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PHILOPATRY, SITE FIDELITY, DISPERSAL, AND SURVIVAL OF SPOTTED SANDPIPERS

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ABSTRACT.—We assessed philopatry, site fidelity, dispersal, and survival during the last eight years of an 18-year study of Spotted Sandpipers (*Actitis macularia*). The first 10 years of the study were of an island population. For the last eight years of the study, we expanded the study area to include a mainland subpopulation, 7 km from the primary island population. We also assessed between-site movement. Yearlings made up 7 to 36% of breeders recruited annually, and yearling return was negatively associated with number of fledglings the previous year. We found male-biased philopatry when all yearling returns were included, but no significant sex bias of birds that returned and bred. Return rate for males that successfully bred was 63%; for males that were not successful, 29% returned. For females, the return rate of successful breeders was 63% and for unsuccessful breeders 26%. Females changed territories between clutches more often after nest failure, and birds moved more often to the island than to the mainland. We used hatch and fledging success, philopatry, and site fidelity rates to construct male and female life tables, separating successful and unsuccessful breeders. From U.S. Fish and Wildlife Service recovery records, dispersal distances ranged from 3.6 to 147 km. We conclude that expanding our study site gave a more accurate picture of philopatry, dispersal, and site fidelity. Birds apparently treated all study areas as a single site, with the island preferred to the mainland for breeding. *Received 8 May 1992, accepted 28 January 1993.*

LOCAL POPULATION dynamics are a result of synergistic interactions among birth rate, survival, philopatry, site fidelity, dispersal, emigration, and immigration (Lack 1954). Philopatry is returning to your birth or hatch site, and dispersal is unidirectional movement of an individual from one geographic location to another (e.g. Greenwood and Harvey 1982, Rockwell and Barrowclough 1987). In practice, processes determining population dynamics are not always distinguishable, particularly for mobile species, such as birds. For example, surveying for birds away from the banding site is required to differentiate dispersal from mortality (Pienkowski and Evans 1985). As an animal moves away from its natal territory, the area that must be searched to determine whether it dispersed or died increases parabolically, thereby reducing the likelihood of detection (Barrowclough 1978). In addition, field restrictions reduce the practicality of trying to find long-distance dispersers (Moore and Dolbeer 1989).

Dispersal data are notoriously difficult to obtain, and details of short-distance dispersal, within a range that could be considered philopatric (e.g. Shields 1983), have not been addressed for most migratory species. Although natal and breeding dispersal data exist for some shorebirds (e.g. Dunlin [*Calidris alpina;* Soikkeli 1967, 1970a, b], Piping Plovers [*Charadrius melodus;* Haig and Oring 1988a, b, c]), few detailed studies have examined short-distance dispersal patterns or documented long-distance dispersal records. Our goals were to assess dispersal, philopatry, breeding-site fidelity, and survival in Spotted Sandpipers (*Actitis macularia*) using data from an 18-year study. We were particularly interested in assessing local movements among neighborhoods within our study area and addressing whether short-distance natal movement in this species should be considered philopatry or dispersal. Our objectives were to (1) quantify philopatry, (2) look for density-dependent and sex-biased return, (3) quantify breeding-site fidelity, (4) use philopatry and fidelity rates to estimate age-specific survival, (5) assess movement among distinct neighborhoods within our study area, and (6) quantify records of dispersal for this species at other sites.

SHOREBIRD PHILOPATRY AND DISPERSAL

Shorebirds are a well-studied group of migratory species that have a wide variety of mating systems and dispersal patterns (Oring and Lank 1984). Reported philopatry in shorebirds typically ranges from 0 to 10% (Soikkeli 1967, 1970a, b, Schamel and Tracy 1977, Oring and

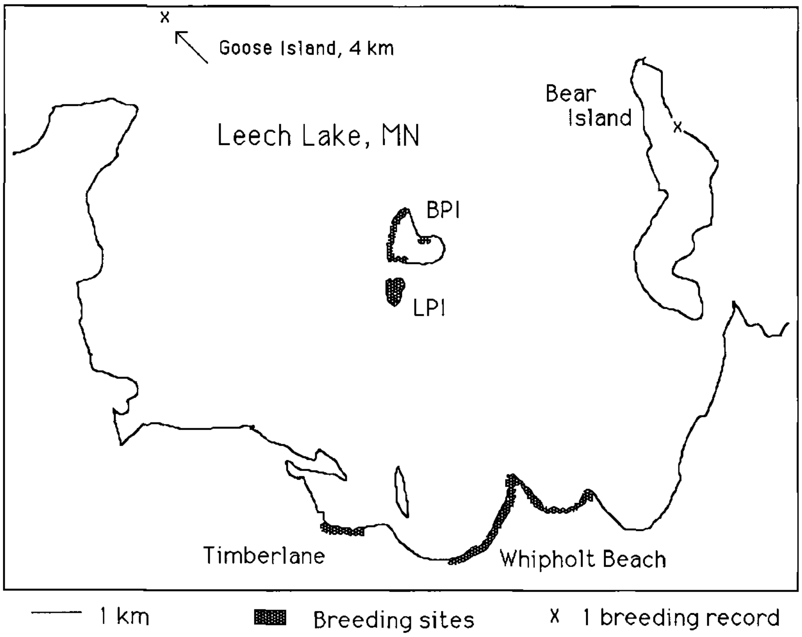

Fig. 1. Study area for 1983-1991. LPI is Little Pelican Island, and BPI is Pelican Island. LPI, BPI, Whipholt Beach, and Timberlane are considered neighborhoods within single population.

Lank 1982, 1984, Gratto 1988, Haig and Oring 1988a, Thompson and Hale 1989), although phalaropes (*Phalaropus* spp.) can be an exception, especially at permanent wetlands where philopatry can be as high as 24% (Colwell et al. 1988). Breeding-site fidelity varies widely among shorebirds, ranging from less than 10% to greater than 90% (Oring and Lank 1984, Thompson et al. 1988).

Variability in site fidelity is determined by resource distribution and predictability, which also affects mating systems and parental-care patterns (Emlen and Oring 1977, Powell 1989). Shorebird species with uniparental care, and little territorial behavior, typically return at relatively low rates (e.g. Colwell and Oring 1989a), although exceptions occur (Colwell et al. 1988). Species with biparental care and strong territoriality return at higher rates. For example, Piping Plovers have 70% return (Haig and Oring 1988a), Common Sandpipers (*A. hypoleucos*) 79% (Holland and Yalden 1991), and Eurasian Oystercatchers (*Haematopus ostralegus*) 90% (Safriel et al. 1984).

Not all species with biparental care and territoriality return at high rates, however. American Avocets (*Recurvirostra americana*) and Black-necked Stilts (*Himantopus mexicanus*) have biparental care, but return at rates of less than 30% (Sordahl 1984). These species breed in ephemeral wetlands, which would not be compatible with high site fidelity. Return rates also can vary strongly among years (e.g. Gratto et al. 1985), and with reproductive success and mate fidelity (Soikkeli 1970a, Hildén 1979, Oring et al. 1983, Gratto et al. 1985, Thompson et al. 1988).

Traditional theory predicts female-biased philopatry when females defend resources, and female-biased dispersal when females defend mates (Greenwood 1980, 1983). These generalities appear to hold for scolopacids, although observed biases are small (Oring and Lank 1984). For Spotted Sandpipers, females defend both resources and males (Oring et al. in press), so there might be no reason to expect bias (cf. Ostfeld 1987).

Study Site and Species

Data were collected from 1973 to 1991 on uniquely color-banded Spotted Sandpipers on Little Pelican Island (LPI), Leech Lake, Minnesota (47°07'N, 94°21'W). LPI's small size (ca. 1.6 ha) and open habitat allowed us to determine arrival and departure dates, mating success and reproductive success (i.e. eggs laid, hatch and fledging successes), and to monitor behavioral interactions, including those associated with territorial intrusion. We also monitored breeding birds on Pelican Island (BPI) 200 m north of LPI starting in 1979, and breeders at two mainland sites 7 km south of LPI starting in 1983 (Fig. 1). We considered this entire area as a single population, and distinguished different breeding locales (LPI, BPI, Timberlane, and Whipholt Beach) as neighborhoods within the population. Every year we banded all new breeding adults and all chicks. In this analysis, we used 1983-1991 data because all neighborhoods were monitored in these years. In some cases data from previous years are included for comparative purposes. The primary differences between data presented here and those presented in earlier studies are size of the study site, and the number of years. Here we are working with a larger study area and more years to examine movement and returns in greater detail.

Spotted Sandpipers are sex-role reversed (Maxson and Oring 1980), and females at LPI typically arrive and establish breeding territories before males do. Males then establish territories within female territories (Oring et al. 1983, Oring and Lank 1986). Although Spotted Sandpipers have been classified as resource-defense polyandrous (Emlen and Oring 1977), they actually have an experience-based mating system (Oring et al. in press). Females defend an all-purpose territory that includes: (1) shoreline, for drinking, bathing and display; (2) semiopen habitat for nesting (Oring et al. 1983); and (3) patches of dense vegetation for cover for chicks (Maxson and Oring 1980). Foraging occurs on all parts of the territory. Once a female has laid a clutch, she sometimes subdivides her territory to permit a second mate to settle (Oring 1982, 1986). In our study areas, females had one to four mates, with 33 to 100% of females having more than one mate annually (Oring and Knudson 1972, Oring et al. 1983, 1991).

When no males are available, females often help incubate and brood, but their contribution at our study site does not appear to affect annual reproductive success (Oring et al. 1991). Older females have higher mating success (Oring and Lank 1986, Oring et al. 1991a), and more experienced females have higher reproductive success (Oring et al. 1983, 1991a, Oring and Lank 1986). Mate availability limits annual female reproductive success (Lank et al. 1985), and females assess potential future breeding sites, apparently by male abundance (Reed and Oring 1992).

Using data from LPI before the study area was expanded, L.W.O. and associates found no sex difference in annual site fidelity (Oring et al. 1983, Oring and Lank 1984), that successful breeders returned more often than unsuccessful breeders (Oring and Lank 1982), and that older males returned more often than older females (Oring and Lank 1982). Oring and Lank (1982) also reported female-biased philopatry for yearlings that bred. Oring (1988) found chick return to be negatively related to number of chicks fledged. Here we reassess these relationships using data from the expanded study site.

Little is known about Spotted Sandpiper dispersal at other sites, or dispersal distances greater than those monitored in this study. The only reported long-distance movement was 12 km by a hatch-year bird (Oring 1988).

METHODS

Philopatry.—We examined return rates for males and females fledging from LPI from 1974-1990, and fledging from the entire study area from 1983-1990. We were primarily interested in a sex bias in philopatry, and density-dependent return rates. We considered return to any of the neighborhoods to be philopatry because we believed the entire site to be within the area of natal experience (cf. Reed 1993). However, we distinguished return to different neighborhoods (Fig. 1) in order to understand the fine structure of philopatry.

From 1983-1991, philopatric yearlings annually made up 7 to 36% (2-9) of recruited breeders (Fig. 2). We tested for sex bias in philopatry using different subsets of data (Table 1) and three statistical tests: (1) *G*-test (Sokal and Rohlf 1981) on observed and expected numbers of males and females returning for all years combined. We used Emigh's (1980) correction for continuity. This test has the weakness of being influenced by extreme values. (2) Wilcoxon signed-rank test (Hollander and Wolfe 1973), with each year having a value for male and female return, is less sensitive to extreme years. (3) Fisher's sign test (Siegel and Castellan 1988). This test is not influenced by extreme years, but does not make use of the magnitude of the difference. In our analyses, all tests were in agreement about direction, or lack, of sex bias.

Site fidelity.—We examined movement among neighborhoods within a population within and among years by breeders banded from 1983-1990; we also included post-1982 movement for birds banded before 1983. For testing sex bias in among-neighborhood movement following nest success or failure, we considered nest loss in different neighborhoods to be independent events. We recognize that our numbers underestimate the number of birds moving following failure because we did not know how many birds left the study site following failure. A bird with many successes that did not move was counted only once. We defined success for males as fledging at least one young that year, and for females as hatching at least one young. Definitions differ because females often desert males and probably have less accurate information regarding nest success. Nests with unknown fates were omitted from analysis.

Dispersal.—To examine dispersal at other breeding sites, we obtained band recovery records for Spotted Sandpipers through 1990 from the U.S. Fish and

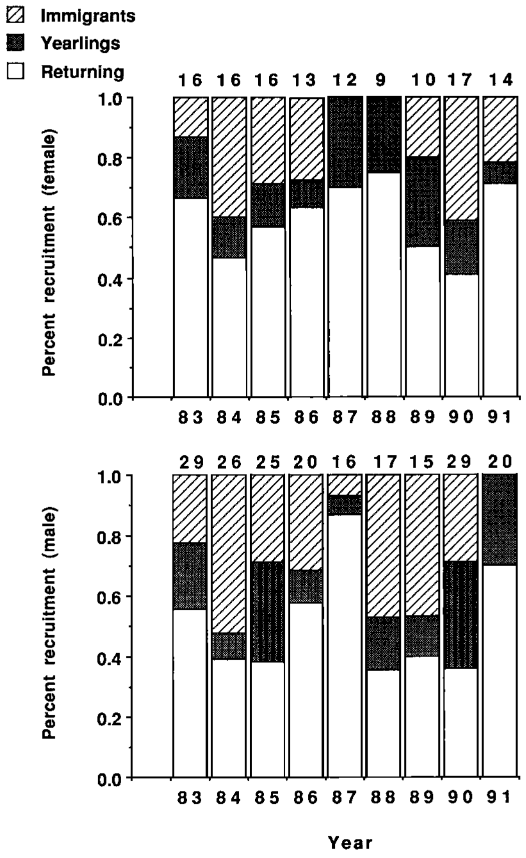

Fig. 2. Proportion of breeding Spotted Sandpipers in study population each year that were returning breeders, recruited yearlings, and recruited immigrants. Numbers of breeders appear at tops of columns.

TABLE 1. Philopatry data, whether or not birds bred, in the year following fledging.

	Born on LPI and returned			Born on expanded study area and returned		
Born	Male	Female	Unknown	Male	Female	Unknown
1974	0	0	-			
1975	0	0	-			
1976	3	1	-			
1977	1	2	-			
1978	3	2	1			
1979	1	4	-			
1980	5	8	2			
1981	3	1	2			
1982	0	1	-			
1983	0	1	-	1	3	-
1984	3	1	-	6	3	1
1985	0	0	-	2	2	-
1986	0	2	-	3	3	-
1987	2	0	-	4	1	-
1988	2	1	-	4	3	-
1989	2	1	-	7	3	-
1990	3	0	-	5	1	-
Total	28	25	5	32	19	1

Wildlife Service, Laurel, Maryland. To narrow records to include only breeding dispersal, only those in which birds were banded and resighted/recovered between 1 May and 10 July were used. We determined distances between banding and recovery using the methods of Moore and Dolbeer (1989). In addition, a single visual sighting reported to L.W.O. was included.

Survival.—We are unable to know true age-specific survival rates because we do not know fates of birds dispersing from our study area. Therefore, we calculated age-specific values for the minimum number known to be alive. This was done with combined cohort data across years (method 2 of Caughley 1977: 91). The portions of the survival schedule we could estimate accurately were hatching and fledging probabilities. These were calculated only for clutches where we knew chick fates through fledging using cohort data from 1983–1990. Age-specific return was determined directly for ages 1 to 4; older age classes were combined to get a single age-specific survival rate. We considered nine to be the oldest achievable age because it was the oldest observed during our 18-year study ($n = 3$; 1 female, 2 males).

Minimum survival to age 1 was the number of yearlings seen that came from clutches where chick fate through fledging was known. Yearlings from a clutch with an unknown number fledging were not included in first-year survival, but were included after that. We included birds born before 1983 on our study site in determining age-specific survival for their ages after 1982.

We regularly banded immigrants and transient birds (short-term visitors); transients often returned to breed in subsequent years (Reed and Oring 1992). We hypothesized that immigrants and transients were yearlings, and compared their age-specific survival to birds of known age. Only transients that returned to our study area and bred were considered. We included immigrants from 1983–1990; those banded before 1983 were included in determining age-specific survival for their ages after 1982.

We determined survival schedules separately for males and females and, within each sex, for birds that were successful versus unsuccessful breeders. Minimum survival rates were compared between successful and unsuccessful breeders, between sexes, and between immigrants and known-aged birds.

TABLE 2. Sex ratios of known yearling breeders versus other breeders at study site.

	Yearling breeders			Other breeders		
Year $x + 1$	Males	Females	M/F	Males	Females	M/F
1984	1	2	0.5	25	14	1.8
1985	6	1	6.0	19	15	1.3
1986	2	0	—[a]	18	13	1.4
1987	1	2	0.5	15	10	1.5
1988	3	1	3.0	14	8	1.8
1989	2	3	0.7	13	7	1.9
1990	7	2	3.5	22	15	1.5
1991	5	1	5.0	15	13	1.2

[a] Undefined.

RESULTS

Philopatry.—If we analyze only yearling Spotted Sandpipers born on LPI that returned to LPI, there is no indication of sex-biased philopatry during early (1974–1982), late (1983–1990), or combined years (Table 1. **1974-1982:** $G_{adj} = 1.708$, df = 1, $P > 0.1$; Wilcoxon signed-rank test, $T^+ = 7$, $n = 7$, $P > 0.78$; Fisher's sign test $P > 0.1$. **1983-1990:** $G_{adj} = 0.18$, df = 1, $P > 0.1$; Wilcoxon signed-rank test, $T^+ = 17$, $n = 7$, $P > 0.078$; Fisher's sign test $P > 0.1$. **1974-1990:** $G_{adj} = 0.118$, df = 1, $P > 0.1$; Wilcoxon signed-rank test, $T^+ = 45.5$, $n = 14$, $P > 0.09$; Fisher's sign test $P > 0.1$). Because some philopatric birds returned to different neighborhoods (breeders shown in Fig. 3), a bias could be hidden. When the entire study area is analyzed, there is slight male-biased philopatry that is nearly statistically significant, 1.68:1.00 with 32 males and 19 females (Table 1. **1983-1990:** $G_{adj} = 3.096$, df = 1, $P < 0.1$; Wilcoxon signed-rank test, $T^+ = 4$, $n = 8$, $P < 0.078$; Fisher's sign test $P < 0.109$). This analysis included all birds that returned, regardless of breeding status, and ratios were compared to an expected equal return rate.

When we analyze sex ratios of philopatric birds that returned and bred as yearlings, using the breeding adult sex ratio during the return year from 1984–1991 as expected values (Table 2), we find no sex bias ($G_{adj} = 1.308$, df = 1, $P > 0.1$; Fisher's sign test $P > 0.26$). For the sign test, we evaluated annual philopatric sex ratios to see if they were above or below annual sex ratios of the balance of breeders that year (Table 2).

Some birds born on the study area were not seen as yearlings, but were seen in subsequent years. Males born in the early years of the study (1973–1982) sometimes were seen for the first time six years later; females were never seen for the first time more than two years after fledging (Table 3). After expanding the study area, such interrupted sightings decreased (Table 3).

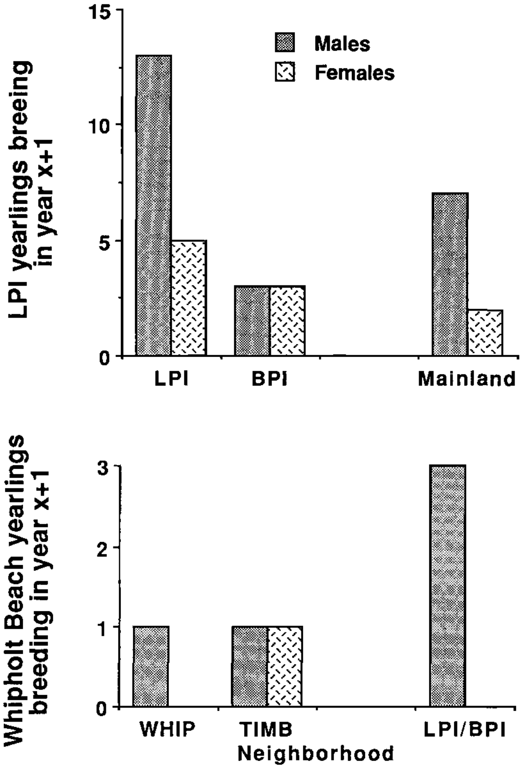

Fig. 3. Yearling breeding philopatry: number of yearlings born on LPI (upper) and Whipholt Beach (lower) that bred in each neighborhood the year following fledging. In upper panel, BPI refers to Pelican Island, and Mainland to Whipholt Beach and Timberlane; in lower panel, WHIP is Whipholt Beach, TIMB is Timberlane, and LPI/BPI references Little Pelican Island and Pelican Island.

Increased fledgling production was associated with decreased chick return (Spearman rank correlation $r^2 = 0.51$, $P < 0.05$; Fig. 4). This relationship was not attributable to a single sex (male, $r^2 = 0.33$, $P = 0.42$; female, $r^2 = 0.24$, $P = 0.57$). As an additional test, we divided fledgling production years into high-production (>35 fledglings produced, $n = 4$ years) and low-production (≤ 35 fledglings, $n = 4$ years) years. (High-production years occurred when there were more females and/or when no predator

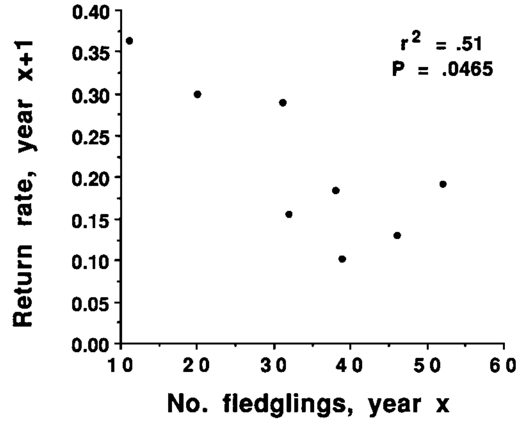

Fig. 4. Proportion of Spotted Sandpipers returning (whether or not they bred) the year following fledging relative to number of fledglings. Spearman rank correlation coefficient presented.

visited LPI.) There is a suggestion that low-production years were associated with higher chick return (G_{adj} = 2.938, df = 1, $P < 0.1$), with the difference approaching statistical significance.

Site fidelity and dispersal.—Return rates for males were 63 and 29% for successful and unsuccessful breeders, respectively; rates were similar for females, 63% for successful breeders and 26% for unsuccessful breeders. Successful breeders of both sexes returned at significantly greater rates than did unsuccessful breeders for ages 1 to 3 (Table 4).

TABLE 3. Spotted Sandpiper chicks hatched (year x) on LPI from 1973-1982, and on entire study site from 1983-1989 that were first resighted more than one year after fledging.

Sex	$x + 2$	$x + 3$	$x + 4$	$x + 5$	$x + 6$
		1973-1982			
Male	6	2	2	1	1
Female	3	—	1	—	—
		1983-1989[a]			
Male	4	—	—	—	—
Female	3	—	—	—	—

[a] One unknown sex.

Of 41 males and 27 females that bred in multiple years after 1982, 12 males (29.3%) and 6 females (22.2%) bred in different neighborhoods (Fig. 5). Three males (7.3%) and three females (11.1%) changed neighborhoods multiple times. We found no difference between sexes in their tendency to move as breeders (G_{adj} = 0.26, df = 1, $P > 0.1$). Site fidelity differed between LPI and Whipholt Beach, with birds having greater fidelity to LPI (Rice's conditional binomial exact test [CBET], two-tailed, sexes combined, $P = 0.008$; Rice 1988).

Males moved significantly more often following nesting failure (9/20) than following nesting success (1/22; Rice's CBET, two-tailed, $P = 0.003$). Females showed a similar pattern, with

TABLE 4. Minimum number of Spotted Sandpipers known to be alive, separated by age, sex, and whether a bird was reproductively successful. Survival equal to return rate; birds included are those hatched or banded after 1982, and returns after 1983 of birds banded before 1983.

	Male					Female				
	Successful[a]		Unsuccessful			Successful		Unsuccessful		
Age	n_x[b]	Survive[c]	n_x	Survive	P[d]	n_x	Survive	n_x	Survive	P
1	41	23	33	9	0.007	25	15	15	5	0.056
2	19	14	16	4	0.002	20	14	5	1	0.029
3	12	8	5	1	0.008	15	9	5	1	0.008
4	6	3	6	3		9	7	2	0	
5	4	4	7	3		7	4	—	—	
6	4	4	2	0		1	0	1	1	
7	2	1	3	1		—	—	3	0	
8	1	0	—	—		2	1	—	—	
9	1	0	1	0		1	0	—	—	
Total[e]	48		53			44		26		

[a] Successful nests: for males, those from which young fledged; for females, those from which young hatched.

[b] Number of birds in each age class contributing to survival to next age. Because birds could switch success categories between ages, and birds banded before 1983 were included in older age classes (after 1983), values in this column do not decrease monotonically, and some gaps are present.

[c] Number known to be alive (i.e. returning) the following year.

[d] Comparing successful with unsuccessful birds using Rice's (1988) CBET (one-tailed, df = 1 for all).

[e] Number of birds contributing to each survival schedule. See footnote b regarding why these numbers cannot be summed to get total number of birds contributing to life table. Overall, n_x was 91 males and 61 females.

TABLE 5. All dispersal records for Spotted Sandpipers from U.S. Fish and Wildlife Service band-recovery records through 1990 from outside our study site. Only birds banded and recovered during breeding season included; sex unknown for all records.

Year			Distance dispersed (km)
Banded	Recovered	Age[a]	
1953	1953	Chick	3.6
1953	1957	Chick	3.6
1956	1959	Chick	4.3
1971	1971	AHY	22.8
1923	1927	HY	61.5
1932	1933	HY	84.0
?[b]	1990	?	113.4
1945	1948	HY	146.7

[a] Age at banding: chick, young bird incapable of sustained flight; HY, postfledging hatch-year bird; AHY, adult of unknown age.

[b] Bird observed but not collected. Missing bands prevented individual identification; dispersal distance listed is shortest one to where Spotted Sandpipers were banded.

4 of 6 moving after failure, and 7 of 25 moving after success (Rice's CBET, two-tailed, $P = 0.061$).

Eight recovery records fit our criteria for dispersal. Dispersal distances ranged from 3.6 to 147 km (Table 5). All birds except one were banded as either chicks or hatch-year birds.

Survival.—Approximately one-half of the eggs laid at our study site hatched, and 83% of those that hatched fledged (43% of eggs laid; Table 6). For nests where we knew the chicks' fates, survival from fledging to age 1 was 0.17 ± SD of 0.07 (Alberico et al. 1992). Because the sex ratio of philopatric birds was 1.68 (males/female), male survival rate from fledging to age one was 0.107, and for females was 0.063, assuming an equal yearling sex ratio. We incorporated 152 adults with known nest fates in our life table (91 males and 61 females; Table 4).

We distinguished natal birds from immigrants, males from females, and successful from unsuccessful nesters. To determine if immigrants could be pooled with birds born locally, we assumed immigrants were banded as yearlings, and compared their return rates to locally hatched birds. Returns were not significantly different between ages 1 and 2 (which had the largest sample sizes) in each success and sex category (Rice's CBET, two-tailed, successful males, age 1 $P = 0.92$, age 2 $P = 0.67$; unsuccessful males, age 1 $P = 0.36$, age 2 $P = 0.80$; successful females, age 1 $P = 0.45$, age 2 $P = 0.19$; unsuccessful females, age 1 $P = 0.22$, age 2 $P = 0.71$). Thus, we pooled immigrant and local-born survival data for analyses.

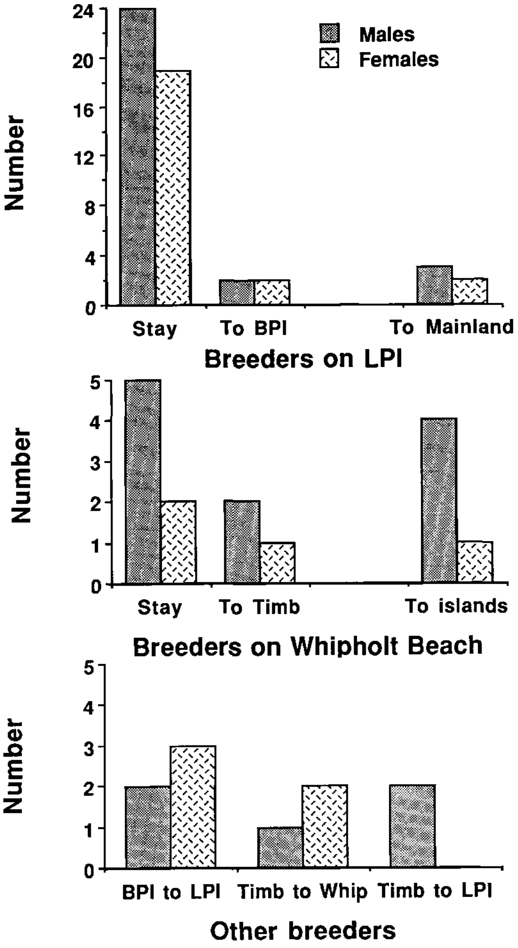

FIG. 5. Interclutch movements, or lack of movements, between and within years of 41 male and 27 female Spotted Sandpipers that bred in multiple, consecutive years after 1982.

Successful males returned more often than unsuccessful males (Rice's CBET, one-tailed, age 1 $P = 0.007$, age 2 $P = 0.002$, age 3+ $P = 0.008$, df = 1 for all; Table 4). Females followed a similar survival pattern (Rice's CBET, one-tailed, age 1 $P = 0.056$, age 2 $P = 0.029$, age 3+ $P = 0.008$, df = 1 for all; Table 4). These data were used to construct survival curves (Fig. 6).

DISCUSSION

The Spotted Sandpiper philopatry rate at our study site was high relative to reports for other sandpiper species (usually not above 10%; see earlier references), with 14% probability that

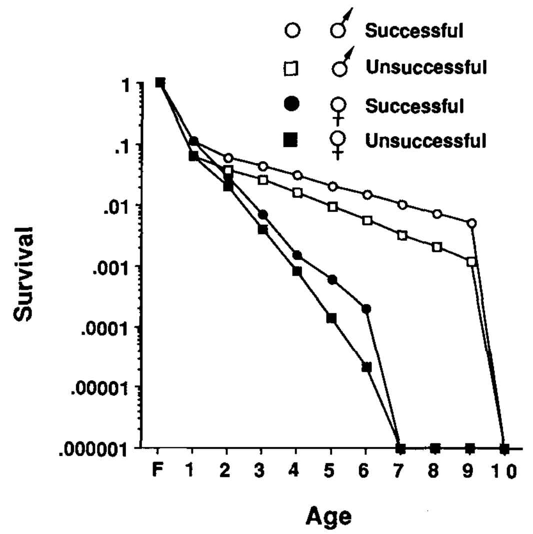

Fig. 6. Survival (log scale) of male and female Spotted Sandpipers that were successful and unsuccessful nesters (F = fledging). Survival curves based on data from Tables 4 and 6, and from Alberico et al. (1992).

chicks would return as yearlings. The high site fidelity observed here fits the general pattern in shorebirds of high return rates among territorial species with biparental care and low return rates among nonterritorial species with uniparental care (Oring and Lank 1984). Spotted Sandpipers have strong territoriality and often have biparental care for a female's terminal clutch of the year; successful breeders at our site returned at annual rates of 55 to 74%. Within our study area, we found higher site fidelity following breeding success. This pattern has been observed in some, but not all, shorebird species (e.g. higher fidelity following breeding success for Long-billed Curlews [*Numenius americana*; Redmond and Jenni 1982] and Semipalmated Sandpipers [*Calidris pusilla*; Gratto et al. 1985]; no reported effect for Dunlin [Heldt 1966, Soikkeli 1967, 1970b], Eurasian Oystercatcher [Safriel et al. 1984], Piping Plover [Haig and Oring 1988a], or Redshank [*Tringa totanus*; Thompson and Hale 1989]).

It seems probable that return rates for successful breeders represented natural survival rates for Spotted Sandpipers. We observed sandpipers up to 9 years of age, short of the longevity record for this species of 12 years (Clapp et al. 1982). Scolopacids can live longer, with a record of 16 years for a Least Sandpiper (*Calidris minutilla*; Miller and Reid 1988).

Expanding a study area can have important effects on observed dispersal and philopatry patterns (Cunningham 1986). Expanding our study site had a noticeable effect on observed return rates and sex ratios (Table 1). If we include only LPI, return rates by sex were almost identical, consistent with typical sandpiper patterns (Oring and Lank 1984, Thompson and Hale 1989). However, with the expanded study site, yearling returns were male biased, which previously had been observed only for Long-billed Curlews (Redmond and Jenni 1982). Male-biased philopatry opposes Greenwood's (1980) model, given that female Spotted Sandpipers typically defend resources. However, there was no significant sex-ratio bias in philopatric yearlings that bred.

TABLE 6. Numbers of eggs, chicks, and fledglings produced within our study area from nests for which fates were known through fledging.

Year	Number of			Number of fledglings	
	Eggs	Chicks	P_x[a]		P_x[b]
1983	97	35	0.361	11	0.113
1984	43	39	0.907	35	0.814
1985	55	48	0.873	41	0.745
1986	105	52	0.495	48	0.457
1987	110	37	0.336	32	0.291
1988	60	50	0.833	39	0.650
1989	64	55	0.859	52	0.813
1990	136	30	0.221	29	0.213
Total	670	346		287	
Mean P_x			0.511		0.428

[a] Number of chicks/number of eggs. SD of P_x was 1.30.

[b] Number of fledglings/number of eggs. SD of P_x was 1.30.

Yearling return rates at our study site were not independent. Siblings returned more often than expected from independent individual returns (Alberico et al. 1992). The cause of this pattern is unknown, but Alberico et al. (1992) suggested it might be a result of siblings spending time together after fledging. Nonrandom sibling return, coupled with no sex-biased philopatry of breeders and high breeding-site fidelity should result in relatively high coancestry. This prediction is corroborated by relatively high band-sharing coefficients from DNA fingerprints of individuals from our study site (Oring et al. 1992).

One thing not changed by expanding the study area was the negative relationship between Spotted Sandpiper fledgling production and percent return the following year (Oring 1988, this study Fig. 4). This relationship is consistent with the hypothesis of density-dependent return, but we do not know the mechanism(s) driving the relationship.

Our study presents the only published long-distance dispersal data for Spotted Sandpipers. Long-distance dispersal is important to gene flow (e.g. Haig and Oring 1988b) and can strongly affect effective-population-size estimates (Payne 1990). Soikkeli's (1967, 1970a, b) work on Dunlins, the most thorough study of dispersal in a shorebird, reported dispersal of 280 km, while Haig and Oring (1988c) reported a Piping Plover dispersed 595 km between breeding sites. Our longest record for Spotted Sandpipers was 147 km. Although limited, these data indicate that long-distance dispersal could be an irregular but important part of shorebird population ecology.

Neighborhood dynamics.—Breeding-bird movements indicated that all neighborhoods in our study area were not equally suitable. It appears that both Whipholt Beach and LPI were acceptable as breeding sites, but that LPI was preferred. LPI consistently had more breeders, and adults tended to move away from Whipholt Beach and to stay on LPI. Furthermore, Timberlane and BPI had relatively few breeders, and high predation rates (L.W.O. unpubl. data).

This movement pattern is consistent with Fretwell and Lucas's (1969) hypothesis that habitats vary in quality and that suboptimal habitat will be filled by birds unable to settle in better habitat. However, breeder movement among neighborhoods after nest failure is not unidirectional, and our neighborhoods might act as sink-source "populations" (Pulliam 1988). However, Spotted Sandpiper population dynamics are probably different in important ways from both theoretical models. Natal dispersal away from LPI is primarily a result of relatively late yearling arrival (Lank et al. 1985) and intense competition for mates. Adult movement is generally a response to breeding failure, but within a season can result from mate acquisition attempts (Colwell and Oring 1989b, Oring et al. in press). Spotted Sandpipers move among neighborhoods in an attempt to maximize mating and reproductive success, and movement is associated with mate availability, competition, and nest-depredation probabilities (Oring et al. in press). This study of short-distance movement patterns, which is rare for a migratory species, provides information necessary for understanding local population dynamics.

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