

NATAL DISPERSAL IN HOUSE SPARROWS: POSSIBLE CAUSES AND CONSEQUENCES

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Dispersal is an important factor in determining the population structure of a species, and when it represents gene flow, may significantly influence the species' evolution (Wright 1940, Mayr 1963, Ehrlich and Raven 1969, Shields 1982). Several studies have documented dispersal in birds (see Barrowclough 1980, Greenwood and Harvey 1982 for review), but few have examined its causes and/or consequences (but see Dhondt 1979, Greenwood et al. 1979, Keppie 1979, Weise and Meyer 1979). Dispersal rates may be affected by intrinsic or extrinsic factors (Howard 1960, Johnston 1961). Intrinsic factors include genetic influences (Greenwood et al. 1979), sex (Greenwood 1980, Lowther 1979b), age, body size, or social rank (Monaghan 1980). Environmental factors which may be important include population density (Tompa 1964, Gaines et al. 1979, Greenwood and Harvey 1982), resource levels (Grant 1978), or potential for breeding success (Freer 1979).

Dispersal may function to reduce inbreeding, or any reduction may be merely a consequence of dispersal (Greenwood et al. 1978). There is likely some risk for dispersers when they leave the local population, and greater mortality of dispersers has been documented in Blackbirds (*Turdus merula*; Greenwood and Harvey 1976), but has not been found in Great Tits (*Parus major*, Dhondt 1979, Greenwood et al. 1979) or Spruce Grouse (*Canachites canadensis*; Keppie 1979). Selection on certain traits may be greater in dispersers, thus making them differ from non-dispersers in these traits.

We present here data gathered from an extensively investigated population of House Sparrows (*Passer domesticus*) in eastern Kansas (Murphy 1978a,b, Lowther 1979a, Johnston and Fleischer 1981, Fleischer and Johnston 1982, Fleischer 1983a,b). Sparrows banded during breeding studies and later recovered provide the data base. Breeding data from Lowther (1979a) supplied information on nestling, nest, and colony characteristics. Banded birds from this study provided known familial relationships. Skeletal measurements and genotypes at up to four polymorphic, putative allozyme loci were taken from collected specimens. These same birds also provided data for Lowther's (1979b) report. Lowther (1979b) presented the distribution of dispersal distances of birds banded as nestlings and compared dispersers and non-dispersers in terms of sex and a number of nest and nestling variables. Here we emphasize data which explore morphological and genetic characteristics of dispersers and non-dispersers. Additionally, we use the familial identification to calculate a correlation of dispersal distance between nest mates (i.e., a nest effect).

METHODS AND MATERIALS

Study area.—The breeding study and collections were made at 7 farms (each was a separate colony) in Leavenworth County, Kansas (Fig. 1; Lowther 1979a,b; Johnston and Fleischer 1981, Fleischer 1983a,b). The farms fit within a rectangular area of about 12 km². Nine other farms in the area had sparrows. Average distance between study farms and their nearest neighbor farm (study or otherwise) was 576 ± 243 m. Mean distance between study farms and their nearest neighbor study farm was 1039 ± 425 m. Farms varied in a number of resource and population parameters (Lowther 1979a, Fleischer 1983a).

Bandings and recoveries.—About 3360 nestlings were color-banded and survived nestbox life on the 7 study farms over the 4-year breeding study. In addition, about 200 adults were netted and banded. Of all of these banded birds, 46 were resighted on study farms at least 90 days after being banded (i.e., after the typical period of natal dispersal, see below) and 85 specimens were collected from study farms during the latter half of November 1978, and March 1979. An additional 351 unbanded specimens were taken during these periods (see Fleischer 1983b, Johnston and Fleischer 1981 for details). Of the 85 banded individuals collected, 63 had been banded as nestlings and also could be used for morphometric analysis (i.e., they had complete skeletons). Other analyses used the entire sample of recovered birds banded as nestlings ($n = 112$).

Individuals were classified as dispersers if they were found at a study farm different from the one at which they were banded. Non-study farms were, unfortunately, not sampled. Since study farms were relatively small and discrete (Fig. 1), dispersal distance was measured as a straight-line interfarm distance. Previous work indicated that most natal dispersal in House Sparrows occurs during late summer and early fall (Summers-Smith 1963, Will 1969). Juvenile sparrows on a farm form flocks and move through the surrounding cropland until about October, when they either return to their natal farm or disperse. Springtime and adult dispersal are rare. Our discussion here relates only to natal dispersal (dispersal of juveniles from site of hatching to site of breeding).

Morphologic analyses.—In addition to nestling 7-day weight used by Lowther (1979b), 4 skin and 14 skeletal measurements (Johnston and Selander 1971) were made on adults recovered. The 14 skeletal variables were assessed multivariately using principal components analysis. Loadings and complete interpretation of the axes are presented elsewhere (Fleischer and Johnston 1982, Fleischer 1983b). Generally, principal component 1 (PC1), with 51% of the variance, represents overall body size, PC2 (17%) represents a core-to-limb ratio, and PC3 (14%) represents relative head size. PC scores were grouped by sex, age (i.e., first-year fall birds versus birds having survived at least one winter), and dispersal status, and means and variances were computed. Means were compared using *t*-tests. In addition, PC scores were regressed against dispersal distance.

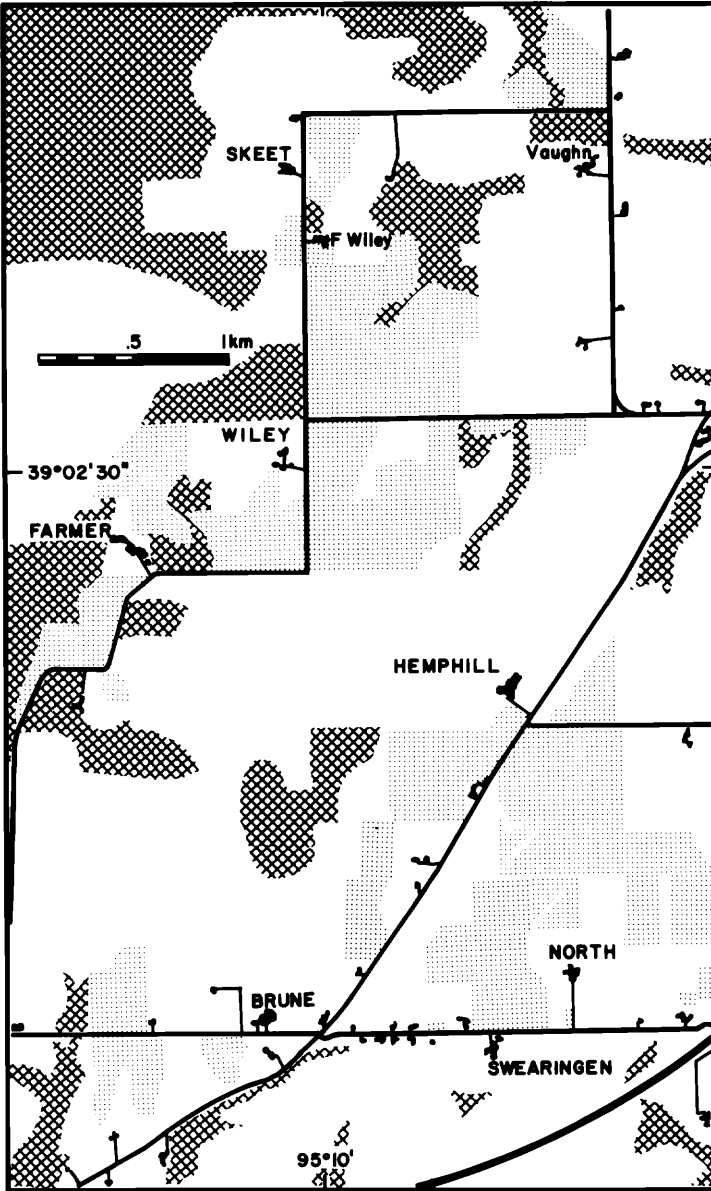


FIGURE 1. Map of the Leavenworth County, Kansas study area (northeast of Lawrence, Kansas). Capitalized names are farms included in the study. For more information on study site see Lowther, 1979a.

Electrophoretic techniques and analyses.—Electrophoretic techniques, local allele and electromorph frequencies for the four allozyme loci, and statistics of genetic structure are presented elsewhere (appendices 1 and 2, Fleischer 1983a,b). Four polymorphic, putative loci were resolved: esterase-1 (EST), isocitrate dehydrogenase-2 and -3 (IDH-2, IDH-3), and fluorescent esterase (Fl-EST). A freezer malfunction and aging of tissues decreased the sample size from the original 436 specimens to a maximum for any one locus of about 340, and only 21 of the 66 natal specimens were scored for all 4 loci. Allele and heterozygote frequencies of dispersers and non-dispersers were compared for each of the 4 loci. In addition, overall heterozygosity was compared for the 21 specimens with complete genotypic information.

Estimation of nest effect.—Among the recoveries banded as nestlings (112), 43 were close relatives. There was one family with 4 probable siblings, 3 families with 3 probable siblings, and 15 pairs of siblings. Of 30 related pairs, 12 were siblings from the same brood and 18 were from different broods, but were from the same nestbox and year. These were probably full siblings. Of the 30 "sibships," 9 were female-female, 10 were male-male, and 11 were male-female. Of the 12 intra-brood siblings (as opposed to intra-nest siblings), 4 were female-female, and 5 were male-male.

Two ways of assessing a nest effect on dispersal were used. First, the heritability of dispersal distance for full sibs was estimated as $h^2 \leq 2t$ (i.e., twice the intraclass correlation coefficient; Boag and Grant 1978, Falconer 1981:151). Since broods should be randomly crossfostered to remove potential maternal or environmental effects, only an upper level of genetic determination may be approximated. However, if heritabilities are not significant, then it is doubtful that there are consequential genetic causes of variation, or any important nest effects.

Because of sexual dimorphism in dispersal level (Lowther 1979b), mixed-sex pairs, in theory, should not be included in the estimation of heritability. A second way of looking for non-random associations of dispersal behavior among sibs eliminates this problem. We calculate a simple, conditional probability to allow comparison of observed and expected distributions of same sex and mixed-sex sibships, where both sibs dispersed or did not disperse, or one sib of either sex dispersed. This is done as follows. The proportion of dispersers and non-dispersers within each sex are computed. In order to determine the probability of certain sibling pairs, the frequencies of each category are multiplied (e.g., the probability of a sibling pair wherein 2 females dispersed is calculated as the square of the frequency of female dispersers). This value multiplied by the total number of sibling pairs (in this case 30) provides the expected numbers. The observed numbers are compared to the expected with a χ^2 test.

RESULTS

Sex, age, and nest characteristics.—As reported by Lowther (1979b), females disperse more than males. Of the 112 recoveries of birds banded

as nestlings, 22 of 42 females (52%) dispersed, and 19 of 70 males (27%) dispersed ($\chi^2 = 7.2$, $P < .01$, 2×2 contingency table). Of the 63 individuals that were collected and measured, 11 of 23 females (48%), and 12 of 40 males (30%) dispersed ($\chi^2 = 2.0$, $P > .1$). Numbers differ slightly from Lowther (1979b) because individuals resighted fewer than 90 days from banding were removed from the analysis. Adults dispersed significantly less than first-year birds (only 1 of 15 recoveries banded as adults was recovered at a different farm).

Lowther (1979b) reported no significant relationship between date of fledging and dispersal. Also, no relationships were found between clutch size or rank in brood and dispersal. For both sexes, dispersers came from nests which had greater fledging success (number young fledged/clutch size) than nests from which came non-dispersers. This difference was nearly significant for males (disperser mean = .88, $n = 12$, non-disperser mean = .76, $n = 28$; $t = 1.81$, $P = .08$).

Body size and mortality.—Dispersing males had slightly larger 7-day weights than non-dispersing males, and dispersing females had slightly smaller 7-day weights than non-dispersing females, but neither was significantly different (Lowther 1979b). Adult size, as assessed by PC scores based on skeletal measurements of collected birds, showed similar patterns (Table 1). Principal component scores were also regressed on dispersal distance, and size (PC1) was negatively correlated with distance dispersed in females (Table 2, Fig. 2). For these same birds, 7-day weight shows an even stronger relationship (Fig. 3), but not for females from the entire sample of recoveries (Lowther 1979b). The relationship was dissected even further (Table 3): birds were grouped into those recovered as fall first-year birds (based on level of skull ossification; Nero 1951; i.e., no winter experience), and those recovered either as adults or in spring (i.e., at least one winter of experience). No differences were apparent among the classes for females, however, adult male dispersers were significantly larger than adult male non-dispersers and all fall first-year males. This likely indicates greater mortality of male dispersers of small body size.

The proportion of recovered birds dispersing was significantly lower among males recovered as adults than among males recovered as fall first-year birds (19% versus 50%, $\chi^2 = 4.1$, $P < .05$, 2×2 contingency table). Females, however, had equal frequencies of dispersers among both classes. When the entire data set is examined, 62% of birds recovered as fall first-year are dispersers, whereas only 32% of those recovered as adults are dispersers ($\chi^2 = 8.4$, $P < .01$). Because most or all dispersal in House Sparrows occurs during the late summer and early fall (before these recoveries were made; Summers-Smith 1963), this difference in frequency of dispersal may represent greater mortality of dispersers over non-dispersers.

Allozymic heterozygosity.—One allozyme locus showed a significantly greater level of heterozygosity among dispersers, and 3 of the 4 loci

TABLE 1. Mean PC^a scores for dispersers and non-dispersers within each sex. No *t* values are significant at .05 level.

	n	PC1 (SD)	PC2 (SD)	PC3 (SD)
Females				
Non-dispersers	12	-0.537 (0.77)	-0.001 (0.60)	0.254 (0.84)
Dispersers	11	-1.050 (1.24)	0.261 (0.97)	0.420 (0.88)
<i>t</i>		1.19	0.79	0.46
Males				
Non-dispersers	28	0.019 (0.99)	-0.410 (1.33)	-1.336 (0.79)
Dispersers	12	0.576 (1.15)	-0.137 (0.68)	-0.094 (0.99)
<i>t</i>		1.55	0.67	1.20

^a From a principal component analysis consisting of 436 specimens from Lawrence, Kansas, over a suite of 14 morphologic variables; the 63 birds in the table are a subset of the whole.

exhibited greater levels of heterozygosity among dispersers than among non-dispersers (Table 4). When the 21 individuals with complete allozyme information are compared, dispersers show a markedly higher level of heterozygosity ($G = 11.0$, $P < .005$). Heterozygosity averaged over individuals is higher in dispersers ($\bar{H} = .34 \pm .17$; non-dispersers $\bar{H} = .10 \pm .13$; $t = 3.6$, $P < .01$). When heterozygosity is computed for individuals with 3 or 4 loci known, and averaged, the total sample is increased to 32, and the relationship remains (disperser $\bar{H} = .29 \pm .19$; non-disperser $\bar{H} = .16 \pm .15$; $t = 2.1$, $P < .05$).

Nest effect.—Correlation coefficients between siblings' dispersal distances were calculated for several subsets of the data. The correlation for all 30 probable sibships is .20 (NS). The correlations for same sex sibships are .50 for females ($n = 9$, NS) and $-.11$ for males ($n = 10$, NS). For sibships from the same brood $r = .46$ ($n = 12$, NS), and when this is divided by sex, the correlation for females is .88 ($n = 4$, NS), and males cannot be evaluated because no individuals among the 5 pairs in this group dispersed. None of these correlations is significantly different from zero.

The second method examined whether pairs of dispersing and non-dispersing sibs occur to a greater extent than predicted by chance. The expected and observed frequencies of the 10 sex/dispersal classes of

TABLE 2. Pearson product-moment correlations (r) between dispersal distance and PC scores from House Sparrows from Lawrence, Kansas 1978-1979.

	n	PC1	PC2	PC3
Males	40	0.29	0.12	0.08
Females	23	-0.42*	-0.11	0.10

* $P < .05$.

TABLE 3. Scores on PC1 of morphology (overall body size) for dispersing and non-dispersing House Sparrows, recovered either as first-year birds in fall, or as adult birds in spring or fall.

	Fall first-year ^a		Adults ^b	
	n	Mean PC1 (SD)	n	Mean PC1 (SD)
Females				
Non-dispersers	7	-0.435 (0.69)	5	-0.678 (0.93)
Dispersers	6	-1.011 (0.75)	5	-1.085 (1.77)
<i>t</i>		1.45		0.45
Males				
Non-dispersers	7	0.089 (1.27)	21	-0.004 (0.93)
Dispersers	7	0.050 (0.97)	5	1.313 (1.04)
<i>t</i>		0.06		2.79**

** $P < .01$.^a No winter experience.^b One or more winters of experience.

sibling pairs are presented in Table 5. Although the samples are small, there is no significant difference between the distributions ($\chi^2 = 5.57$, $P > .5$). Thus, there appears to be neither a significant nest effect nor a measureable heritability associated with dispersal in the House Sparrow.

Environmental factors.—Environmental factors affecting dispersal were difficult to assess, as it was virtually impossible to calculate an unbiased estimate of dispersal rate from all of the farms. Some isolated cases, however, point to potential breeding success and population size as factors promoting philopatry in sparrow colonies. For example, the Wiley farm (in Fig. 1) had the lowest breeding productivity (per female) and the smallest population size of any of the study farms (Lowther 1979a, Fleischer 1983a). Of 13 specimens collected from this farm, none had been banded on the farm, and all 5 recoveries of Wiley nestlings occurred at surrounding farms (Farmer, Skeet, Brune, or Hemphill). On the other hand, the Farmer farm (which I present here because of its proximity to the Wiley farm, i.e., <1 km distant) had the second highest breeding productivity and population size of the 7 farms. Of 90 specimens from this farm, 28 (31%) had been banded as nestlings there ($\chi^2 = 3.9$, $P < .05$ for comparison with Wiley farm), and only 8 Farmer birds were recovered at the 4 surrounding farms (Wiley, Skeet, Brune, or Hemphill; $\chi^2 = 12.3$, $P < .005$ for comparison with Wiley farm).

DISCUSSION

Intrinsic factors.—The main intrinsic factors affecting dispersal rates in House Sparrows are not easily elucidated. It appears that factors common to a nest, such as brood size, success, or hatch date cannot be

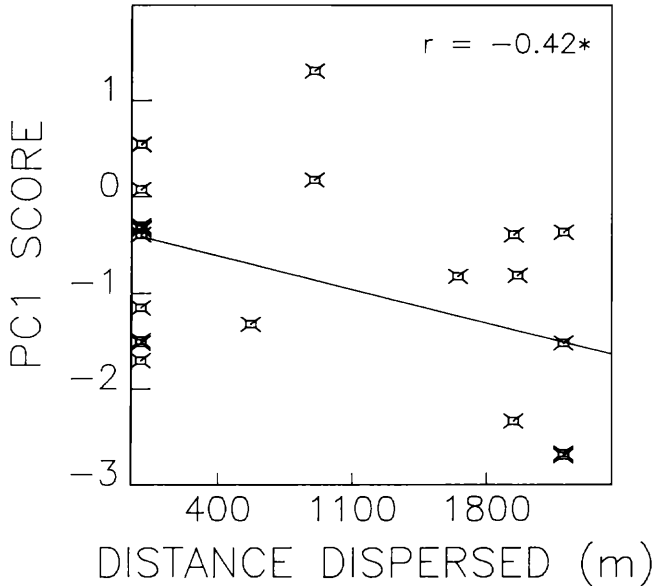


FIGURE 2. Relationship between female body size at time of recovery (assessed by score on PC1, see text) and the distance dispersed.

implicated as primary causes of dispersal. The lack of a significant nest or genetic component to variation in dispersal does not match previous results. Both Greenwood et al. (1979) and Dhondt (1979) note significant correlations among relative's dispersal tendencies in the Great Tit. Greenwood et al. calculate a parent-offspring heritability that averages between 50 and 60%. Dhondt found a sibling nest effect or maximal heritability of about 30%, and the intraclass correlation and the analysis of variance provide significant results.

The lack of heritability or nest effect in House Sparrows may be an artifact of the limited sample size or because of a misidentification of siblings. The sample size of 30 sibling pairs, however, is about two-thirds as large as the 44 pairs used by Dhondt (1979), and about $\frac{1}{2}$ as large as the average sample of 58.5 parent-offspring duos used by Greenwood et al. (1979). Even if our assumption that broods from the same nest and year have the same parents is incorrect, the analyses using just the 12 intrabrood sibling pairs also provided no significant results.

If there actually is no consequential genetic basis for variation in dispersal level, then selection on such variation can have no evolutionary importance. It is possible that dispersal is entirely environmentally induced, or that environmental effects on other characters (such as body size or aggressiveness) in turn induce dispersal. Alternatively, sibling pairs may differentially disperse to reduce the chances of sib-sib mating,

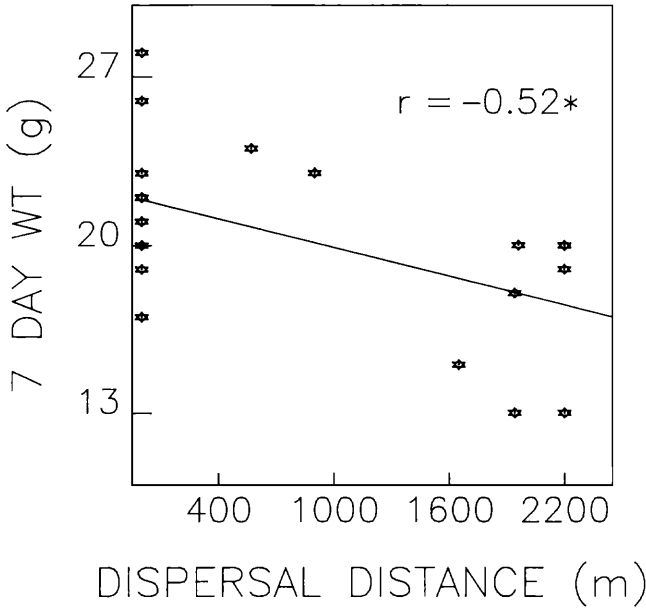


FIGURE 3. Relationship between female 7-day weight (as a nestling) and the distance dispersed. Pearson $r = -.52$, $P < .05$.

sibling competition for resources, or other negative inter-sibling interactions. If such were always the case, then the correlation among sibling pairs should be negative, rather than effectively zero.

Intrinsic factors that provide the strongest links to dispersal are small body size in females and perhaps overall heterozygosity at allozyme loci. The latter may strictly be a consequence of dispersal rather than a cause of it. This could be manifested in two ways. One, if there is heritability of dispersal, then parents of dispersing birds probably also dispersed, and were thus "outbred" compared to non-dispersers. Their offspring would probably be of greater heterozygosity. Since we have no evidence for genetic determination of dispersal, this explanation is unlikely.

Alternatively, as dispersers likely face greater environmental challenges than non-dispersers, greater allozyme heterozygosity may act as a buffer against these rigors, and enhance survival (Lerner 1954). There is, however, no significant difference in heterozygosity levels between the entire fall and spring samples of the study (i.e., the 436 collected birds, Fleischer, unpubl.). Sample sizes are too small to adequately compare fall first-year and adult classes within the present set of 21 recoveries. The result may be an artifact of some other variable or unknown bias.

One consequence of dispersal for small males appears to be higher mortality. Previous analyses, using all 436 specimens, showed that males

TABLE 4. Heterozygosity levels of dispersers versus non-dispersers in House Sparrows from Lawrence, Kansas. See text for locus designations.

	Dispersers		Non-dispersers		χ^2
	n	% heterozygote	n	% heterozygote	
EST	17	0.47	30	0.50	0.04
IDH-2	15	0.20	21	0.05	2.06
IDH-3	14	0.43	16	0.07	6.00**
Fl-EST	16	0.07	22	0.04	0.05

** $P < .025$.

average significantly larger in the spring than in the fall (Johnston and Fleischer 1981; Fleischer and Johnston 1982). In contrast, females of small size were selected for. Thus, for males, dispersal-related mortality may have accentuated selection on body size: large male dispersers have a higher probability of survival than small male dispersers. Non-dispersers appear not to exhibit differential size selection. This suggests that males who disperse suffer from greater winter stress. Note that mortality occurred *after* the act of dispersal. What mortality occurs *during* dispersal could not be assessed in this study.

Why selection for larger size? For indepth discussion see Fleischer (1983b) or Johnston and Fleischer (1981). Here we suggest that in dispersers it is probably due to the introduction of males into a new social situation. Males establish winter roost and future nest sites in fall (Summers-Smith 1963). Resident males with already established sites are presumed to be at an advantage in retaining those sites (Greenwood and Harvey 1982), and may be more able to locate or guard local food resources. Only large dispersing males may be able to obtain a suitable

TABLE 5. Expected and observed frequencies of the 30 sibships within groupings of sex and dispersal status. $\chi^2 = 5.57$, $P > .5$.

Combination ^a	Exp	Obs
f disp/f disp	1.6	2
f disp/f non-disp	4.1	4
f non-disp/f non-disp	2.7	3
f disp/m disp	0.6	1
f disp/m non-disp	5.8	2
f non-disp/m disp	0.8	0
f non-disp/m non-disp	7.6	8
m disp/m disp	0.1	0
m disp/m non-disp	1.3	2
m non-disp/m non-disp	5.3	8
Total	30.0	30

^a f = female; m = male; disp = disperser; non-disp = non-disperser.

roost site or survive the winter conditions without one (Kendeigh 1976). Large male House Sparrows are dominant to small ones in interactions over food (Cink 1977). The relationship is also found for females. Perhaps the smallest females disperse farther as a response to domination by larger birds of both sexes. Alternatively smaller females may be able to disperse farther or for a longer period of time because of reduced energetic requirements.

Environmental factors.—There is a trend in which farms with large populations and high breeding productivity have lower rates of emigration and higher rates of immigration. Thus it appears that birds may be able to assess resources and/or the probability of breeding success on a farm, and make a decision to remain or disperse. Alternatively, aggression from resident birds may be greater in resource-stressed areas, and so force juveniles to disperse to a greater extent, than in richer areas.

Resource depletion resulted in increased dispersal in rodents (Grant 1978) and increased potential for breeding success was related to high philopatry in Bank Swallows (*Riparia riparia*, Freer 1979). Increased density has been shown to result in increased dispersal from an area (Gaines et al. 1979, Greenwood et al. 1979, Watson and Moss 1979, Greenwood and Harvey 1982), but how density relates to population size on our study farms is unknown.

Conclusions.—These data suggest that dispersal may ultimately influence the genetic and morphological structure of sparrow populations. Greater dispersal, mediating increased gene flow, can effectively reduce intercolony allozyme differentiation (Fleischer 1983b) and presumably decrease inbreeding within sparrow populations. In addition, homozygous dispersers may suffer greater mortality, and thus cause an increase in heterozygosity. Finally, selection against small dispersing males (Table 3) may result in (or at least emphasize) major morphological shifts toward large male size (Johnston and Fleischer 1981; Fleischer and Johnston 1982).

SUMMARY

Some causes and possible consequences of natal dispersal among colonies of House Sparrows in Kansas were examined. Two types of factors are considered: intrinsic and extrinsic. Among intrinsic factors, no nest effects could be detected, and the primary factors affecting dispersal were sex (greater female dispersal), age (greater juvenile dispersal), and smaller body size within females. Among environmental factors, farms with low breeding productivity and population size had lesser levels of colonial philopatry. Differential frequencies of dispersers among adult recoveries versus first-year recoveries suggest that dispersers suffer greater mortality than non-dispersers. This mortality appears to be higher in small males: dispersed adult recoveries (survivors) were significantly larger than non-dispersed adult recoveries, but pre-winter subadults

showed no such difference. Dispersers had greater allozyme heterozygosity at 4 putative loci.

ACKNOWLEDGMENTS

We appreciate the field or preparatory assistance of M. T. Murphy, W. B. McGillivray, C. S. Lowther, J. Stramel, J. Senegas, S. L. Stewart, and B. Bellringer. We thank M. Gaines for use of laboratory facilities and M. A. Jenkinson for ensuring skeletonization of specimens. W. Shields, J. Hamrick, and M. Gaines read and commented on earlier drafts. The National Science Foundation (NSF DBS-7912412) and the General Research Fund of the University of Kansas supplied funding.

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