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PHILOPATRY, NATAL DISPERSAL, AND INBREEDING AVOIDANCE IN AN ISLAND POPULATION OF SAVANNAH SPARROWS

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Abstract. Over a 9-yr period, we studied dispersal of young banded Savannah Sparrows (*Passerculus sandwichensis*) from their natal nest to the site where they first bred 1 yr later in a population on an isolated archipelago in the Bay of Fundy, Canada. On a broad geographic scale, young birds were highly philopatric, returning from wintering grounds several thousand kilometers away to nest on the same island and often in the same field where they had hatched the year before. In some cases, birds chose nest sites within a few meters of their natal nest. The median dispersal distance between a bird's natal nest and its first nest as an adult was 228 m, a distance equivalent to about six times the diameter of an average territory. Nearly three-quarters of the breeding birds in the study population had been banded as nestlings or fledglings within a 10-ha area on one island, which suggests that most birds in the population originated within the 127-ha archipelago.

Within the archipelago, males and females dispersed similar distances from their natal site. There was no correlation between natal dispersal distances of parents and their offspring, nor was there a correlation between natal dispersal distances of siblings, which indicated that natal dispersal has low heritability. Sex, hatching date, fledging mass, and population densities during the previous and current years were all poor predictors of natal dispersal distance. Males that were strongly philopatric recruited significantly more offspring during their lifetime than males raised outside the study area, although there were no differences between philopatric and dispersing females.

Birds tended to shift to distinct parts of the island to breed if their parents of the opposite sex still occupied the territory where they had hatched. Dispersal was not affected by return of same-sex parents. Distances between nests of siblings raised the same year were farther apart than expected by chance, based on Monte Carlo simulations. Although many birds in the population had the opportunity to pair with kin, some mechanism, yet to be determined, enabled birds to avoid inbreeding: in 1073 nesting attempts involving birds of known parentage, no individuals were known to have paired with close relatives (coefficient of kinship >0.125). Because complete inbreeding avoidance occurred in <1% of Monte Carlo simulations, the absence of inbreeding among Kent Island Savannah Sparrows is unlikely to be due to chance.

Understanding natal dispersal in birds requires a combination of models: ecogenetic models at broad geographic scales (e.g., adaptation to local environments), ecological constraints and neutral models at smaller spatial scales (e.g., unavailability of territories within particular habitats), and genetic models (e.g., inbreeding avoidance).

Key words: Canada; inbreeding; islands; Kent Island; natal dispersal; Passerculus sandwichensis; *philopatry; Savannah Sparrow; scale.*

INTRODUCTION

Many migratory birds show a remarkable tendency to return each year to breed in the same location (Nice 1937, Lack 1954, Haukioja 1971, Greenwood 1980, Nagata 1993). Models for the evolution of such site fidelity, or philopatry, fall broadly into three groups: ecological, ecogenetic, and genetic (Greenwood 1987). Ecological models assume philopatry is advantageous because familiarity with a particular area makes a bird more successful at acquiring food, escaping predators, locating mates, and reproducing (Hinde 1956, Mayr

1963, Greenwood 1980, Weatherhead and Forbes 1994). Ecogenetic models emphasize that philopatry increases the probability of producing offspring that are well adapted to local conditions in spatially heterogeneous environments (Greenwood 1987). Genetic models of philopatry, which are based on the presumption that philopatry coupled with random mating increases the probability of breeding with close relatives, consider inbreeding to be the main function of philopatry, not a mere consequence, because of the advantage of mating with genetically similar individuals, preserving co-adapted gene complexes, and reducing the cost of meiosis (Shields 1982, 1987). Most authors, however, consider inbreeding depression as a

risk of philopatry (Charlesworth and Charlesworth 1987, Pusey 1987, Harvey and Read 1988, Ralls et al. 1988).

In some cases, philopatry may be unavoidable because of isolation or saturation of suitable breeding habitats. If breeding with relatives reduces reproductive success compared to breeding with nonrelatives, selection should favor the ability to recognize kin and avoid mating with them (Harvey and Ralls 1986, Hepper 1991, Pusey and Wolf 1996, Pärt 1996). Dispersal to areas away from kin (i.e., a lack of philopatry, at least at a local scale) has been interpreted as an adaptation to avoid risk of inbreeding (Greenwood and Harvey 1982, Bollinger et al. 1993). An alternative interpretation of dispersal, especially if dispersal away from relatives of the opposite sex is no greater than dispersal away from same-sex relatives, is that moving away from locally high population densities serves to reduce resource competition (e.g., Lambin 1994).

Natal dispersal and breeding dispersal are generally considered separately. Natal dispersal, the subject of this study, refers to the net movement between site of birth and site of first breeding, whereas breeding dispersal refers to the distance between locations of successive reproductive attempts by adults (Greenwood and Harvey 1982). Various studies of vertebrates have attempted to quantify movement of young away from their birth site, to interpret its adaptive significance (if any), and to measure its effect on population age structure, gene flow between populations, and persistence of small populations (Greenwood 1980, Fleischer et al. 1984, Lande and Barrowclough 1987, Johnson and Gaines 1990, Payne 1990, 1991a, Nagata 1993). In a recent review, Weatherhead and Forbes (1994) showed that natal philopatry (as measured by proportion of young banded on a given study area that were seen there in subsequent years) was less common in migratory songbirds than in resident songbirds, and they found little support for Shields' (1982) optimal-inbreeding hypothesis.

In a growing number of bird populations, genetic relationships among individuals are known, information necessary to determine the frequency of inbreeding in relation to natal dispersal (Koenig and Pitelka 1979, van Noordwijk and Scharloo 1981, van Tienderen and van Noordwijk 1988, Gibbs and Grant 1989, Payne 1991a, Potti and Montalvo 1991, Alberico et al. 1992, Rowley et al. 1993, Russell and Rowley 1993, Lessells et al. 1994, Pärt 1996). In this study, we investigated natal dispersal and inbreeding avoidance by focusing on a highly philopatric bird population nesting under natural conditions in an isolated archipelago. Our 9-yr study of the Savannah Sparrow (*Passerculus sandwichensis*), a native migratory North American bird species, demonstrates that, in this population at least, birds of all ages are highly philopatric at the scale of geographic regions and individual islands. Nonetheless, despite numerous opportunities for breeding with

their parents or siblings, young Savannah Sparrows appeared to avoid incest by dispersing more when their opposite-sex parents were still alive, and by pairing exclusively with nonrelatives.

METHODS

Study area

Our main study area was located on Kent Island, an 80-ha island located 9 km south of Grand Manan Island, New Brunswick, Canada (44°35′ N, 66°46′ W), where we observed all Savannah Sparrows nesting in two open fields (North [1 ha] and South [6 ha]) separated from each other by 150 m of spruce-fir (*Picea glauca, P. rubens, Abies balsamea*) woods. At least once a year we censused the rest of Kent Island as well as neighboring Sheep Island (17 ha, 100% open habitat) and Hay Island (30 ha, 30% open habitat), which lie <0.5 km from Kent Island. Together those islands comprise an isolated archipelago called the Three Islands. Every other year we also censused several other small islands that occur within 3–6 km of Kent Island. Census involved 3–5 observers spending 2–3 h slowly walking 20–40 m apart, flushing and observing each Savannah Sparrow using 10× binoculars. We counted ~50–70 individuals per census; the number of birds observed varied little among years. In 10 yr of censuses on islands surrounding Kent Island, we never found >2 birds/yr that had been banded as nestlings on Kent Island, and only on a few occasions encountered a banded bird that had been overlooked in earlier censuses. As a result, more intensive sampling would be unlikely to turn up many more birds that had dispersed from Kent Island. Even though a large proportion of nestlings return to Kent Island as adults (see *Results: Natal philopatry and dispersal*), many must also disperse undetected to Grand Manan or to the mainland of Nova Scotia and Maine, 20 km away.

Study species

Savannah Sparrows winter mainly in southern United States and return to the breeding area in late April or early May. Adults that have previously bred generally return to the same territory where they tend to pair with their mate from the previous year if it is still alive. The basis on which yearlings select mates and/or territories is complex and incompletely understood. Males tend to arrive on the breeding grounds several days earlier than females, establishing and maintaining territories through song, displays, chases, and aggressive interactions. Yearling males that fail to attract a mate or claim a territory sometimes wander inconspicuously until they locate an unpaired (and usually yearling) female, which they mate-guard vigorously; the new pair may subsequently settle to breed wherever their presence is uncontested (Wheelwright and Rising 1993). About 30% of males mate with >1 female (Wheelwright et al. 1992). Females build cryptic nests

on the ground in fields, in vegetation along the shore-line, and in other open habitats within their mate's territory, and defend their own, smaller territories against other females. Population densities can be as high as 15 nesting females/ha. On Kent Island ~30% of females produce a second clutch, 2–3 wk after fledging young from the first brood. After they leave the nest ~10 d after hatching, fledglings remain with their siblings and parents within or near their natal territory for another 10–25 d. As they become independent of their parents, they join loose juvenile flocks that wander around the island until, 4–8 wk after independence, birds depart on their southward migration. Males and females are reproductively mature at the age of 1 yr, and virtually all returning adults breed (Stobo and McLaren 1975, Dixon 1978, Bédard and LaPointe 1984, Wheelwright and Rising 1993, Wheelwright and Schultz 1994, Wheelwright et al. 1994). Both sexes forage and use other resources such as shelter in similar ways, so resource competition (other than for mates) is not necessarily appreciably greater among individuals of the same sex compared to individuals of the opposite sex.

Field methods, data analysis, and simulations

Between 1987 and 1995, all adult birds in the study area were captured in mist-nets and marked with U.S. Fish and Wildlife Service aluminum bands and a unique, randomly assigned combination of plastic color bands ($N = 3459$ individuals). Throughout the breeding season, population censuses were conducted every other day on Kent Island to determine the reproductive status of individuals, including identity of their mates and location and fate of all nests ($N = 917$ nests). Every nestling that fledged within the study area was banded. Adults of both sexes could usually be detected within a few days of arriving on the breeding ground because of their vigorous territorial and mate-guarding behaviors, especially given that the vegetation on Kent Island remains sparse and low until early June.

The adult female incubating at a nest and later feeding nestlings and fledglings was assumed to be their mother. The adult male mate-guarding that female, defending the territory around her nest, and later feeding the same nestlings and fledglings was designated her mate and the father of the nestlings for the purpose of this study. DNA fingerprinting (Freeman-Gallant 1996a; J. Sevigny, D. Westneat, and N. T. Wheelwright, *unpublished data*) demonstrates that intraspecific brood parasitism is rare but that extra-pair fertilizations (EPFs) regularly occur, so our assignment of genetic fathers was probably inaccurate for as many as 25% of offspring. However, we believe that the imperfection of our genealogies does not pose a major problem for this study, for the following reasons. In terms of studying natal dispersal per se, establishing genetic parentage is irrelevant. As for inbreeding avoidance, our study does not enable us to detect cases where indi-viduals mated with relatives produced by EPFs in other nests. Nonetheless, the absence of matings between brood-mates is consistent with inbreeding avoidance, even if brood-mates are not always genetically related, because nestlings probably use the same criteria for determining degrees of relatedness that we did—presumably they identify the birds that brood, feed, and protect them as their parents, and identify those nestlings occupying the same nest and sharing parental care through the fledgling stage as their siblings (see Hepper 1991). There is no published evidence that birds rely on genetic markers to recognize close relatives. In any event, females associated with a particular nest were in almost all cases the genetic mothers of all male nestlings in that nest because intraspecific brood parasitism is so rare in this population. The absence of matings between such females and male offspring from their nests is therefore evidence of inbreeding avoidance, even if EPFs are common.

When nestlings were 7 d old, they were measured and banded ($N = 2316$ nestlings; see Wheelwright et al. 1992 for additional details on capturing, marking, and measuring birds). Altogether, we measured and banded 1615 nestlings that had hatched before 1993 and for which the identity of at least one parent was known (for 1515 nestlings, both parents were known). Taking advantage of genealogies of marked birds, we searched for cases of pairing between close relatives: between full siblings or parents and offspring (coefficient of kinship $\phi = 0.25$), or between half-siblings, uncles and nieces, aunts and nephews, or grandparents and grandoffspring ($\phi = 0.125$) (coefficient of kinship $= 1/2$ coefficient of relatedness, r; Greenwood 1987). Because of low annual adult survival rates and short life expectancies (Wheelwright and Rising 1993), chronologically more distant relatives, such as individuals and their great-grandparents ($\phi = 0.068$), are seldom alive at the same time; matings between them would be expected to be exceedingly rare even if there were no inbreeding avoidance. In any case, because our genealogies for distant relatives were less complete and the magnitude of inbreeding depression due to such matings likely to be slight (Gibbs and Grant 1989), we considered only cases of close inbreeding ($\phi \geq 0.125$).

The location of all nests was plotted on field maps (scale 1:1200; accuracy estimated to within 3 m), digitized, and used to calculate distances between nests. We defined natal dispersal distance as the distance between an individual's natal nest and its first adult nest. We also determined distance between an individual's first adult nest and the nest of each of its close relatives that were alive at the same time.

To evaluate the probability that observed dispersal patterns and pairings could have occurred by chance, we used Monte Carlo simulations (Manley 1991). Every 1-yr-old Savannah Sparrow in a particular year was randomly assigned a first adult nest from the pool of nests actually occupied by 1-yr-old birds that year. Our

model thus assumed that older birds were dominant and their nest sites were not available to 1-yr-olds. However, because there is no obvious spatial relationship between nest site and age (Wheelwright et al. 1993), this assumption did not affect our results. No nest was used more than once in the simulation. The distance between the 1-yr-old's randomly assigned first adult nest and its actual natal nest was then determined. Population means (±1 standard deviation) were calculated separately for each simulation of natal dispersal distances; we also calculated medians to reduce the disproportionate influence of the few extreme values (e.g., truncation effects; Payne 1990). Finally, we tested our observed median natal dispersal distances (calculated from actual field observations) against the expected distribution of medians of 1000 Monte Carlo simulations to determine exact probabilities. The same procedure was used to evaluate distances between nest locations of individuals and their relatives.

To test whether observed patterns of mating could have happened by chance, we performed additional Monte Carlo simulations, randomly pairing individuals with other adults of the opposite sex known to be alive at the same time. In designing null models, assumptions about mating status, time of arrival, and other factors are crucial (Pärt 1996). In the case of Savannah Sparrows on Kent Island, the population is female-biased and 20–40% of the males attract more than one mate, regardless of the timing of arrival (Wheelwright et al. 1992). Unlike the case of birds that depend on natural cavities or artificial nest boxes (Pärt 1996), sites for the ground nests of Savannah Sparrows are unlimited. Therefore, in our simulations we allowed males to mate with more than one female, once all males had at least one mate (all males are paired in this population; Wheelwright et al. 1992). The choice of mates in successive nesting attempts (first vs. second broods within a season, broods in different years) is not strictly independent, because pairs typically remained together as long as both members of the pair were still alive (although mate-switching between clutches during the same breeding season occurred in the case of ~5% of females; N. T. Wheelwright, unpublished data). Therefore, as a more conservative test we repeated simulations, selecting only the initial nesting attempt per pair (N = 548 unique pairs) and omitting subsequent nesting attempts involving the same pair. Our tests of inbreeding avoidance were also conservative because our sample did not include individuals that bred outside the study, even though they were known to have paired with birds that were unbanded and therefore unlikely to have been relatives.

RESULTS

Natal philopatry and dispersal

Of 1615 nestlings whose parentage was known, 180 (11.2%) returned to breed on Kent Island the following year. Further evidence of strong philopatry comes from the fact that none of the >7000 Savannah Sparrows banded at Kent Island since 1964 was recovered during the breeding season at a distance >3 km from where it was first banded (Dixon 1978, Wheelwright et al. 1994, Freeman-Gallant 1996b). Annual censuses of nearby islands showed that dispersal between islands was uncommon. On Sheep and Hay Islands (both of which are within several hundred meters from Kent Island and accessible by foot at low tide), birds banded as nestlings on Kent Island never accounted for >2% of breeding birds in any given year; on the three Green Islands (3–7 km away), recruits from Kent Island accounted for 0–1% of breeding birds.

During the first two years of the study, the proportion of new recruits that had first been banded as nestlings or juveniles was relatively small but then increased once the study area was expanded and more birds were marked. Between 1990 and 1995, an average of 73% of all newly breeding males and 71% of newly breeding females within the study area were known to have been 1-yr-olds raised within or adjacent to the study area the previous year (Table 1). The other new recruits were believed to be yearlings as well (based on wing length and flight feather shape, as well as the fact that older birds do not tend to change territories once they have begun to breed (Wheelwright et al. 1994; N. T. Wheelwright and R. A. Mauck, unpublished data). These new recruits could have originated from the Three Islands but outside the study area, given the fact that our study area only covered about half of the available breeding habitat in the Three Islands.

Although strong philopatry was evident at the scale of the Three Islands archipelago, within Kent Island itself yearlings appeared to disperse random distances from their natal nest and, in some cases, to avoid their natal area (Fig. 1). The median natal dispersal distance for yearlings was 228.5 m (N = 143 birds; Table 2) and did not differ between years of the study (ANOVA: P = 0.32). Median natal dispersal distances were <228.5 m in 82% of the Monte Carlo simulations that paired actual natal nests with randomly assigned yearling nests of the same year. As a second comparison, we randomly paired nests using all nests from 1988–1993 (N = 731 nests) and calculated distances between members of each pair, repeating the simulation 100 times. For each simulation, we calculated median and mean distances between nests for the population as a whole. The averages of those simulation statistics were 186.3 m for median and 235.6 m for mean natal dispersal distance. Mean distances between two random nests were less than those observed between actual natal and first adult nests in 75% of the simulations. Note, however, that our random nests were restricted to nests from within our 7.6-ha study area. Had we used random points from within suitable nesting habitat anywhere on the Three Islands or just Kent Island, natal dispersal would appear highly philopatric even at the

TABLE 1. Histories of the population of breeding Savannah Sparrows in the Kent Island study area between 1988 and 1995.

Year	Total no. breeding birds		No. new recruits		Minimum no. recruits known to be local		Minimum frequency of recruits known to be local	
	Males	Females	Males	Females	Males	Females	Males	Females
1988	48	69	29	40	9	7	0.31	0.18
1989	53	77	30	35	13	12	0.43	0.34
1990	57	73	35	31	22	19	0.63	0.61
1991	62	75	31	35	25	24	0.81	0.69
1992	43	58	22	29	16	18	0.73	0.62
1993	35	54	17	27	11	19	0.65	0.70
1994	39	51	16	25	13	23	0.81	0.92
1995	44	54	21	30	17	23	0.81	0.77
1990–1995	280	365	142	177	104	126	0.73	0.71

Notes: Estimates for number and frequency of new local recruits (recruits known to have been raised in the area, i.e., first banded as nestlings or juveniles) are minimum because it is likely that the majority of the unbanded new recruits actually were raised within the Three Islands archipelago but outside the study area, as indicated by low frequencies before 1990 when our marked population was first being established. Therefore, data are analyzed separately for 1990–1995.

scale of Kent Island. As a comparison to natal dispersal, breeding dispersal by adults was negligible once they established a territory (median distance between nests within breeding seasons: 16.9 m, $N = 227$ females; between breeding seasons: 31.8 m, $N = 173$ females

FIG. 1. Frequency distribution of natal dispersal distances for male and female Savannah Sparrows.

[N. T. Wheelwright and R. A. Mauck, *unpublished data*]).

Natal dispersal distances can also be quantified in units of territory diameters. The average diameter of male Savannah Sparrow territories on Kent Island was 38 m (N. T. Wheelwright and R. Rynning, *unpublished data*). Therefore, a median natal dispersal distance of 228.5 m represents the traversal of about six territories. Shields (1982) classified a species as philopatric if median natal dispersal distance was <10 territory diameters. However, if instead one were to chose as the null hypothesis that there are advantages to extreme philopatry, an assumption strongly suggested by the fact that adults scarcely move between breeding attempts (see also Hinde 1956, Pärt 1996; N. T. Wheelwright and R. R. A. Mauck, *unpublished data*), young birds would be expected to settle as near as possible to their natal nest. In this case, one could conclude from the observed natal dispersal distances that Savannah Sparrows avoided selecting a breeding territory too close to their natal site. Assuming for simplicity that territories are roughly similar in size and hexagonal in shape and occupy all available habitat, a given territory would be surrounded by a ring of six adjacent territories and beyond that by another ring with 12 territories, and so forth. Given that 55% of adult males and females fail to return to reclaim their territory each year (Wheelwright et al. 1994), at least three of the territories immediately adjacent to a yearling's natal site would be expected to be uncontested by the previous occupant of the same sex. Six from the next ring, <80 m away from the yearling's natal nest, should also be vacant. The probability that a yearling would be have to go a distance of more than six territory diameters from its natal nest site to find an unoccupied territory would be exceedingly small, given the null hypothesis of preferring to establish a territory as close as possible to one's natal territory (see Waser 1985, Payne 1991a).

Sex differences in natal dispersal

Yearling males and females returned in roughly equal numbers. There were no differences between sexes in
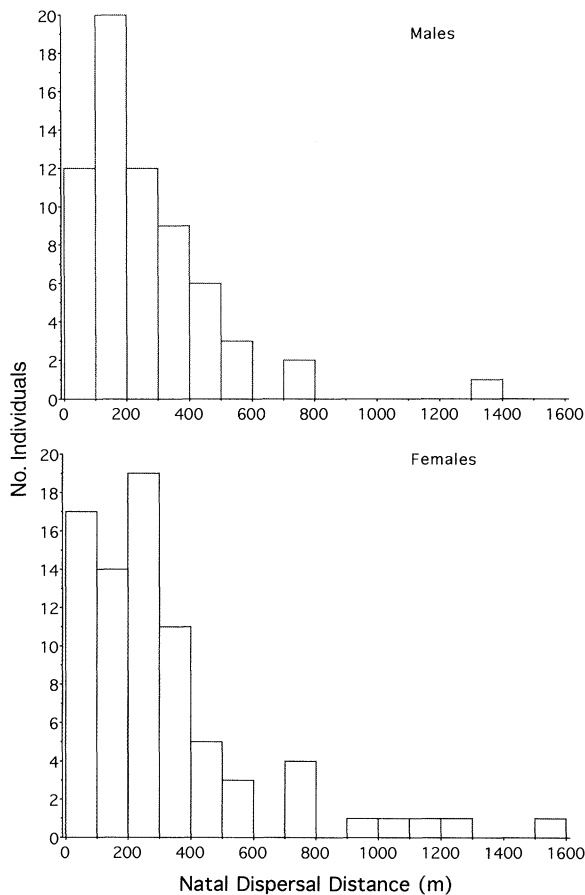
TABLE 2. Natal dispersal distance (distance between natal nest and first adult nest) for the study population of Savannah Sparrows. All birds were uniquely banded as nestlings on Kent Island and had returned to the island 1 yr later to breed.

Sex	Natal dispersal distance (m)†					
	Median	Mean	1 SD	Minimum	Maximum	N
Males	202.8	261.8	215.6	6	1381	65
Females	248.4	309.0	290.8	7	1540	78
Both sexes combined	228.5	287.5	259.6	6	1540	143

† Differences in dispersal distances between sexes were not significant (Mann-Whitney U test: $P = 0.62$).

the probability of dispersal out of the area, given the 1:1 nestling and juvenile sex ratios in this population (Wheelwright et al. 1994). On a smaller scale, there was also no significant difference in natal dispersal distance between males and females that returned to the Three Islands. Males dispersed a median of 202.8 m, compared to 248.4 m for females (Table 2). Females were more likely than males to remain in their natal field (Table 3), which suggests (given the similarity in median dispersal distances between the sexes) that if a female did change from the North to the South field (or vice versa), she tended to move farther than males that changed fields (Fig. 1).

Influence of population density, hatching date, and fledging mass on natal dispersal

If natal dispersal were influenced by competition for limited territories, one might expect a difference in dispersal distance between years of low and high population densities, between birds that had fledged early vs. late, and between heavy and light fledglings (e.g., Rabenold et al. 1991). However, we found no relationship between population density and median natal dispersal distance for birds that had hatched that year (Spearman rank test, $P > 0.40$) or the previous one, even though population sizes fluctuated by a factor of two to three between years (Wheelwright and Rising 1993). There was also no relationship between an individual's natal dispersal distance and the date it

TABLE 3. Natal dispersal between fields for (a) male and (b) female Savannah Sparrows on Kent Island. Numbers refer to individual 1-yr-old males and females; thus, 19 males changed fields between their natal and first adult nest.

Location of adult nest	Location of natal nest	
	South field	North field
a) Males		
South field	43	7
North field	12	3
b) Females		
South field	54	11
North field	5	8

Notes: Males showed no tendency to return preferentially to the field where they had hatched (χ^2 test: $P = 0.57$); females, in contrast, showed relative philopatry with respect to natal field ($P = 0.006$).

hatched or its mass at 7 d of age (Spearman rank test, $P > 0.10$).

Behavioral observations of independent juvenile Savannah Sparrows suggested that territory selection and even defense may have begun to take place within 1 mo after hatching. Vigorous chases similar to those between adult males occurred between juvenile males, which by 28 d of age were already noticeably longer-winged and heavier than adult and juvenile females (Wheelwright et al. 1994). Adult males frequently defended their territories against juveniles in July and early August. In addition, juveniles were often repeatedly captured in mist nets at the same site over a period of several weeks. As a preliminary test of the hypothesis that juveniles begin to select future territories at an early age, we compared an individual's natal dispersal distance to the distance between its first adult nest and the place where it was last observed as a juvenile. Individuals located their first adult nest closer to the site of their last sighting as a juvenile the previous year than to their natal nest (paired t test: males, $P = 0.015$; females, $P = 0.018$).

Heritability of natal dispersal

In the case of 55 yearlings for whom natal dispersal distances were known, we also knew natal dispersal distance of at least one of their parents. For 25 yearlings, only maternal natal dispersal distance was known; for 20 yearlings, only paternal natal dispersal distance was known. For 10 yearlings, both maternal and paternal natal dispersal distance were known; in the latter case we averaged the two distances to get mid-parent values. A linear regression of offspring vs. parent natal dispersal distance had a positive slope but was not significant, suggesting low heritability of the trait (slope = 0.36, $P = 0.32$, $N = 55$ parent-offspring pairs) (see van Noordwijk 1984). We repeated the analysis using each parent only once, regressing individuals' natal dispersal distances against those of their mothers or fathers, but there was no significant relationship in either case (maternal regression: slope = 0.38, $P = 0.41$, $N = 35$ mother-offspring pairs, Fig. 2a; paternal regression: slope = -0.08, $P = 0.91$, $N = 30$ father-offspring pairs, Fig. 2b). Because of the rarity of intraspecific brood parasitism (see Methods:
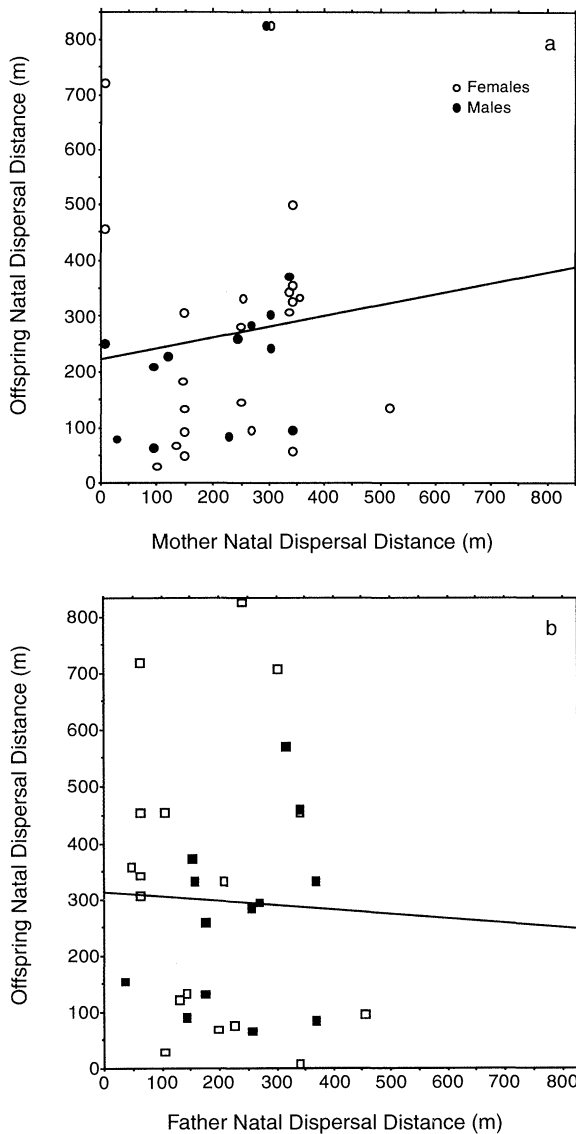
FIG. 2. Regression of offspring vs. maternal (a) or paternal (b) natal dispersal distances for male and female Savannah Sparrows ($N = 35$ and 30 birds, respectively). Open symbols = female offspring; closed symbols = male offspring. The two points at the top of Fig. 2a represent a male that dispersed 1381 m and a female that dispersed 1540 m; the point at the top of Fig. 2b represents a female that dispersed 1247 m.

Field methods, data analysis, and simulation), maternal regressions avoided the potential problem of extra-pair paternity. Low heritability was also implied by the lack of a correlation between natal dispersal distances of siblings from the same year (Spearman rank test, $P >$ 0.40, $N = 18$ sibling pairs).

Natal dispersal in relation to the location of relatives

If natal dispersal functions chiefly to reduce the likelihood of mating with parents (Greenwood 1980, Pusey

TABLE 4. Natal dispersal between fields for Savannah Sparrows on Kent Island, relative to movements of parent.

Location of first adult nest	Status of opposite-sex parent		Status of same-sex parent	
	Returned	Did not return	Returned	Did not return
Changed sites	23	11	19	16
Did not change sites	44	61	52	54

Notes: Birds tended to change sites (fields) when their parent of the opposite sex returned and to show relative philopatry when their opposite-sex parent did not return (χ^2 test: $P = 0.01$). Movements appeared to be independent of the return of their parent of the same sex ($P = 0.73$).

1987), males whose mothers returned from migration might be expected to disperse farther than males whose mothers had failed to return. The same should be true for females and their fathers. However, there should not necessarily be a relationship between dispersal and return of parents of the same sex (Ralls et al. 1986, Pusey 1987, Ralls et al. 1988). Alternatively, if natal dispersal is driven by intrasexual competition for territories, food, or mates (local resource competition; Gowaty 1993), the opposite prediction should hold true: birds should disperse farther when their same-sex parents returned than when their opposite-sex parents returned (Waser 1985). In our study, yearlings were more than twice as likely to nest in a field other than their natal field if their opposite-sex parent returned than if it did not return, but the probability of changing fields was apparently unaffected by whether or not their same-sex parent returned (Table 4). The presence of a parent of either sex did not appear to affect natal dispersal distance per se, however (Table 5; Mann-Whitney U test, $P > 0.28$ for all comparisons).

Birds nested significantly farther from siblings raised the same year than expected by chance. Distances between a yearling's first nest and the nest of its nearest sibling of either sex were as follows: same year, same nest (327.9 m [median] and 399.8 ± 378.4 m [mean ± 1 SD], 15 sibling pairs); same year, different nest (338.5 m and 332.4 ± 261.0 m, 21 sibling pairs); different year, different nest 123.9 m and 281.2 ± 261.2 m, 18 sibling pairs). Only 8 of 1000 Monte Carlo simulations produced median distances between all same-year siblings that exceeded observed values (observed median = 333 m, expected median = 190 m; $P <$ 0.009, $N = 36$ pairs of returning siblings). Unaccountably, siblings unfamiliar with each other (those raised in different years) actually nested closer to each other than expected by chance ($P = 0.014$, $N = 18$ sibling pairs). The mean distance between the first adult nests of siblings of the same sex was less than that of siblings of the opposite sex (274.3 ± 147.6 m [$N = 15$ same-sex sibling pairs] vs. 517.6 ± 445.3 m [$N = 13$ opposite-sex sibling pairs]; one-tailed t test, $P < 0.03$), although differences between medians (266.7 m vs. 460.7 m) were not significant due to small sample sizes

TABLE 5. Natal dispersal distance for Savannah Sparrows on Kent Island as a function of whether or not their father or mother returned that year.

| | | Natal dispersal distance (m) | | | |
		Median	Mean	1 SD	N
Sex	Status of parents				
Males	Father returned	214.8	232.9	147.3	34
	Father did not return	183.7	283.5	269.8	30
	Mother returned	199.1	252.0	189.6	31
	Mother did not return	202.8	264.5	242.0	31
Females	Father returned	275.7	340.0	322.6	36
	Father did not return	214.8	286.8	263.1	41
	Mother returned	250.3	260.9	210.3	37
	Mother did not return	238.3	354.6	348.9	40

Notes: Sample sizes vary because the identity of father or mother was unknown for four birds. The presence of a parent of either sex did not appear to affect natal dispersal distance per se in male or female birds (Mann-Whitney U test: $P >$ 0.19; however, see Table 4).

(Mann-Whitney U test, $U = 0.09$). There is no evidence that birds from earlier broods interact with their younger siblings as helpers-at-the-nest or in any other way (Wheelwright and Rising 1993; see Gowaty 1993, Komdeur 1996).

Inbreeding avoidance

There were numerous opportunities for individuals to breed with close relatives. For example, in 1994, a year in which both parents were known in the case of 57 of the 114 adults in the breeding population, 4 males and 11 females had parents of the opposite sex still alive; there were also 12 possible pairings between full siblings and 9 more between half-siblings. But in 96 breeding attempts that year, and 917 observed from 1987 to 1995, we found no cases of pairing between full siblings, parents and offspring, half-siblings, uncles and nieces, aunts and nephews, or grandparents and grandoffspring, even though ~20% of adults had one or more close relatives breeding in the population at the same time. In 1996, when there were 62 nest attempts, a male was observed mate-guarding his sister, but her nest failed at the egg stage and both birds disappeared; in 1997, there were no records of pairing with relatives in 94 nest attempts. In an independent sample of >600 nest attempts, C. R. Freeman-Gallant (*unpublished data*) found no cases of pairings between close relatives, and none were reported by Dixon (1978) in her 4-yr study of the same population. Note that the results of the present study refer only to social pairing, which leaves open the possibility of extra-pair fertilizations between relatives. However, in a separate study of the Kent Island Savannah Sparrow population using DNA fingerprinting, Freeman-Gallant (1996*a*) found no examples of EPFs involving relatives.

To assess whether the absence of pairing between relatives was due to chance rather than active inbreed-

ing avoidance, we simulated random pairing in each year using all nesting attempts observed through 1995 ($N = 917$ nests). Only 9 of 1000 simulations produced zero cases of close inbreeding ($\phi > 0.125$) as observed in this study ($P < 0.01$). Based on the simulations, the probability of observing fewer than two cases of close inbreeding if pairing were random was 0.05. As a more conservative test, we included only a single nesting attempt involving the same pair. Based on 1000 simulations, we found that the probability of observing zero cases of close inbreeding was 0.06. If Savannah Sparrows chose mates without regard to their relatedness, the level of close inbreeding expected would have been 2.40 ± 1.24 cases [mean ± 1 SD, range = 0–8 cases].

Natal philopatry and lifetime reproductive success

A common assumption of ecological models of philopatry is that philopatry is adaptive because of advantages of familiarity with a particular location (Hinde 1956). Accordingly, one might expect reproductive success to be higher in individuals that returned to breed near their natal site than in birds that dispersed greater distances. We examined the relationship between natal dispersal and total number of nests, eggs, fledglings, and recruits produced over their lifetimes by individuals that bred in the study area. Birds that were known to have been raised in the study area (banded on site as nestlings) we considered most highly philopatric. Birds raised near but not in the study area (banded as juveniles) were considered intermediate in philopatry. Birds not raised in the study area and possibly not even nearby (banded as yearlings) were considered least philopatric. Age at first breeding was the same (1 yr) for all three groups, based on banding records, wing length, and feather shape. Males raised within the study area recruited significantly more offspring than those raised outside the study area ($P < 0.02$). Trends were in the same direction, although not statistically significant, for other measures of reproductive success (Table 6). Our measure of lifetime reproductive success did not take into account the possibility that individuals may have achieved or been the victim of EPFs (e.g., Freeman-Gallant 1996*a*). However, unless for some reason there were a strong relationship between philopatry and the probability of EPFs, these results would not be affected by including extra-pair paternity in our measure of lifetime reproductive success. For females, our measure of lifetime reproductive success was probably quite accurate, given the rarity of intraspecific brood parasitism. We found no apparent fitness advantage of natal philopatry for females (Table 6).

DISCUSSION

Natal dispersal in Savannah Sparrows on Kent Island can be viewed in different ways, depending upon the scale of analysis. On the one hand, yearlings showed

TABLE 6. Lifetime reproductive success (excluding possible extra-pair paternity) in Savannah Sparrows as a function of natal philopatry, determined by initial banding age.

Lifetime reproduction	Sex	Age at banding			P
		Nestling	Juvenile	Adult	
Total nests	Males	3.5 (3.3)	3.2 (1.9)	2.9 (2.3)	0.43
	Females	2.5 (1.8)	2.9 (2.0)	2.9 (2.2)	0.39
Total eggs	Males	14.8 (14.5)	13.6 (8.0)	11.9 (10.2)	0.34
	Females	10.4 (8.0)	12.6 (8.8)	11.1 (9.5)	0.39
Total fledglings	Males	9.6 (8.5)	9.2 (5.7)	7.4 (6.6)	0.20
	Females	6.7 (5.2)	7.7 (5.5)	6.8 (6.5)	0.64
Total recruits	Males	1.1 (1.5)	0.8 (0.9)	0.5 (0.8)	0.02
	Females	0.6 (0.8)	0.7 (0.9)	0.6 (1.2)	0.87

Notes: Birds banded as nestlings (N = 86 males, 125 females) located their first adult nests in one of the two same fields as their natal nests and therefore were presumably most familiar with the area. The natal nests of birds banded as juveniles (N = 33 males, 33 females) had to have been from outside the study area but nearby, as juveniles were banded within the study area shortly after independence. The natal nests of birds first banded as yearlings (N = 61 males, 63 females) also had to have been from outside the study area; the fact that they were not observed in the study area until the age of 1 yr suggests that they were least familiar with the area. Data are presented as means ± 1 SD and include birds banded 1988–1994 (except for "total recruits" [the number of offspring that were later captured as breeding adults], which includes only birds breeding in 1988–1993 [banded as nestlings, N = 74 males, 109 females; juveniles, N = 32 males, 26 females; adults, N = 58 males, 61 females]). P values refer to results of one-way ANOVA testing the effect of banding age within sexes.

excellent homing abilities and impressive philopatry, most birds returning from distant wintering grounds to breed within several hundred meters of their natal nest (see Able and Able 1996). More than 11% of 7-d-old nestlings returned to breed on the island, and >70% of all new recruits into the breeding population were known to have been raised nearby. Among passerines 11% is considered to be a high rate of survival for the first year of life beginning at 7 d of age (see references in Newton 1989). If we were to expand our study site and band all nestlings on Kent Island and the islands immediately surrounding it, the fraction of locally raised recruits would probably be higher. For example, during the last two years of our study, yearling recapture frequencies increased, at least for females, apparently because the area searched for Savannah Sparrow nests was expanded when an independent study of Savannah Sparrows was started (Freeman-Gallant 1996a, b). In combination, these observations suggest that the majority of surviving Savannah Sparrows that hatch on Kent Island subsequently return to breed in the Three Islands archipelago or on nearby islands. In mainland populations recapture rates of 1-yr-old Savannah Sparrows banded as nestlings are far lower (Ross 1980, Bédard and LaPointe 1984), which suggests that strong philopatry may be more common in island populations (Eliason 1986, Weatherhead and Forbes 1994). Genetic differentiation and even subspeciation of Savannah Sparrow populations in insular habitats illustrate the potential evolutionary consequences of philopatry (Stobo and McLaren 1975, Zink et al. 1991, Wheelwright and Rising 1993, Freeman-Gallant 1996b; see also Chepko-Sade and Shields 1987). Even at the scale of Kent Island, young Savannah Sparrows were highly

philopatric, settling disproportionately within the study area vs. outside of it.

Within the study area, however, Savannah Sparrows distanced themselves several hundred meters from the immediate area of their natal site. Because >50% of adults fail to return each year and Savannah Sparrow territories on Kent Island are <40 m in diameter, yearlings should not have had to disperse so far if there were advantages to choosing a territory as close as possible to their natal site. There was no difference in natal dispersal patterns between males and females, as evidenced by equivalent return rates to Kent Island and natal dispersal distances within the study area (see also Ross and McLaren 1981). In this respect, natal dispersal in Savannah Sparrows on Kent Island differs from that of the majority of passerine birds studied thus far, in which females tend to disperse farther than males (Greenwood 1980, Greenwood and Harvey 1982, Gowaty 1993). In the White-crowned Sparrow (*Zonotrichia leucophrys*), one of the few sparrow species in which dispersal has been thoroughly investigated, there is a nonsignificant tendency for females to disperse greater distances than males (Morton et al. 1991, Morton 1992). The usual explanation for female-biased dispersal in birds (in contrast to male-biased dispersal in mammals) is that female birds searching for prospective mates benefit by moving away from their natal site and by assessing a variety of territories and males, whereas male birds benefit by claiming a familiar territory (i.e., one near their natal site) (Greenwood and Harvey 1982, Johnson and Gaines 1990). The relatively small size of Kent Island and the fact that Savannah Sparrows there spend much of their time foraging off territory in undefended common areas such as the in-

tertidal zone (Wheelwright and Rising 1993) may allow females to select among available mates without having to disperse greater distances than males. Interestingly, the 1:1 secondary sex ratio in the population (Wheelwright et al. 1994) and the lack of a sex bias in natal dispersal are consistent with the predictions of Gowaty's (1993) model of differential dispersal due to local resource competition.

Many of our results parallel those of Payne (1991a, b), whose long-term study of Indigo Buntings (*Passerina cyanea*) at a mainland site is one of the few to quantify dispersal distances against the background of information on relatedness between birds breeding under relatively natural conditions. Indigo Buntings, migratory songbirds related to Savannah Sparrows (Sibley and Ahlquist [1990] place both species in the same subfamily, Emberizinae) with 15% of males being polygynous (Payne 1991b), showed no difference in natal dispersal distance between the sexes, and males and females were equally likely to return to breed in their natal area (Payne 1991a), just as in Savannah Sparrows. Like Payne (1991a), we found no evidence to support the idea that young birds disperse because they are slower to return to the breeding area or are subordinate to older birds, even at high population densities (social competition hypothesis). In fact, many yearling Savannah Sparrows arrived on the breeding grounds as early as older birds but apparently bypassed opportunities to occupy uncontested territories near their natal nest. Moreover, the social competition hypothesis predicts longer natal dispersal distances for birds in poorer condition or under crowded conditions, but we found that natal dispersal distances were unrelated to a bird's condition at fledging or at the time of territory establishment, to the date it fledged (often used as a measure of condition; C. R. Freeman-Gallant and N. T. Wheelwright, *unpublished manuscript*), or to population density (see also Potti and Montalvo 1991).

In other respects, our results were quite different from Payne's (1991a) study. In Indigo Buntings, natal dispersal was independent of whether a bird's parents or its siblings of either sex returned. Moreover, buntings apparently chose mates without regard to their degree of relatedness. The behavior of Indigo Buntings thus seemed most consistent with a neutral model rather than the social competition or inbreeding avoidance models (Payne 1991a).

The neutral model is insufficient to explain certain aspects of natal dispersal and inbreeding avoidance in Savannah Sparrows on Kent Island. Random movements obviously could not account for strong philopatry at the scale of the islands surrounding Grand Manan Island, the scale of Kent Island, or the scale of the study area. Nor did the neutral model apply to adult Savannah Sparrows, given that on average birds moved less than half a territory diameter between nesting attempts. Presumably, there are benefits for extreme philopatry, even at the scale of the territory. Those same benefits may apply to yearlings making decisions about dispersal from their natal site, but yearlings, which are far less philopatric than adults, may face constraints that are different from those of older birds, such as lower social status or higher risks of close inbreeding. Alternatively, extreme philopatry may be less of an advantage for yearlings than it is for birds that have previously chosen territories and invested in learning where to forage, display for mates, or hide from predators.

More interestingly, the neutral model was contradicted in this study by the significantly increased likelihood of changing breeding sites when opposite-sex parents were present. Lambin's (1994) work on Townsend's voles (*Microtus townsendii*) is one of the few other studies to show that animals disperse farther when their opposite-sex parents are alive. Other evidence that dispersal and pairing in Savannah Sparrows were nonrandom include the greater-than-expected distances between the nests of opposite-sex siblings, the greater-than-expected distances between the nests of familiar siblings, and the absence of a single incident of close inbreeding out of 1073 breeding attempts. The rarity of inbreeding in the Kent Island Savannah Sparrow population would have been even more significant if we were to have included birds of known parentage that settled outside the study area and were known to have mated with nonrelatives.

It is important to note that even individuals that dispersed several hundred meters from their natal site tended to be within sight and hearing of at least one relative, and that about half of the adult birds that survived from year to year returned to find that their mate from the previous year had failed to return. Yearlings were not relegated to peripheral areas; their territories were interspersed among those of older birds. Consequently, opportunities for pairing with relatives were common. In many natural populations (Ralls et al. 1986, Gibbs and Grant 1989), random dispersal and demographic factors (high adult mortality, in particular) may be sufficient to account for low levels of inbreeding, but our study seems to implicate active avoidance of mating with kin. In the absence of a single known event of pairing with a close kin, we could not estimate inbreeding depression, but presumably breeding with relatives reduces fitness in Savannah Sparrows as it does in other species (Pusey and Wolf 1996, although see Shields 1982).

A prerequisite for active inbreeding avoidance (vs. passive inbreeding avoidance by dispersing away from the natal area) is the ability to recognize relatives. Such an ability might develop in Savannah Sparrows over the course of the 10-d nestling period and the 2–3 wk during which fledglings are fed by their parents on their natal territory, and become reinforced during the following 1–2 mo that juveniles spend near their natal territory. Male Savannah Sparrows often sing immediately after feeding their fledglings (N. T. Wheel-

wright, M. Swett, P. Kane, and D. Kroodsma, *unpublished data*), which would provide females a mechanism to learn their fathers' song. If song characteristics are inherited (genetically or culturally), females might be able to recognize and avoid mating with siblings that had hatched in different years. Based on a preliminary analysis, however, the correlation between fathers and sons in several song characteristics appears to be low, although males sing the same song throughout their lives (N. T. Wheelwright, M. Swett, P. Kane, and D. Kroodsma, *unpublished data*). The precise criteria that females use in choosing among males are still not understood, but philopatry itself appears to play a large role in determining which male a female ends up pairing with (Eliason 1986; see also Freeman-Gallant 1996a, b).

Observations of chases and fights among juveniles, as well as the early expression of sexual dimorphism (Wheelwright et al. 1994) and the proximity of the location where a juvenile was last seen and where it ultimately settled as a breeding bird the following year, suggest that young males may be staking out the location of future territories during this period. Alternatively, an indirect mechanism to explain inbreeding avoidance could be that parents that are unlikely to survive until the following year (e.g., due to poor nutritional condition) may be less likely to drive juveniles from the natal area during the period when juveniles are evaluating future territories (R. Payne, *personal communication*).

Our behavioral observations provide a mechanism to explain the results of a concurrent study of Savannah Sparrows on Kent Island, several neighboring islands, and the Canadian mainland (Freeman-Gallant 1996b). Island Savannah Sparrow populations prove to be phenotypically and genetically distinct from mainland populations and show concordant patterns of morphological and genetic variation, as might be expected with strong regional natal philopatry. Nonetheless, island populations prove to be no more inbred than mainland populations based on band-sharing frequencies. Freeman-Gallant's (1996b) results are consistent with the hypothesis that birds that exhibit such strong philopatry have also evolved mechanisms to avoid inbreeding (Ralls et al. 1986, Hepper 1991).

If the Savannah Sparrows on Kent Island are representative of other isolated populations of passerine birds with respect to natal dispersal, our study may give insights about species that are more difficult to study. Information about dispersal and inbreeding is lacking for most birds. With the exception of Gibbs and Grant (1988) and Payne (1991a), the few studies that exist have focused on species with unusual social systems (Koenig and Pitelka 1979, Russell and Rowley 1993, Lessells et al. 1994), species that are colonial and/or cavity-nesting and affected by extreme parasite loads or limited availability of nest sites (DuPlessis 1992, Brown and Brown 1992), species with abnor-

mally high population densities due to the provision of artificial nest sites (van Noordwijk and Scharloo 1981, van Tienderen and van Noordwijk 1988, Drilling and Thompson 1988, Nilsson 1989, Lundberg and Alatalo 1992, Pärt 1996), or species occupying highly disturbed or evolutionarily novel habitats (Fleischer et al. 1984). We know very little about populations from fragmented habitats, although we do know that island populations of a variety of species are highly philopatric (Stobo and McLaren 1975, Eliason 1986, Arcese 1989, Nagata 1993, Pärt 1996).

Of particular concern are certain sparrows and other grassland birds that have recently been restricted to island-like habitats (Vickery 1995). To the extent that their demography and behavior are similar to those of Savannah Sparrows on Kent Island, the effective population sizes (N_e) of many bird populations could be appreciably lower than currently believed (Grant and Grant 1992). N_e in Kent Island Savannah Sparrows, for example, is reduced not only because of strong breeding area philopatry, as shown in this study, but also because of a skewed (female-biased) population sex ratio, a polygynous mating system, and large variation in reproductive success between individuals (Wright 1969, Wheelwright et al. 1992, Wheelwright et al. 1994). For example, Freeman-Gallant (1996b) has used multilocus DNA fingerprinting data to calculate N_e of only 37 for Kent Island and surrounding islands. Populations with small N_e are particularly prone to local extinction through demographic stochasticity, loss of genetic variability, and increased homozygosity (Soulé 1987). The population density of Savannah Sparrows on Kent Island appears to have remained relatively stable over three decades (Dixon 1978, Wheelwright et al. 1997). If the population had earlier passed through a "bottleneck" that eliminated most deleterious recessive alleles, selection for inbreeding avoidance should be weak (R. Payne, *personal communication*). However, if inbreeding depression is a hazard (e.g., Keller et al. 1994), differential dispersal away from opposite-sex relatives and kin recognition could reduce that risk (Pusey and Wolf 1996). What we do not yet know is whether incest avoidance is primarily a feature of populations with an evolutionary history of relative isolation (although see van Noordwijk and Scharloo 1981, van Tienderen and van Noordwijk 1988, Gibbs and Grant 1989), or whether small mainland populations, newly isolated by habitat fragmentation, can forestall the loss of genetic variability by avoiding mating with relatives.

In conclusion, ecological constraints such as territoriality can explain to some extent why birds disperse from the immediate vicinity of their natal site, and ecogenetic models such as local adaptation can explain population-level philopatry. Those models fall short in accounting for cases such as the present study, which found that dispersal was nonrandom with respect to the presence of opposite-sex parents and siblings. A com-

bination of ecological, neutral, and genetic models is necessary to explain the natal dispersal of birds at different scales (Dobson and Jones 1985, Greenwood 1987, Payne 1991a, Weatherhead and Forbes 1994). The failure to observe a single incident of close inbreeding over a 9-yr period in the Kent Island Savannah Sparrow population strongly suggests that some birds may be more adept at recognizing their relatives than previously believed. Although natal dispersal may partly explain incest avoidance, it remains to be determined whether birds are able to recognize relatives and, if so, the cues they might use.

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