Oecologia (Berlin) (1987) 71:325–331

Oecologia

Interspecific competition between introduced house finch populations and two associated passerine species

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Summary. House Finches (*Carpodacus mexicanus*), natives of western North America, have expanded their range in the eastern United States since their 1940 release in New York City. Range and the relation of House Finch population growth to the population dynamics of House Sparrows (*Passer domesticus*) and Purple Finches (*Carpodacus purpureus*) were examined, using data from the Breeding Bird Survey and the Christmas Bird Count. The House Finch population grew exponentially throughout its eastern range. Significant negative relationships in population density, relative to spatial and temporal control populations, were found between House Finches and House Sparrows in summer and winter, and between House Finches and Purple Finches in summer. Purple Finch and House Sparrow populations outside of the House Finch range appeared to have no effect on each other throughout the study. Neither changes in 74 weather variables, nor changes in forest, field or developed habitat explained the observed trends in population density. The results indicate that House Finches compete with these two species, but winter migration complicates the picture.

Key words: Interspecific competition – Introduced finches – Carpodacus – Passer

A number of workers (e.g. Conner and Simberloff 1979; Connell 1980) have recently questioned whether interspecific competition is an important force shaping community structure, both in species composition and in patterns of resource use, partially because of the weak methods used to test competition in the field. Experimental work, usually involving population manipulation, has been employed in the last two decades to more rigorously determine the importance of competition (e.g. Connell 1961; reviewed by Connell 1983; Schoener 1983). Experimental methods generally require study organisms that possess high reproductive rates and limited mobility. These conditions usually cannot be met in avian studies, although a few experimental studies under limited conditions have been successful (Davis 1973; Garcia 1983). An alternative is to investigate population interactions during a species introduction, although rigorous controls are often absent and replicates of the treatment are usually not available (Dunham 1980; Moulton and Pimm 1983). Such systems also allow the investigation of species interactions on a scale much larger than is possible experimentally (470,000 km^2 in this study).

This study examines the House Finch (*Carpodacus mexicanus*) introduction in the eastern United States. Cage bird dealers, to avoid prosecution under the International Migratory Bird Treaty Act, released House Finches in New York City in 1940 (Elliot and Arbib 1953; Aldrich and Weske 1978). Since its establishment, the eastern population has grown rapidly in range and size (Bock and Lepthien 1976; Bystrak and Robbins 1978; Mundinger and Hope 1982). Several authors suggest that House Finches may compete with the exotic House Sparrow (*Passer domesticus*) and the closely related Purple Finch (*Carpodacus purpureus*) because of similarities in diet and habitat use in the eastern United States (Elliot and Arbib 1953; Cant 1962; Katholi 1967; Kalanoski 1975). Kricher (1983) found a negative relationship between House Finch numbers and House Sparrow numbers in five northeastern states using Christmas Bird Count (CBC) data, but also found a decreasing trend in House Sparrow numbers in four southeastern states outside of the House Finch range.

House Finches forage primarily on the ground, and their California diet consists of 86.2% seeds, 10.5% fruit, 2.4% animal matter and 0.9% miscellaneous (Beal 1907, cit. in Bent 1968). The diet of the ground-foraging House Sparrow consists of 96.6% vegetable matter, and is composed primarily of seeds (Martin et al. 1951; Bent 1958). Purple Finches, congeners of House Finches, also feed on seeds, buds and fruit, but are less dependent on seeds than House Finches (Martin et al. 1951). Both House Finches and Purple Finches feed their young seeds rather than insects (Beal 1907, cit. in Bent 1968).

House Finches inhabit brush margins, open woodlands, desert, scrub, open areas with scattered trees and shrubs, and areas of human habitation in their native western North America (Salt 1952). In eastern North America, they live in areas of human activity, nesting around buildings, particularly in ivy on walls, under eaves, and, in more rural areas, in conifers (personal observation; Bent 1968; Bull 1974; Kalanoski 1975; Kricher 1983). House Sparrows also occur in areas of human habitation, and nest around buildings, but nest in bird boxes and cavities rather than conifers in rural areas (personal observation; Bent 1958; Kalanoski 1975; Kricher 1983). Purple Finches inhabited coniferous

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forests and areas of human activity in eastern North America prior to the House Finch introduction, but inhabited only coniferous forests in western North America where the native House Finch population was present, suggesting competition induced habitat partitioning (Salt 1952).

This study examines evidence for interspecific competition between House Finches and both House Sparrows and Purple Finches by considering the population dynamics of House Sparrows and Purple Finches over time in response to the House Finch introduction. By assuming that the House Finch population increase is a result of its exposure to a previously unexploited area, rather than the result of some extrinsic factor (e.g. climate and other factors are not causing the increase), this system can be considered analagous to a population manipulation, with both temporal (before vs. after House Finches) and spatial (inside vs. outside House Finch range) control populations. House Finches have subsequently invaded the control areas used for this analysis, hence, unlike "natural experiments" which compare areas with and without a particular species in a static situation, this system does not automatically have a confounding difference (the factor preventing a potential competitor from inhabiting the control area) between areas with and without House Finches. If interspecific competition occurs between House Finches and the other species, then with the increased House Finch abundance in the eastern United States, growth rates of competing populations should be depressed relative to those before House Finch arrival and those of populations outside of the House Finch range.

Methods

Data bases

Analyses were performed on two avian data bases consisting primarily of data collected by volunteer observers: the Breeding Bird Survey (BBS), directed by the United States Fish and Wildlife Service (USFWS), and the Christmas Bird Count (CBC), sponsored by the National Audubon Society. In the BBS (reviewed by Robbins and VanVelzen 1967; 1969), observers travel by car over assigned routes, spread evenly within each state, on one day during June and make 50 3-min stops at 0.8 km intervals, recording any bird detected. CBC observers go into the field during a specified 24-h period in late December or early January and record any bird seen or heard in a specified area ("count") 24 km in diameter. Count compilers also make a measure of effort, the party hour (PH), defined as the total time spent searching for birds by separate groups of observers (J. Confer pers. comm.). American Birds (formerly Audubon Field Notes) publishes the yearly count results. In this study, the CBC year refers to the calendar year in which the count ends.

The validity of using volunteer-based data programs has received attention because of the problems of observer variability, coverage biases in relation to human population centers, discontinuous yearly observations, and differences in observer effort both between counts and within counts between years. Reviews of the BBS (Bystrak 1981) and the CBC (Bock and Lepthien 1974, 1976; Bock and Root 1981; Drennan 1981) have concluded that large geographic coverage and large sample size of routes or counts reduce any errors inherent in the data collection methods. Because this study consisted of large samples from a wide geographic area, utilization of these data bases seems appropriate.

Population analyses

I derived each range map by recording whether House Finches occurred within each count or route during the two year period covered by the map (e.g. 1979 and 1980 for 1980 maps). Population growth for 1966 to 1979; years for which BBS data were available, was determined by plotting yearly means for routes where House Finches were observed at any time. Linear regression was performed on log-transformed House Finch data to derive the population growth curve.

I plotted yearly average House Finch numbers against yearly average numbers of other species within the 1983 (CBC analysis) or 1979 (BBS analysis) House Finch range and performed Spearman Rank Correlations to test for negative relationships over time between House Finches and potentially competing species. I also performed correlation analysis between House Sparrow and Purple Finch populations outside of the House Finch range to determine whether these two species interacted with each other. To determine qualitatively the shape of any relationship, I plotted a curve of best fit, using linear regression on log-log or inverse-inverse (i.e. 1/X) transformed data. The BBS data used were yearly means for the northeastern states (Virginia and north), corresponding to USFWS region 5. The CBC analysis was limited to 1968–1983 data from counts in which House Finches were present more than four years, allowing trends to develop in each count, while reducing potential jumps in the data resulting solely from the initiation or discontinuance of counts during the overall period of the analysis. I used birds observed per party hour (total numbers of birds divided by total party hours) as units, which provides a better measure of relative abundance than number of birds alone (Bock and Lepthien 1974, 1976).

Species which exhibited a negative relationship to House Finch population levels in the BBS analysis were examined outside of the House Finch range to determine whether the population also decreased in the absence of House Finches. I calculated an average trend (% change) over time for each state and province surrounding the 1979 BBS House Finch range (North Carolina, Tennessee, Kentucky, Indiana, Michigan, New Brunswick, and southern Quebec and Ontario), and weighed the percentage change in each state or province in relation to its area to derive an average overall trend. If I found a negative trend outside of the House Finch range, I factored it out of the data from inside the range by adding the product of the first year's density and the annual percent population change from outside of the range to the density of the subsequent year, and continued the procedure with each adjusted value so that the percentage change was cumulatively added to each subsequent value.

In the case of CBC data, if I found a negative relationship between House Finches and another species, I examined the population of potential competitors over time to determine if it had been changing at the same rate prior to House Finch arrival. Linear regression was performed on populations over time in individual counts in which House Finches had been present for more than 10 years.

I compared slopes within each count before and after House Finch arrival, and used a binomial test (Snedecor and Cochran 1980) to ascertain whether there was a higher proportion of counts than randomly expected in which the slope after House Finch arrival was less than the slope prior to their arrival.

Weather and habitat analyses

To determine if observed population trends were caused by changes in weather, I regressed yearly BBS population levels on average monthly and annual values of minimum temperature, maximum temperature, average temperature, temperature fluctuation, precipitation, and (October through May) snowfall for the whole eastern House Finch range (U.S. Environmental Data Service 1966–1979). Any variables with significant relationships were inspected in three states outside of and at similar latitudes to the eastern House Finch range (Indiana, Kentucky and Washington state). If weather were a factor, the same trends should also have appeared in these reference areas. If any one of the populations in these states showed a significant trend, I performed multiple regression to ascertain whether House Finches and/or weather had a significant influence on the species' population within the House Finch range.

I examined rates of habitat change to determine whether differences in these rates presented a confounding factor acting on control populations and populations associated with House Finches. I compared changes in percent area of forest, field, and residential lands between states inside and outside of the 1979 BBS House Finch range between 1964 and 1979 (United States Department of Agriculture 1968, 1984), using a t-test. I also compared changes in CBC coverage of these three habitats before and after House Finch arrival by examining habitat data from the individual CBC counts used to compare population trends before and after House Finch arrival.

Results

From 1979 to 1983 to House Finch range expanded in all directions, but primarily grew to the southwest and, to a lesser extent, the west (Fig. 1). Patterns of colonization in southern Ontario and Nova Scotia indicated that House Finches will fly across large bodies of water. The range expanded to the south and west in the winter and contracted in the summer. Part of this seasonal difference might be a result of higher total observer time in the CBC compared to the BBS, which favors detection of rare species in the winter.

The total population grew geometrically with an intrinsic annual rate of increase (r) of 0.24, and doubled every three years (BBS data, Fig. 2). Both Bock and Lepthien (1976) and Bystrak and Robbins (1978) found a similar rate of increase during the 1960's and early 1970's.

Summer and winter densities of House Sparrows declined significantly with increasing House Finch density over time ($P<0.005$ in both cases, Fig. 3a and b). Summer House Sparrow density decreased an average of 1.05%/year outside of the House Finch range (reference area), but this decrease was not statistically significant ($0.2>P>0.1$, one-tailed t-test of slope). Furthermore, House Sparrow density inside of the House Finch range compensated by 1.05% per year still had a significant negative relationship to House Finch density ($P<0.005$), thus the rate of decline of House Sparrows outside of the House Finch range does not explain the House Sparrow decline in the presence of House Finches. Slopes of winter densities of House Sparrows after House Finch arrival plotted against time were

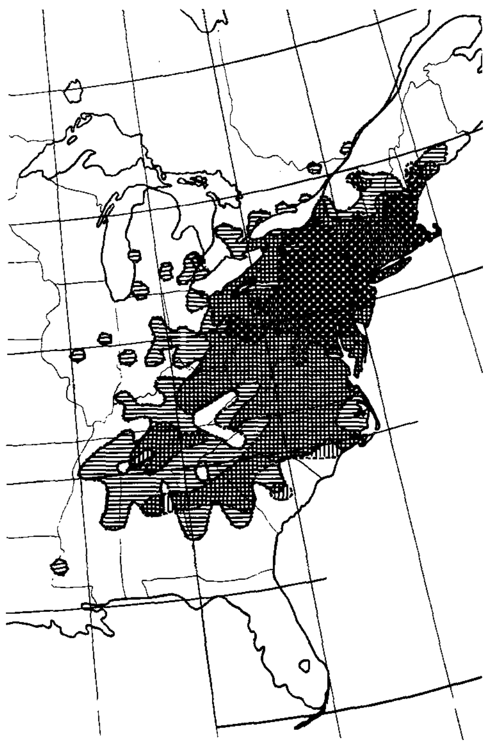

Fig. 1. Range of the eastern House Finch population over time. Dotted area – 1979–1980 summer (BBS) range; vertically-lined area – 1979–1980 winter (CBC) range; horizontally-lined area – 1982–1983 winter (CBC) range. Winter observations from Yarmouth (1979–1980 and 1982–1983) and Halifax (1982–1983), Nova Scotia, are not shown

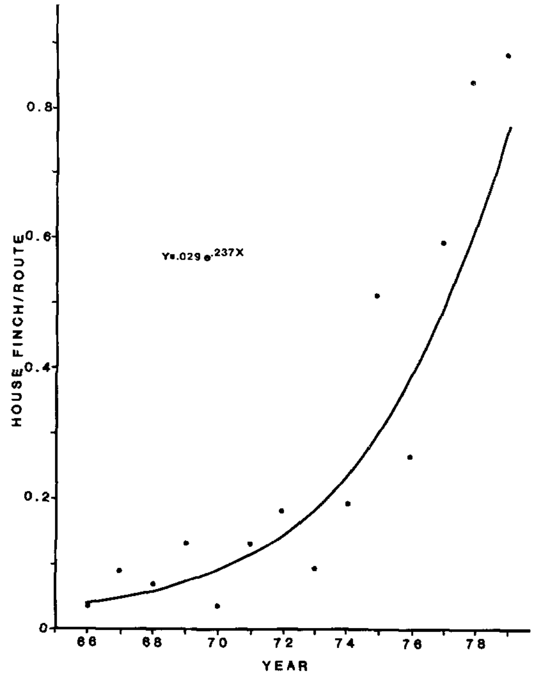

Fig. 2. Population growth of the eastern House Finch population 1966–1979. Data taken from the BBS

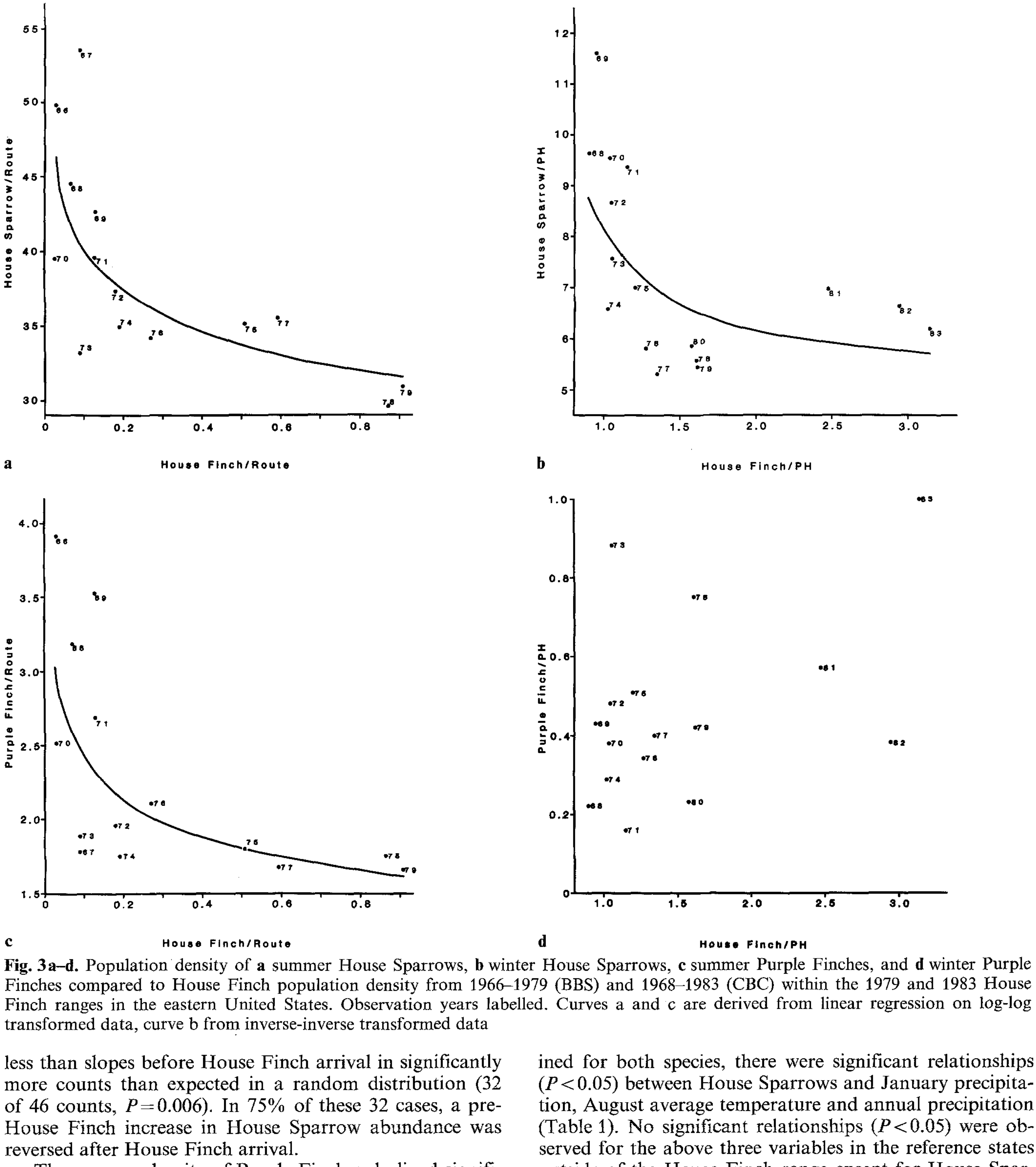

Fig. 3a–d. Population density of **a** summer House Sparrows, **b** winter House Sparrows, **c** summer Purple Finches, and **d** winter Purple Finches compared to House Finch population density from 1966–1979 (BBS) and 1968–1983 (CBC) within the 1979 and 1983 House Finch ranges in the eastern United States. Observation years labelled. Curves a and c are derived from linear regression on log-log transformed data, curve b from inverse-inverse transformed data

less than slopes before House Finch arrival in significantly more counts than expected in a random distribution (32 of 46 counts, $P=0.006$). In 75% of these 32 cases, a pre-House Finch increase in House Sparrow abundance was reversed after House Finch arrival.

The summer density of Purple Finches declined significantly over time with increasing House Finch density ($P<0.005$, Fig. 3c), but winter densities of Purple Finches and House Finches were not significantly related (Fig. 3d, $P>0.5$). The summer Purple Finch population outside of the House Finch range increased at an average rate of 0.7%/year. Purple Finch and House Sparrow populations were not correlated outside of the House Finch range ($P>0.1$).

Long term changes in weather did not cause changes in species abundances. Of the 74 weather variables examined for both species, there were significant relationships ($P<0.05$) between House Sparrows and January precipitation, August average temperature and annual precipitation (Table 1). No significant relationships ($P<0.05$) were observed for the above three variables in the reference states outside of the House Finch range except for House Sparrows and January precipitation in Kentucky (but not Indiana or Washington). The slope found in this case ($b=-3.23$) differed significantly from the slope inside of the House Finch range ($b=-0.06$, $P<0.025$, t-test between slopes). Multiple regression indicated that House Finch density had a significant relationship to House Sparrow density ($P<0.01$) whereas January precipitation did not ($P>0.1$).

Habitat change did not appear to be responsible for differences in growth rates of different House Sparrow or

Table 1. Slopes (b) and probability values for regressions between weather variables and House Sparrow populations. All regressions are significant ($p < 0.05$) inside of the House Finch range (the other 145 regressions with House Sparrows and Purple Finches were not)

Regression	January Precipitation		August ave. Temperature		Annual Precipitation	
	b	p	b	p	b	p
House finch range	−0.06	<0.05	−2.49	<0.03	−0.29	<0.03
Indiana	−0.33	>0.2	−0.02	>0.1	4.58	>0.4
Kentucky	−3.23	<0.005	−0.04	>0.1	−12.66	>0.2
Washington	−0.02	>0.5	0.16	>0.5	−0.02	>0.5
Multiple regression:						
House finch	−0.09	<0.01	–	–	–	–
Weather	−0.08	>0.1	–	–	–	–

Purple Finch populations. Changes in the area covered by forests, fields and developed areas were similar both between states within and outside of the House Finch range (t-tests, all $P > 0.2$), and within individual CBC counts before compared to after House Finch arrival (binomial tests, all $P > 0.37$).

Discussion

Population growth

The density maps and population graphs indicate that the House Finch population is still growing explosively. The rate of range expansion to the north declines as it approaches the southern edge of the northern boreal forest depicted on USFWS stratographic maps (see Bystrak 1981). A possible cause of this will be discussed below.

Competition with House Sparrows

Competition apparently occurs between House Sparrows and House Finches, as indicated by the negative response of the House Sparrow population in the presence compared to the absence of House Finches during both summer and winter. This competition could be over food or nesting sites. The majority of the adult diet of both species consists of seeds, and vegetable matter as a whole makes up 96.7% and 96.6% of the House Finch and House Sparrow diets, respectively (Bent 1958, 1968; Martin et al. 1951). Kricher (1983) presents antecdotal evidence that House Finches have replaced House Sparrows in some nesting spots.

Interspecific aggression between House Finches and House Sparrows occurs, suggesting that interference competition might occur between these two species. Authors disagree on the outcome of these interactions. Kalanoski (1975) performed experiments on aggression between House Sparrows and House Finches in the laboratory and found that House Sparrows won most of the antagonistic encounters, supporting field observations from the western United States (Bent 1968), but he noted that high density cage conditions in the study might have increased aggressive activity above natural levels. In the eastern United States, observers report a standoff during aggressive encounters between the two species (personal observation; Elliot and Arbib 1953; Katholi 1967). A difference in aggressiveness between the eastern and western House Finch populations may be responsible for this pattern.

Competition with Purple Finches

Purple Finches present a more complicated picture: the Purple Finch population shows a negative relationship to the House Finch population in summer but not winter. A possible explaination for this seasonal difference is that Purple Finches are migratory, with their major wintering grounds to the south of the bulk of the House Finch range; House Finch interactions occur with different portions of the population at different times of the year. Purple Finch migration, particularly to the northern portion of the wintering range, is erratic (Bent 1968); a significant trend is unlikely to be found in winter on the basis of this fact alone. Thus, Purple Finches appear to compete with House Finches for habitat or resources in the breeding season. Both species eat seeds, buds, and fruit, but Purple Finches are less dependent on seeds than are House Finches (Martin et al. 1951; Salt 1952; Bent 1968). Both species feed seeds to their young and usually situate nests in conifers.

Habitat separation may be occurring between Purple Finches and House Finches. As mentioned earlier, Purple Finches may have a wider range of habitats during the breeding season in eastern compared to western North America because of the original absence of House Finches in the eastern United States. If habitat separation is taking place, then the decline of the Purple Finch population is expected in areas outside of the conifer/mixed forest, where the House Finch population is now expanding. Furthermore, the range maps indicate that growth of the House Finch range has slowed as it approaches the coniferous forest zone in the Adirondack Mountains, southern Ontario and Quebec, and northern Maine, consistent with the habitat separation hypothesis. Salt (1952) has suggested that winter weather affects both species in a similar manner, but in summer each species is competitively superior in its preferred habitat because of physiological adaptations.

Alternative factors

One problem with observing a species introduction is that replicates of the "treatment" are often unavailable, and control populations may not be distributed randomly, so that different rates of change of other environmental factors may cause confounding differences between the dynamics of different populations. However, in this study, a difference in the rate of change of some environmental factor is unlikely to have coincidentally tracked the expansion of the House Finch population through time across 46 widely spread (up to 1,240 km apart) CBC replicates. Differences between House Sparrow and Purple Finch populations inside and outside of the House Finch range might be influenced by different rates of change of some environmental factor. As mentioned earlier, one confounding factor present in "natural experiments", the factor limiting the range of any potentially dominant competitor, is absent in this comparison. House Finches have invaded most of the control area after 1979 (Fig. 1, unpublished nesting data), the year in which I last made comparisons, thus no environmental difference appears to affect House Finches in the two areas. To further test the possibility of confounding factors, I examined rates of change of the two factors most likely to have an effect on populations: weather and habitat.

Changes in weather between years of this study are not an important factor in House Sparrow and Purple Finch population dynamics. The significant relationships found represent 2% of the regressions performed, less than 5% expected by chance alone. Only one significant trend in these three comparisons occurred in only one of three reference areas, and this specific relationship was different from that inside the House Finch range. These facts and the multiple regression results indicate that the House Finch population level is an important variable, but that the relationship between weather conditions and population dynamics are spurious or, at best, unimportant.

Differences in the rate of habitat change were apparently not responsible for declines of House Sparrow and Purple Finch densities in the presence of House Finches. Rates of change in forest, field, and developed lands were not different between states within the House Finch range and in the control area, nor in individual CBCs before compared to after House Finch arrival.

Interactions between House Sparrows and Purple Finches

If House Finches compete with both House Sparrows and Purple Finches, competition may also occur between the later two species. Alternatively, mutualism between House Sparrows and Purple Finches may explain concurrent declines in these two populations, rather than competition with House Finches. Bent (1968) provides qualitative reports that Purple Finch populations declined sharply with the introduction of the House Sparrow during the late 1800's, suggesting that competition, but not mutualism, may occur between these two species. I found no correlation between House Sparrows and Purple Finches outside of the House Finch range, suggesting that neither of these interactions was important during the duration of the study.

In conclusion, the House Finch population is still growing exponentially and expanding its range. Population density curves and comparisons between spatial and temporal controls indicate that competitive interactions may occur between House Finches and both House Sparrows and Purple Finches. Evidence exists suggesting that interference competition may occur between House Sparrows and House Finches, but not between House Finches and Purple Finches. Weather and habitat changes do not explain the observed population trends.

To test further whether competition occurs in this system and if it produces changes in resource use or species distributions, three predictions must be examined in future work: 1) there is a common limiting resource (probably food or nesting sites), 2) a shift in the use of this resource will be seen inside compared to outside of the House Finch range, and 3) as the House Finch range expands into areas previously unoccupied, the same shift will occur in these areas. More quantitative data on diet and habitat preference of the species in this paper also are needed to determine the resources over which competition occurs and the extent resource overlap.

Questions pertaining to populations that are hard to manipulate can be investigated in a system such as this and it should be exploited as fully as possible while the House Finch population increase is still occurring. This system has the advantage of being well documented by the volunteers who participate in programs such as the BBS and CBC. This study involved more than 1 million person hours in the field, and clearly could not have been done by one person or research group alone. Unfortunately these programs are largely overlooked in the scientific community as an important source of data, although their value, despite their shortcomings, can be great.

Acknowledgements. I would like to thank T. Cade, P. Gowaty, C. Hall, G. Orians, R. Paine, D. Schluter, T. Schoener, J. Wetterer, N. Wheelwright, and two reviewers for helpful suggestions on various versions of the manuscript and during the study. I would also like to thank C. Bock for preliminary CBC data, and C. Robbins and the rest of the BBS staff for providing computerized BBS data. Finally, I would especially like to thank the hundreds of volunteer observers who collected the field data. This study was supported in part by an honors thesis grant from the Cornell University College of Agriculture and Life Sciences, and a portion of this paper was written during tenure on an NSF graduate fellowship.

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Received May 5, 1986