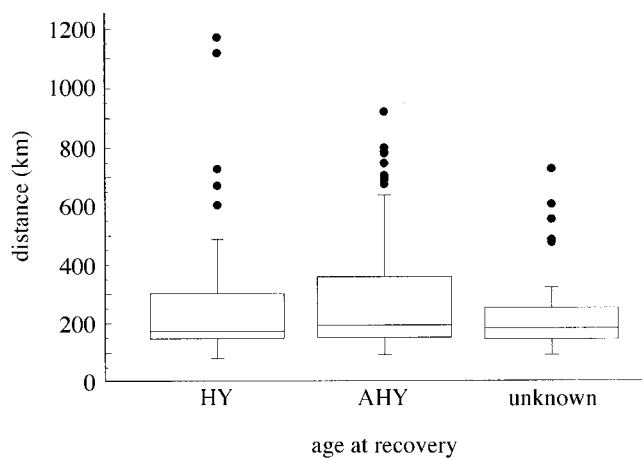


Figure 7. Distance of banding recoveries (more than 80 km from banding site) of the eastern population of house finches by age. HY, birds recovered prior to their first breeding season; AHY, birds recovered during or after their first breeding season, regardless of the age at which they were banded. $n = 135$ AHY, $n = 98$ HY, $n = 33$ unknown age. Other conventions as in figure 6.

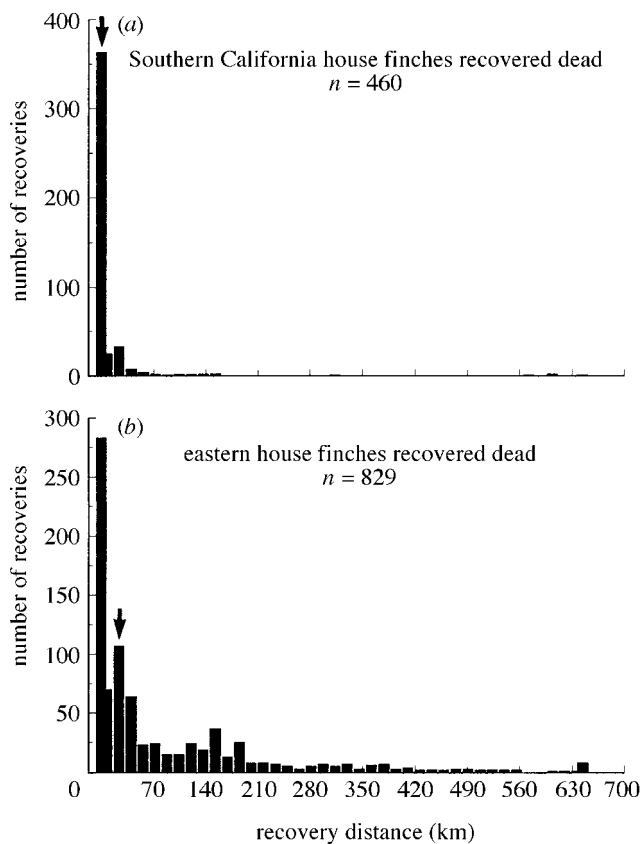


Figure 8. Frequency distribution of recovery distances for all band recoveries involving dead birds. (a) All recoveries of birds banded south of 35° N latitude in California; (b) all recoveries of birds banded in the eastern core range (see legend, figure 1). Arrows indicate the median distance.

80 km of the banding site. The median recovery distance for the population as a whole was 0 km (figure 8a). The proportion of apparently sedentary individuals remained relatively constant over the years and was 82.1% ($n = 145$) (98.0% less than 80 km from the banding site) during the

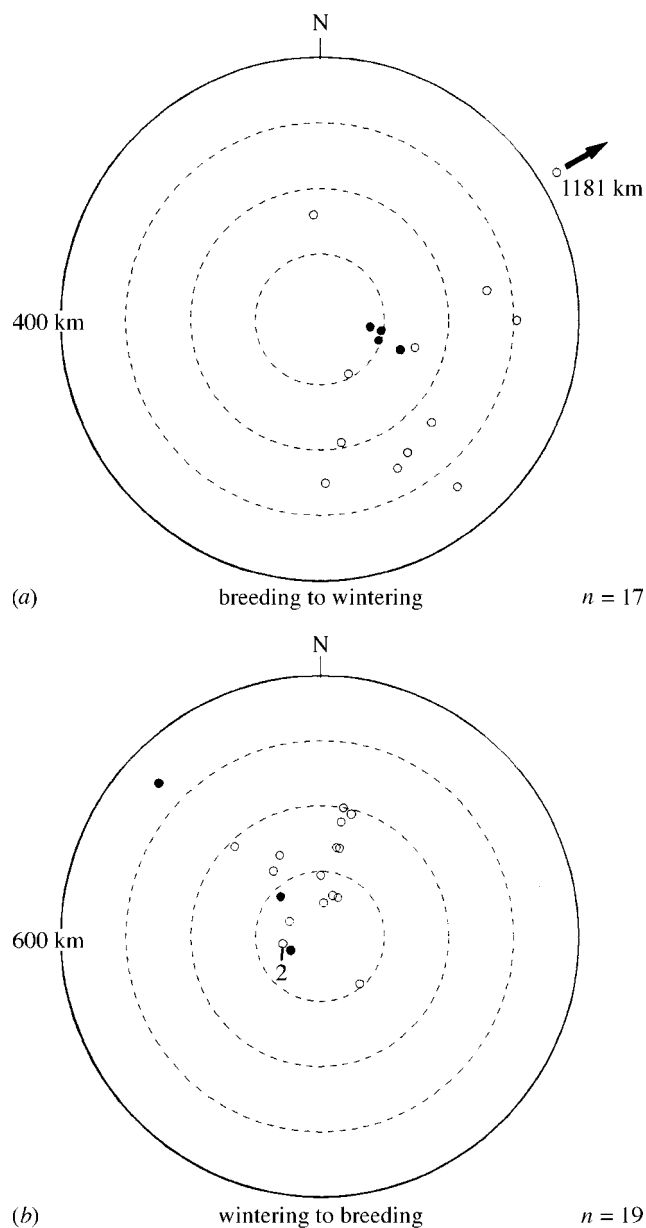


Figure 9. Directions of recoveries (made more than 80 km from banding site) of the western population of house finches. (a) Birds banded during the breeding season and recovered in winter; (b) birds banded in the winter and recovered during the breeding season. Solid circles indicate birds banded south of 35° N latitude in California, open circles denote birds banded elsewhere in California and in the other western states (see text).

period that included the years when the eastern population of birds were released (1936–1945). A very small number were recovered at distances more than 80 km from the site of banding (14 individuals, 3.1% of recoveries from 1922 to 1997) (figure 8a). The mean distance of all recoveries more than 80 km (birds recovered alive as well as dead) was 323 km (s.d. = 343 km) and the longest-distance recovery was 1303 km. A similar plot of recoveries from the core eastern population is significantly different (Kolmogorov–Smirnov test, $p < 0.0001$) (figure 8b). Only 31.4% of birds recovered dead were found within the 10-min block where banded, the median recovery distance for the population as a whole was 28 km, the mean distance of all recoveries more than

80 km was 245 km (s.d.=161 km), and the longest-distance recovery was 1173 km ($n=829$). Thus, although a much larger proportion of the southern California population is sedentary or disperses only a short distance, a few birds moved distances that were at least as great as those in the eastern population. No round-trip migrations are as yet documented by banded birds in western North America.

If we compare southern California recoveries of more than 80 km between breeding and wintering seasons with those between winter and breeding season (as was done for the eastern-population data), the directions of movement are different. Birds banded during the breeding season and recovered in winter moved toward 104° ($r=0.996$, $n=4$), whereas those banded in winter and recovered during the breeding season moved in an approximately opposite direction (mean direction= 296° ; $r=0.900$, $n=3$). The number of recoveries available is, however, too small for statistical analysis or to inspire confidence. If one looks at all of the available data for western North America (including the remainder of California, Oregon, Washington, Utah, Colorado, Arizona and British Columbia), the same pattern is obtained: recoveries between breeding and wintering seasons were orientated towards the south-east (mean direction= 117° ; $r=0.767$, $p<0.001$, $n=17$) (figure 9a), whereas those between wintering and breeding seasons were significantly orientated toward the north-west (mean direction= 338° ; $r=0.649$, $p<0.001$, $n=19$) (figure 9b).

One could argue that these movements, in more or less opposite directions, reflect a tendency towards seasonal migration in a very small number of individuals in these predominantly sedentary western populations. Some support for this can be found in the distribution of directions of short-distance movements (recoveries less than 80 km from banding site). These recoveries are not orientated (southern California only: mean direction= 225° ; $r=0.171$, n.s., $n=73$; all western populations: mean direction= 250° ; $r=0.102$, n.s., $n=182$). This suggests that short-distance dispersal occurs in essentially random directions, whereas the occasional long-distance movements tend to be orientated in directions consistent with seasonal migration in this region.

(i) *Patterns of individual migration in different years*

It is clear from the banding data that some individual house finches from the eastern population perform round-trip migrations of considerable distance. Do some individual birds migrate every year whereas others never migrate (obligate partial migration), or is the behaviour more facultative, with the decision to migrate dependent upon local conditions? Most instructive are the rare records of birds encountered more than once after banding. Banding records for the eastern core population contain 66 such cases, of which 17 provide some insight into migratory behaviour (see electronic Appendix A at <http://www.pubs.royalsoc.ac.uk/publish/probs/nov98pbl.htm>). In ten of these cases, the records document that the birds migrated in some winters and remained at their summer locality in others. Two additional encounters probably fall within this category, but recaptures in the breeding area in November leave open the possibility of migration later

in the season. The records are too few to reveal much in the way of patterns of migration with respect to age. Six of the birds were banded during or after their first breeding season (AHY) and four were of unknown age. However, in all cases, the birds migrated when younger and remained at their summer locality at an older age. Five records documented migration in more than one winter: four of these involved returning to the same overwintering site and one bird overwintered at sites only 19 km apart. One case involved a bird banded in New York in summer which was recaptured at the same Pennsylvania location during three successive winters. In addition, there are many cases of birds banded in midwinter in one locality and recovered in a subsequent midwinter at a distant location. By their nature, these data are qualitative and to some extent, anecdotal. However, they demonstrate unequivocally that some individual house finches from the eastern population migrate in some years and remain in the breeding area in others. Perhaps a smaller proportion of individuals migrates annually, and some of these exhibit winter site fidelity.

4. DISCUSSION

Migration apparently appeared in the eastern population of the house finch shortly after the birds were released on Long Island, NY, around 1940. From the earliest band recoveries, movements between winter and breeding seasons by the eastern population of house finches showed the pattern of directionality typical of the flow of songbird migration in the north-eastern United States, and are consistent with the conclusion that the movements reflect seasonal round-trip migration. Since the early 1960s, the migrating fraction within the core eastern area has fluctuated between 28 and 54%, with no overall trend of increase or decrease. The comparable figure for the southern California population is 2–3%, indicating that the propensity to migrate increased markedly in the eastern population within 20 years of its initial introduction, after which it has remained relatively stable. The average distance moved by birds that were recovered more than 80 km from where they were banded has, however, continued to increase logarithmically to the present time.

The banding data show that the eastern population of the house finch is a partial migrant (Belthoff & Gauthreaux 1991a): in any given year, some individuals migrate to distant wintering areas, whereas others remain at or near the breeding locality. The banding recoveries also show that the same individuals migrate in some years and overwinter in breeding areas in others. The data are not sufficient, however, to conclude whether or not house finches from the eastern population are facultative partial migrants (*sensu* Terrill & Able 1992). The trend revealed by the data is for birds to migrate when younger and to be sedentary when older. Young birds are also more likely to move long distances. Some adults move very long distances, however, so overall there is no difference in migration distance between young and older birds. This behaviour could reflect facultative migratory behaviour induced by external factors in the bird's physical and social environments (Kalela 1954; Ketterson & Nolan 1976, 1979, 1983; Gauthreaux 1978; Myers 1981). However,

because of the age-related trend among the small number of relevant recoveries, the changes in behaviour from year to year might also reflect a genetically based ontogenetic program (Schwabl & Silverin 1990; Berthold 1996). Of course, these two alternatives for the control of partial migration are not mutually exclusive. In most cases, it is likely that the expression of migratory behaviour results from an interaction of an individual's genetic makeup with its physical and social environment (Lundberg 1987; Terrill 1991; Holberton 1993; Berthold 1996; Pulido *et al.* 1996).

One might also expect year-to-year variation in the number of birds migrating and the distance migrated as a function of the severity of winter weather in the breeding area. Unfortunately, the banding data are not sufficiently detailed to reveal patterns at that scale. In recent years, at least, there has existed a statistically significant latitudinal gradient in the winter distribution of the sexes, with females on average spending the winter farther south than males (Belthoff & Gauthreaux 1991a). Because females tend to be dominant to males in this species (Thompson 1960; Brown & Brown 1988; Belthoff & Gauthreaux 1991b), the pattern of winter distribution is not consistent with the behavioural dominance hypothesis (Gauthreaux 1978). Only the body-size hypothesis (Ketterson & Nolan 1976), which predicts that the smaller females would overwinter farther south because of reduced tolerance for cold temperatures, explained the observed pattern. Again, whether this difference in behaviour represents a facultative response to some aspect of the environment or whether it represents a sex-linked heritable difference between males and females (Berthold 1986; Holberton 1993) remains to be determined by studies under controlled conditions.

Interpreting the development of migratory behaviour in the eastern house finch is fraught with difficulty. At one extreme, it could represent rapid evolution under the very different selective regime experienced by southern California birds suddenly faced with the problem of coping with north-eastern winters. At the other, it might have resulted from a direct environmental induction of behaviour for which the genetic and physiological basis already existed, but which was rarely if ever triggered in the source population. Banding data can provide only correlative evidence with regard to the possible roles of genetic and environmental factors. At present, nothing is known about the physiological aspects of house finch migration, e.g. changes in hormone levels, migratory fattening, migratory restlessness, etc.

Captive breeding studies have shown that important aspects of migratory behaviour and physiology can evolve very rapidly (Berthold & Querner 1982; for a review, see Berthold (1996)). Strong artificial selection applied to a partly migratory population of the blackcap (*Sylvia atricapilla*) produced exclusively migrant individuals in three generations and a completely non-migratory line in six generations. Berthold (1996) and Pulido *et al.* (1996) have argued that all bird populations are partly migratory; species that appear to be completely migratory or sedentary contain both residents and migrants, respectively, but at essentially undetectable frequencies. The data from house finches are consistent with this notion. The orientated long-distance movements

of a few western-population house finches suggests that the genetic basis for migration persists at a low level even in apparently sedentary populations, and this could provide the raw material upon which selection in a new environment might operate.

The banding data provide two lines of evidence that are consistent with evolution being at least partly responsible for the increase in migratoriness in the eastern population of house finch. Two components of migratory behaviour, propensity to migrate and migration distance, have changed during the approximately 57 generations since introduction. As the population expanded and new areas were colonized, migration distance as a trait appears to have moved with the dispersing individuals. In fact, the initial migration distances in newly colonized areas were consistently greater than those predicted by the average of the eastern population at the same time. This is to be expected because longer-distance migrants may be more likely to colonize new areas and the existence of migratory behaviour in the eastern population may be partly responsible for the rapidity with which the house finch range has expanded. If migration distance was entirely or largely a function of local environmental conditions (a facultative response), we would expect different distances to be associated with different regions. More southern areas, in particular, should be characterized by shorter migration distances in response to their milder climates and less severe winters. Yet, breeders in this area show the same pattern exhibited by other recently colonized regions: initial migration distances comparable to those of more northern areas and longer than the average of the eastern core population at the same time.

The proportion of individuals migrating also appears to exist as an intrinsic trait that moves with individual dispersants. Newly colonized areas had an initially high proportion of migrants, in all cases except the south-eastern states, greater than the corresponding value for the eastern core population at the same time. Although the number of band recoveries is small, breeders in the southern states showed a propensity to migrate that was similar to that of populations in the north-eastern states. Were the migration entirely or largely facultative, we would expect a higher degree of residency in these southern populations. As breeding populations become established at lower latitudes, we would predict that the proportion of migrants and migration distance will decrease over time.

We can only speculate on why the average migration distance has continued to increase. Examination of data from the Bird Banding Laboratory indicates that it cannot be accounted for by increased capture effort in the south-eastern United States. The trend runs counter to that expected in the face of general climatic warming. It may be the case that migration distance evolves in small increments and that the trait has not reached equilibrium in the eastern population. This is not unlikely, because the population has changed markedly in both numbers and range. The expansion of the breeding population southward may have provided a selection pressure favouring migrants that 'leap-frogged' over those birds and continued to unoccupied lower latitudes.

Berthold (1996) notes a trend in which populations, especially of partial migrants, have become increasingly

sedentary over the past one hundred years. This trend is correlated with general climatic warming and is predicted to increase. In contrast, cases in which migration has appeared in a previously sedentary population seem to be extremely rare: the serin (*Serinus serinus*), which has undergone an extensive northward range expansion in Europe over the last century (Olsson 1969; Berthold 1996), and the eastern-population of house finch are the only documented examples of which we are aware. Providing an example of the appearance and establishment of large-scale migration in a bird population within our lifetime, the eastern-population house finch provides a unique model in which to study the physiological and genetic changes that accompany the development of migratoriness in a population. It may well be that the southern California origin of the introduced eastern population of house finches was an important precondition for the evolution of migration. In the native range of house finches in western North America, birds living at latitudes comparable to those of the eastern population do not migrate (Belthoff & Gauthreaux 1991a; Hill 1993). These birds possess the physiological means to survive harsh winters without migrating. Had the birds introduced into New York come from one of these winter-adapted populations, there may have been no selection pressure favouring migration.

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