

# POPULATION STUDIES OF THE POLYANDROUS SPOTTED SANDPIPER

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**ABSTRACT.**—A color-banded population of Spotted Sandpipers (*Actitis macularia*) was studied over a 10-yr period on Little Pelican Island, Leech Lake, Minnesota. A total of 75 females and 107 males bred for 144 ♀♀ yr and 200 ♂♂ yr. The observed skew in the population sex ratio was due primarily to behavioral exclusion of inexperienced females. Density appeared to limit population size and productivity. Locally hatched chicks accounted for 31% and 40% of the breeding females in the final 2 yr. Females laid eggs for 1.35–2.06 males per year. Experienced females had significantly more mates, eggs, chicks, and fledglings than did inexperienced females. Locally hatched chicks accounted for 21% and 19% of the breeding males in the final 2 yr. Males mated with 1.0–1.4 females per year. Experienced males had more mates and received more replacement eggs than did inexperienced males; in contrast to females, however, inexperienced males had no less hatching or fledging success than did experienced males. Thirty-eight marked females and 16 marked males tried unsuccessfully to enter the population, and 6 females and no males were observed to be nonbreeders all season long. Of 1,142 eggs, 442 hatched and 256 fledged. Experienced birds returned to breed more often in subsequent years than did inexperienced ones (61% vs. 50%). Return rates of successful birds were consistently higher than those of unsuccessful birds, the difference decreasing with age. Young males appeared to be less site-faithful than were females and older males. Successfully breeding females lived an average of 3.7 yr. Relative to other scolopacids with multipurpose territories, the Spotted Sandpiper is considered a pioneering species that quickly and frequently colonizes new sites, emigrates in response to reproductive failure, breeds first at an early age, lives a relatively short time, lays many eggs per female per year, and has relatively low nest success. Received 11 May 1982, accepted 11 November 1982.

HISTORICALLY, long-term population studies of shorebirds have lagged far behind those of passerines (e.g. Nice 1937; von Haartman 1949, 1953; Kluijver 1951) and colonial waterbirds (e.g. Richdale 1957; Coulson and White 1958, 1959; Coulson 1966). In recent years, however, there has been a surge of interest in shorebird biology, and a number of long-term studies have been conducted, including those on Dunlin (*Calidris alpina*; Soikkeli 1967, 1970) and Temminck's Stint (*C. temminckii*; Hildén 1978, 1979). While Dunlin are typically monogamous, Temminck's Stint exhibit *rapid-multi-clutch polygamy* (Emlen and Oring 1977). This paper reports upon population characteristics of a resource-defensive, polyandrous species, the Spotted Sandpiper (*Actitis macularia*; Emlen and Oring 1977, Oring 1982). It is the sec-

ond of two papers dealing with Spotted Sandpiper population biology; the first presented data on arrival times at the breeding grounds, philopatry, and breeding-site fidelity (Oring and Lank 1982).

Spotted Sandpipers breed from the Arctic Ocean to the southern United States. Nests usually are placed in semi-open vegetation near the water's edge, although a variety of vegetation types may be used (Bent 1929, Oring et al. unpubl. data). The suitability of nesting habitat varies from year to year due to flooding, drought, plant succession, and the presence or absence of predators. Breeding habitat often is typified by high invertebrate biomass. Adult flying insects are staple diet elements, but crustaceans, leeches, molluscs, small fish, and carrion are also eaten (Bent 1929, Kuenzel and Wiegert 1973, Rubbelke 1976).

In spring, females arrive before males, establish territories, and mate with one or more males. Homing to breeding and natal sites by both sexes is related to age and previous breeding success (Oring and Lank 1982). Males

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also are territorial, and each provides most or all of the care for a single nest and brood (Hays 1972, Oring and Knudson 1972, Oring and Maxson 1978, Maxson and Oring 1980). The mating and parental-care behavior of individuals varies not only with their own sex, age, breeding experience, and extrinsic factors such as food supply, nest predation, and weather, but also with the sex, age, and experience of other individuals in its local breeding area. In short, Spotted Sandpiper reproductive behavior is characterized by extreme lability, and much of this variability is related to demographic features.

#### STUDY AREA

This study was conducted on Little Pelican Island, Leech Lake, Minnesota (47°07'N, 94°22'W). The island is 1.6 ha in area and is situated 7–8 km from shore. Two other islands are nearby: Pelican Island (36 ha), about 200 m to the north, where 3–5 female Spotted Sandpipers breed annually, and Gull Island (0.3 ha), about 300 m to the southwest, where no Spotted Sandpipers breed. This report covers only birds breeding on Little Pelican Island (LPI).

Vegetation zones on LPI include open beach, semi-open herbaceous cover, dense grasses and sedges, cattails (*Typha latifolia*), shrubs (including *Ribes*, *Rhus*, *Salix*, and *Vitis* spp.) and trees (Rubbelke 1976). Spotted Sandpipers nest in all of these vegetation zones, but most nests are located in the semi-open and the grass-sedge areas.

#### METHODS

Field observations were conducted in 1974–1982 from early May, when the first Spotted Sandpipers returned, through early August, when they completed breeding and left the island. Breeding birds (75 ♀♀, 107 ♂♂; 1973–1981) were captured in mist nests or shoreline funnel traps and were color-banded. Seasonal arrivals and departures, spacing and mating patterns, and hatching and fledging success were determined for each bird. From 1975 on, observations were made from four 3-m towers. Chicks were marked at the nest soon after hatching. In 1973, not all birds were marked, and the study season was brief; consequently, breeding data are less complete than for subsequent years. In 1982, the reproductive effort of the population was experimentally manipulated; thus, only data on the return of 1981 breeders and on the philopatry of chicks are included here.

In 1966 a mink (*Mustela vison*) was trapped on the island, and in both 1976 and 1977 deer mice (*Peromyscus maniculatus*) were trapped on one portion of the island (Maxson and Oring 1978).

In this paper, *experienced* birds are those known

to have bred previously on LPI (vs. *inexperienced* birds). Of the *inexperienced* birds, 8% were 1-yr-olds that had hatched on LPI, 5% were older birds that had hatched on LPI, 10% were birds that had been banded as adults but were not known to have bred locally, and 76% were adults that had been banded in their first local breeding season. The territorial and reproductive behavior of this last group suggests that most of them were first-time breeders. Birds banded as adults in 1973 were not classified in terms of experience.

Some analyses involve a variable called *minimum age*. Birds that had not been banded as chicks were assigned the arbitrary age of 1 yr when first banded, including those marked in 1973.

Birds were considered *mated* if a nest was attributed to the pair. A *nest* was defined as a scrape containing one or more eggs. Nests *hatched* if one or more eggs in them hatched, and *fledged* if one or more chicks from that nest fledged.

Known individuals *returned* to the island when they came back the next year and bred. One experienced, paired female that was killed in a trap and another that died just before egg-laying also were credited with returning. Data on returning birds are classified as a function of previous breeding success. *Success* is defined as the hatching of one or more eggs. This was as good a predictor of return as any other measure of reproductive success (Oring and Lank, unpubl. data).

#### RESULTS

*Annual breeding effort and success: an overview.*—Aspects of the reproductive biology of the Spotted Sandpiper, recorded for 9 yr, are summarized in Tables 1 and 2. In the first 2 yr (1973 and 1974), breeding population density and hatching success were about average, but fledging success was low: 53% of 59 nests hatched, 39% of 31 hatched nests fledged chicks, and 25% of the 84 chicks fledged. Sources of egg and chick loss in 1973–1974 are largely unknown.

In 1975, an adult mink inhabited the island, depredated most of the eggs and the hatchlings. As a result, there were many renestings, leading to the largest number of nests and eggs per female of any year. In 1976, a mink was trapped early in the year; none was seen again on the island until 1981. The number of females (6) and males (12) breeding in 1976 was the lowest recorded in this study, but the breeding sex ratio was the most male-biased we observed (2:1). Following our predator-control effort (Maxson and Oring 1978), reproductive

TABLE 1. Numbers of Spotted Sandpipers breeding on Little Pelican Island, Minnesota, 1973–1981. Numbers in parentheses indicate birds that hatched on the island and returned there to breed.

Year	Totals		Experienced		Inexperienced	
	F <sup>a</sup>	M <sup>a</sup>	F	M	F	M
1973	18	22	—	—	—	—
1974	15	21 <sup>b</sup>	10	8	5 (0)	12 (0)
1975	16	23	8 (0)	10 (0)	8 (0)	13 (0)
1976	6	12	6 (0)	5 (0)	0 (0)	7 (1)
1977	14	23	8 (0)	9 (0)	6 (1)	14 (2)
1978	19	21	8 (1)	16 (1)	11 (3)	5 (1)
1979	17	22	9 (3)	11 (1)	8 (1)	11 (0)
1980	19	24	9 (2)	13 (1)	10 (4)	11 (4)
1981	20	32 <sup>b</sup>	11 (6)	21 (4)	9 (2)	10 (2)
Totals	144	200	69 (12)	93 (7)	57 (11)	83 (10)
$\bar{x}$	16.0	22.2	8.6	11.6	7.1	10.4
C.V. <sup>c</sup>	26.5	22.9	17.5	43.1	48.9	29.1

<sup>a</sup> F = females, M = males.

<sup>b</sup> Including one male of unknown experience class.

<sup>c</sup> Coefficient of variation of annual means.

success was high, especially when calculated on a *per capita* basis (Tables 3 and 4).

The number of breeding birds doubled in 1977 (14 ♀♀, 23 ♂♂) and then remained relatively stable through 1980. The mean fledging success per female was at a maximum in 1976 and remained relatively high from 1977 to 1980 (Table 3). From 1976 to 1980, 51% of the 162 nests hatched, 91% of these 82 nests produced one or more fledglings, and 73% of the 274 chicks fledged.

In 1981, following 5 consecutive years of high breeding success, the number of breeding males and females reached a maximum (Table 1). On 11 July, however, a juvenile mink took up residence on the island, killing nearly all un-

fledged chicks and all those that hatched subsequently. Only 42% of the 81 chicks fledged that year. This mink did not eat eggs.

*Females.*—The total number of females breeding on LPI per year ranged from 6 to 20 (Table 1). Excluding 1976, a year unique in its lack of immigrant females, the number varied from 14 to 20. The number of experienced females varied from 6 to 11 (8–11 excluding 1976), and these birds had the lowest coefficient of variation (CV) of the four sex/experience classes. The number of immigrant females varied from 0 to 11 (6–11 excluding 1976). With the exception of 1976, the percentage of experienced females averaged 53, ranging from 44 to 67 (Table 1). The percentage of breeding females known

TABLE 2. Annual breeding sex ratios, polygamy, reproductive effort, and reproductive success of Spotted Sandpipers on Little Pelican Island, Minnesota, 1973–1981.

Year	Breeding sex ratio	Mean number of mates per		Number of nests found	Nests where eggs hatched	Nests where chicks fledged	Number of eggs		Number of chicks fledged
		Female	Male				Laid	Hatched	
1973	1.22	1.50	1.23	28	19	6	112	55	11
1974	1.40	1.67	1.19	31	12	6	123	29	10
1975	1.44	2.06	1.43	46	1	0	157	3	0
1976	2.00	2.00	1.00	15	12	11	60	40	32
1977	1.64	1.86	1.13	32	19	18	116	57	40
1978	1.11	1.42	1.29	38	13	12	133	42	30
1979	1.29	1.35	1.05	40	17	16	127	63	47
1980	1.26	1.53	1.21	37	21	18	141	72	52
1981	1.60	1.85	1.16	50	26	12	173	81	34
1973–1981	1.39	1.66	1.20	317	140	99	1,142	442	256

TABLE 3. Annual breeding effort and success of female Spotted Sandpipers on Little Pelican Island, Minnesota, 1974–1981.<sup>a</sup>

Year	Mean number per breeding female of							
	Mates		Eggs laid		Chicks		Fledglings	
	EXPER <sup>b</sup>	INEXP <sup>b</sup>	EXPER	INEXP	EXPER	INEXP	EXPER	INEXP
1974	1.70	1.60	8.30	8.00	1.60	2.60	0.70	0.60
1975	2.38	1.75	11.00	8.63	0.38	0.00	0.00	0.00
1976	2.00	—	10.00	—	6.67	—	5.33	—
1977	2.00	1.67	9.75 *	6.33	4.75	3.17	3.25	2.33
1978	1.50	1.36	7.25	6.82	2.38	2.09	1.75	1.45
1979	1.56	1.13	9.56 **	5.13	4.44	2.88	3.44	2.00
1980	1.89 *	1.20	8.78	6.20	4.67	3.00	3.22	2.30
1981	2.27 *	1.33	11.00 *	5.78	4.55	3.44	1.91	1.44
1974–1981	1.91 **	1.40	9.46 **	6.61	3.59 *	2.44	2.32 *	1.48
C.V. <sup>c</sup>	16.6	16.8	13.7	18.4	55.6	47.5	69.6	60.7

<sup>a</sup> Asterisks between columns indicate significant differences between experience groups (*t*-tests); \* =  $P < 0.05$ , \*\* =  $P < 0.01$ .

<sup>b</sup> EXPER = experienced breeders, INEXP = inexperienced breeders (see text); annual sample sizes in Table 1.

<sup>c</sup> Coefficient of variation of annual means.

to have hatched on LPI increased during the study, reaching 32% and 40% in the last 2 yr.

The average number of mates for which females laid eggs, a measure of polyandry, varied from 1.35 to 2.06 per year (Table 2). The annual degree of polyandry obviously is related to the total breeding sex ratio but is not usually identical to it (Fig. 1). Deviations of average polyandry from breeding sex ratio reflect the incidence of sequential polygyny among males. Polygyny may occur following nest loss when the original female is no longer available (Oring et al. unpubl. data). Thus, while the incidence of polyandry was quite

similar in 1975 and 1976, it occurred in different ways. In 1975, nest depredation resulted in the most renesting of any year and a high level of both polygyny and polyandry, albeit the level of what might be called "effective polyandry" (genetically consequential) was fairly low. By contrast, polyandry in 1976 was due to the skewed sex ratio and occurred despite high hatching rates and a complete lack of polygyny.

Overall, experienced females had significantly more mates, eggs, chicks, and fledglings than did inexperienced females (Tables 3 and 5). Two-way ANOVAs, using experience and year as main effects, showed significant expe-

TABLE 4. Annual breeding effort and success of male Spotted Sandpipers on Little Pelican Island, Minnesota, 1974–1981.<sup>a</sup>

Year	Mean number per breeding male of							
	Mates		Eggs obtained		Chicks		Fledglings	
	EXPER <sup>b</sup>	INEXP <sup>b</sup>	EXPER	INEXP	EXPER	INEXP	EXPER	INEXP
1974	1.38	1.08	7.00	5.25	0.75	1.67	0.50	0.42
1975	1.40	1.46	8.10	5.85	0.30	0.00	0.00	0.00
1976	1.00	1.00	6.40	4.00	3.60	3.14	3.20	2.29
1977	1.11	1.14	5.33	4.86	2.22	2.64	1.22	2.07
1978	1.38 *	1.00	6.56	5.60	2.13	1.60	1.63	0.80
1979	1.09	1.00	6.82 *	4.73	2.91	2.82	2.09	2.18
1980	1.31	1.09	5.77	6.00	2.92	3.09	1.77	2.64
1981	1.19	1.10	5.86	4.80	3.05 *	1.70	1.62 **	0.00
1974–1981	1.25	1.13	6.40 **	5.17	2.31	2.04	1.47	1.29
C.V. <sup>c</sup>	12.6	13.7	13.3	13.0	51.9	50.9	64.9	85.0

<sup>a</sup> Asterisks between columns indicate significant differences between experience groups (*t*-tests); \* =  $P < 0.05$ , \*\* =  $P < 0.01$ .

<sup>b</sup> EXPER = experienced breeders, INEXP = inexperienced breeders (see text); annual sample sizes in Table 1.

<sup>c</sup> Coefficient of variation of annual means.

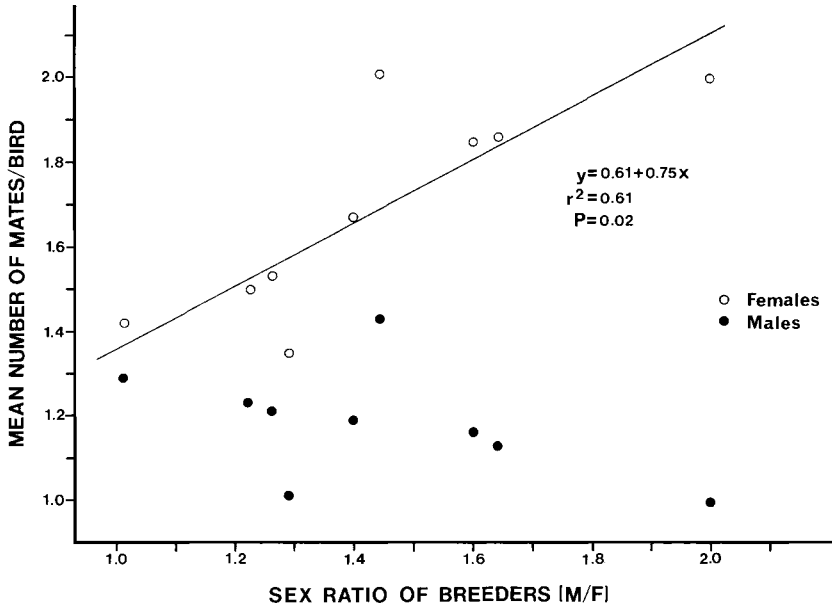


Fig. 1. Relationship between incidence of polygamy and breeding sex ratio.

rience effects for all four reproductive variables (Table 5). Experienced females were more successful than inexperienced females in each measure in each year, except for numbers of eggs hatched in 1974 and numbers fledged in 1975 (when no chicks fledged) (Table 3).

Four possible measures of reproductive success (i.e. mean numbers of mates, eggs, chicks, and fledglings) did not yield similar patterns of annual variability. The CVs of annual means are lower for numbers of mates and eggs laid per female than those for numbers of chicks

and fledglings per female (Table 3). The ANOVAs show significant year effects only for the latter two measures (Table 5). Thus, females of both experience classes obtained nutrients for egg production and mates for incubation at similar rates from year to year, but the success of reproductive efforts varied annually.

*Males.*—The total number of breeding males per year ranged from 12–32 (Table 1). Excluding the two most extreme years, the number was quite constant (20–24). The percentage of experienced males varied more than that of fe-

TABLE 5. ANOVA tables of the effects of year and breeding experience on reproductive effort and success.<sup>a</sup> In each test, the degrees of freedom (year, experience, error) = (7, 1, 111) for females and (7, 1, 160) for males.

Dependent variable	Source of variation	Females		Males	
		F	P <sup>b</sup>	F	P <sup>b</sup>
Number of mates	Year	1.95	ns	1.97	ns
	Experience	17.19	***	3.13	ns
Number of eggs	Year	1.01	ns	1.21	ns
	Experience	21.48	***	10.57	**
Number of chicks	Year	8.18	***	12.12	***
	Experience	8.73	**	1.76	ns
Number of fledglings	Year	7.23	***	9.67	***
	Experience	5.95	*	0.88	ns

<sup>a</sup> There were no significant interactions except in the case of numbers of fledglings per male. This may result from the strong difference seen only in 1981 (see Table 4 and text).

<sup>b</sup> \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

males, averaging 53% and ranging from 42–72% annually. The percentages of locally hatched chicks in the male breeding population was 21% and 19% during the final 2 yr of the study.

On LPI, male Spotted Sandpipers have one mate and nest per season unless their initial nest fails (there has been one exception in 200 male-years). Thus, there is a narrower range for males than females in the mean number of mates, eggs, chicks, and fledglings (Tables 3 and 4), and the degree of polygyny is not significantly correlated with the breeding sex ratio (Fig. 1). The degree to which mates per male exceeds 1.0 measures mate-switching following nest failure (Table 4). In 1976, mates per male equaled 1.0, reflecting the high nesting success of that year. By contrast, in 1975 mates per male equaled 1.43, showing high levels of polygyny due to intense nest predation.

Males in 1976 were less synchronous in arrival and breeding than usual, and arrival was significantly later than in other years (1976:  $n = 12$ ,  $\bar{x} = 3 \text{ June} \pm 15 \text{ days}$ ; other years:  $n = 145$ ,  $\bar{x} = 25 \text{ May} \pm 10 \text{ days}$ ; variances unequal, 11.8 df,  $t = 2.86$ ,  $P = 0.02$ ). The asynchrony of males allowed for an unusually skewed sex ratio (2:1) and a high incidence of polyandry (2.0 males per female).

The number of eggs per male minus 4, the normal determinate clutch size, equals the average number of replacement eggs obtained by males, regardless of mate-switching. This number was highest ( $6.83 - 4 = 2.83$ ) in 1975, the year of least nesting success (0.13 hatching eggs per male), and lowest in 1976 ( $5 - 4 = 1$ ), the year of greatest success (3.33 hatching eggs per male).

Local breeding experience had a smaller effect on the variance of male reproductive variables than was the case for females (Tables 3, 4, and 5). The ANOVAs show significant differences only for numbers of eggs, although number of mates also approaches significance ( $P = 0.08$ ). Experienced males averaged 1.25 mates per year, whereas inexperienced males averaged only 1.13 ( $t$ -test, variances unequal, 163 df,  $t = 1.79$ ,  $P = 0.08$ , Table 4), and experienced males obtained an average of 2.40 replacement eggs per season compared to 1.17 for inexperienced males ( $t$ -test,  $t = 3.25$ , 174 df,  $P < 0.0001$ ). Thus, experienced males obtained and lost more eggs than did inexperienced males.

During this study, egg predation was greater early than late in the season (Maxson and Oring 1978, Oring et al. unpubl. data). Because experienced males had earlier arrival and pairing dates on average than did inexperienced males (Oring and Lank 1982), nests of the former group bore most of this predation pressure. When these seasonal trends were controlled for, the differences in rates of nest loss between age classes disappeared (Oring et al. unpubl. data). Despite their nest losses early in the season, experienced males were able to replace nests and fledged as many chicks as did inexperienced birds (Tables 4 and 5). In 1981, when intense predation on chicks began in mid-season, the earlier breeding, experienced males fledged significantly more chicks than did inexperienced males (1.62 vs. 0.0,  $t$ -test, variance unequal, 20 df,  $t = 4.25$ ,  $P < 0.001$ , Table 4).

*Nonbreeding birds.*—Over the 7-yr period when social behavior was recorded in detail (1975–1981), we documented 38 occasions when marked females tried unsuccessfully to establish territories on the island and 16 occasions when marked males unsuccessfully attempted to enter the breeding population. Comparing these numbers against the number of successful breeding-years for each sex (144 ♀♀, 200 ♂♂, Table 1), there is a significant association between sex and the probability of becoming established on the island ( $\chi^2 = 13.7$ , 1 df,  $P < 0.001$ ). This analysis would be biased if substantially more females than males had been marked in total, but the numbers were almost identical (159 ♀♀, 162 ♂♂, Oring 1982). Most females that failed to obtain a territory shortly after arriving left LPI, and we do not know whether they bred elsewhere. At least six unpaired females, however, were observed throughout the breeding season in nearby areas unsuitable for breeding. No males remained unpaired for the entire breeding season.

*Clutch size and number.*—As with most shorebirds, the normal clutch size of Spotted Sandpipers is four. The distribution of clutch sizes found was 23 with 1 egg, 16 with 2, 26 with 3, 251 with 4, and 1 with 5 eggs. The mean clutch size of  $3.60 \pm 0.9$  (SD) is less than the mode of four, mainly because laying was sometimes curtailed by predation. Females usually laid complete replacement clutches in such cases. The single clutch of five eggs was laid when the first egg was depredated and the female

TABLE 6. Fates of Spotted Sandpiper eggs laid on Little Pelican Island, Minnesota, 1973–1981.

Year	Total eggs laid	Total eggs hatched	Eggs lost from nest due to							Eggs not hatched		
			Mice	Mink	Birds	Deser- tion	Flood	Human	?	Infer- tile	Pipped	?
1973	112	55	—	—	—	—	—	—	52	—	—	5
1974	123	29	15	0	0	12	4	4	51	1	0	7
1975	157	3	10	87	6	5	15	0	30	0	0	1
1976	60	40	13	0	0	0	0	1	1	2	1	2
1977	116	57	40	0	4 <sup>a</sup>	6	0	2	0	1	0	6
1978	133	42	58	0	3	5	0	0	22	0	0	3
1979	127	63	18	0	13	1	8	0	22	0	0	2
1980	141	72	25	4 <sup>b</sup>	23	8	0	0	2	4	3	0
1981	173	81	26	4 <sup>a</sup>	22	8	0	5	19	1	4	3
1973–1981	1,142	442	205	95	71	45	27	12	199	9	8	29
Percentage of total	100	38.7	18.0	8.3	6.2	3.9	2.4	1.1	17.4	0.1	0.1	0.3

<sup>a</sup> Incubating male depredated by predator, but eggs not eaten.

<sup>b</sup> Depredated by otter (*Lutra canadensis*).

continued to lay four eggs in the same nest at the normal rate.

Spotted Sandpiper females laid up to five complete clutches per season, with a mean of  $2.2 \pm 1.1$  (SD), and at least six females are known to have laid none (see above). The average number of clutches per female per year varied from a low of 1.95 in 1980 to 2.88 in 1975.

*Breeding success and failure.*—Of 1,142 eggs found in this study, 39% hatched. The percentage of eggs hatching during 7 yr varied from 2% in 1975 to 67% in 1976 (Tables 2 and 6). The percentage of nests with one or more eggs hatching ranged from 2% (1975) to 80% (1976) (Table 2). Mice, especially *Peromyscus maniculatus* but occasionally *Microtus pennsylvanicus* (Maxson and Oring 1978), were the most consistent source of egg loss (Table 6). In 1975, a mink ate 87 eggs. Blackbirds caused substantial egg loss in the last 3 yr of the study (Table 6). Losses considered as unknown were due primarily to three sources: mice, birds, and the sandpipers themselves carrying off damaged eggs (Maxson and Oring 1978).

Of 442 chicks that hatched during the study, 58% fledged. On LPI, most chick mortality occurred during the first few days of life (Oring et al. unpubl. data). The only known major source of chick mortality was a juvenile mink that killed all chicks hatching after its arrival on 11 July 1981 (total 43). Other sources of chick mortality are unknown (114). Common Grackles (*Quiscalus quiscula*) took at least one chick and one fledged juvenile, and brooding sand-

pipers are unusually aggressive toward this species (Maxson 1977). Five chicks were deserted by the parent, 5 were killed by neighboring adult Spotted Sandpipers, 3 died at hatching, and at least 1 is believed to have starved.

*Survival in the first year.*—From 1973 to 1981, 256 chicks fledged from LPI. At least 51 (20%) of these have been seen in later years (30 ♀♀, 21 ♂♂, 3 of unknown sex). It is not possible to calculate survival in the first year, because substantial juvenile dispersal to other breeding areas almost certainly occurs. Most immigrants to LPI hatched elsewhere: of 93 males and 63 females entering the breeding population from 1974 to 1982, only 14 (22%) of the females and 13 (14%) of the males were hatched on the island. Whether these immigrants dispersed from other breeding areas as juveniles or as older breeders is unknown. If the patterns of breeding-site tenacity documented on LPI (Oring and Lank 1982, Fig. 2) are representative of birds elsewhere, the immigrant population should include some former breeding birds that failed at other sites.

*Estimating age at sexual maturity.*—The age at first breeding on LPI is known for 14 females banded as nestlings: 10 were 1 yr old, 3 were 2, and 1 was 3. The four females first returning to breed at age 2 or 3 may have bred or attempted to breed elsewhere and then returned to the island, just as a large number of unsuccessful inexperienced breeding females fail to return to LPI (77%,  $n = 22$ ). These data show

TABLE 7. Mean minimum ages and annual return rates of Spotted Sandpipers breeding on Little Pelican Island, Minnesota, 1973–1981.

Year	Females				Males			
	$\bar{x}$ minimum age EXPER <sup>a</sup>	Return rate			$\bar{x}$ minimum age EXPER	Return rate		
		EXPER	INEXP <sup>b</sup>	SUCC <sup>c</sup>		EXPER	INEXP	SUCC
1973	—	—	—	0.70	—	—	—	0.39
1974	2.00	0.60	0.50	0.88	2.00	0.50	0.50	0.45
1975	2.75	0.88	0.13	1.00	2.80	0.33	0.15	1.00
1976	3.33	1.00	—	1.00	3.60	1.00	0.43	0.67
1977	4.50	0.38	0.83	0.58	3.78	0.44	0.85	0.73
1978	3.38	0.50	0.45	0.64	3.00	0.60	0.40	0.58
1979	3.22	0.67	0.38	0.64	3.64	0.82	0.36	0.71
1980	3.67	0.50	0.70	0.60	4.00	0.92	0.55	0.81
1981	3.09	0.45	0.66	0.58	4.14	0.48	0.55	0.54
1973–1981	3.51 <sup>d</sup>	0.60	0.52	0.67	3.72 <sup>d</sup>	0.62	0.48	0.62

<sup>a</sup> EXPER = experienced breeders; annual sample sizes in Table 1.

<sup>b</sup> INEXP = inexperienced breeders; annual sample sizes in Table 1.

<sup>c</sup> SUCC = successful breeders; annual sample sizes in Table 1.

<sup>d</sup> Calculated from 1976–1981 only.

that delayed sexual maturity is not a fixed feature of Spotted Sandpiper population biology, despite the polyandrous mating system in which some females are unable to obtain territories and mates.

The age at first breeding on LPI is known for 13 males banded as nestlings: 4 were 1 yr old, 4 were 2, 2 were 3, 2 were 4, and 1 was 6 yr old when first returning to breed. Like the females, older returning males may have bred elsewhere in earlier years, as 80% ( $n = 25$ ) of unsuccessful inexperienced males failed to return to LPI.

*Mortality during the breeding season.*—Mortality during the breeding season was low. During nine summers, 4 males and 2 females died on the island. Two incubating males were killed at night by a mink, one was taken off a very exposed nest by a Northern Harrier (*Circus cyaneus*), and a fourth became ill and died from unknown causes. One female died during egg production, and one was killed in a mink trap. In addition, two females whose legs were seriously crippled during fights involved with mate acquisition bred but did not return the next year.

*Return to the island and nonbreeding survival rates.*—Return rates of the four sex and experience classes varied from year to year (Table 7). Return rates of males and females did not differ significantly in any single year, although the difference approached significance between experienced females and males return-

ing after the unsuccessful year 1975 (7/8 females returned vs. 3/9 males surviving the breeding season returned; Fisher's exact test, two-tailed,  $P = 0.08$ ). Overall, experienced birds returned in subsequent years more often than did inexperienced ones (61% vs. 50%,  $\chi^2 = 3.83$ ,  $P = 0.05$ ). The most striking exception to this pattern was 1977, when inexperienced males and females returned at apparently greater rates than did their experienced counterparts. There were no differences between the return rates of inexperienced males and females.

Return data, classified by sex and breeding success, are plotted as a function of minimum age in Fig. 2. The return rates of successful birds were higher overall than those of unsuccessful birds (Oring and Lank 1982). Return rates averaged 67% for successful females of all ages and 62% for all males (Table 7). Despite the similarity of these overall patterns of return at different ages, there appear to be differences in the age-specific return probabilities of successful males and females. Figure 2 shows that successful females returned at a rate of 65–70% at all ages. In contrast, successful males breeding at 1 and 2 yr returned less often than did older males (52% vs. 70%,  $\chi^2 = 4.62$ , 1 df,  $P = 0.03$ ). Successful males breeding in their first year appear to have returned less often than did successful females (52% vs. 70%,  $\chi^2 = 3.08$ , 1 df,  $P = 0.08$ ).

Without accurate information on the rate of dispersal, we can estimate nonbreeding season



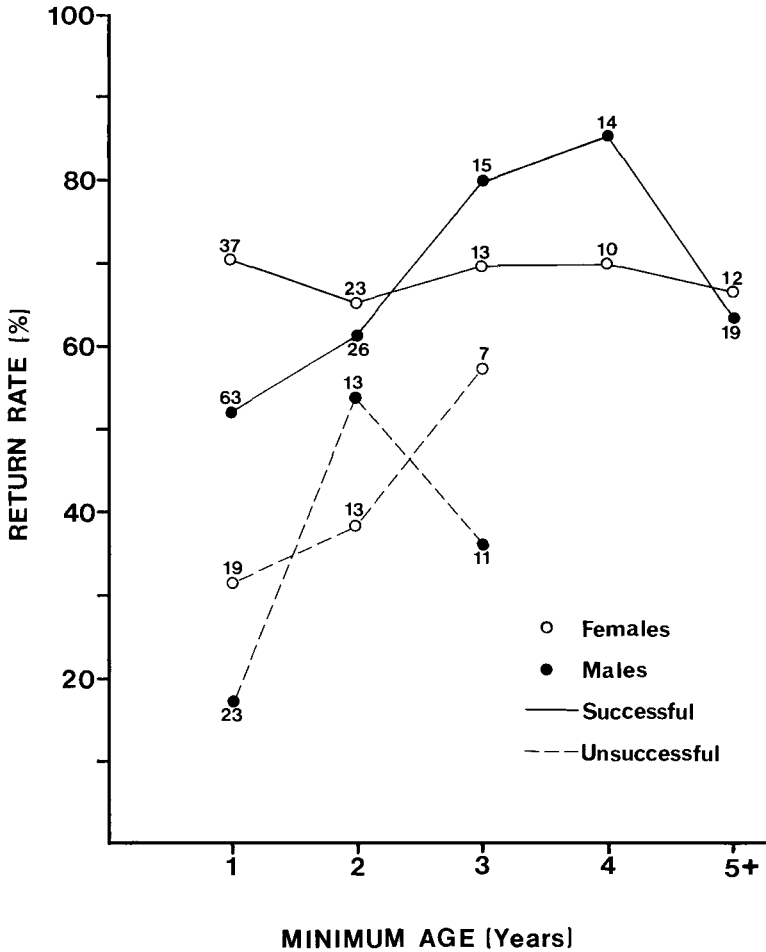


Fig. 2. Age-specific return rates of Spotted Sandpipers breeding on Little Pelican Island, Minnesota. The 5+ points combine information from 8 individual females and 13 individual males. Numbers indicate sample sizes.

survival rates only from groups of birds that always return if alive. This clearly does not apply to unsuccessful Spotted Sandpipers of either sex, especially inexperienced ones. Evidence presented above suggests that successful first- and second-year males either are less site faithful or are suffering higher mortality than are older males and that first-year males are less site faithful than first-year females. We believe that decreased site faithfulness is the primary explanation for sex differences in return rates because: (1) male chicks are less philopatric than female chicks, and (2) 6 males but only 2 females have skipped years and then returned to the island. We do not feel that we can calculate survival rates for males due to their varying

site tenacity with age. On the other hand, in the case of successful females, there is no age-specific change in site tenacity—apparently all, or nearly all, successful experienced females attempt to return. Consequently, it is possible to estimate longevity for this group. These females returned at an average annual rate of 68.4% and bred an average 2.7 yr after first breeding (calculated using the method of Soikeli 1970).

An alternative way of looking at survivorship involves consideration of the mean minimum ages of experienced birds (Table 7). By excluding inexperienced birds from consideration, this number summarizes the post-banding life expectancy for a group of birds that is

strongly site attached (with the possible exception of some males with a minimum age of 2). Minimum ages are artificially low for the first few years, because all experienced birds in 1974 were automatically 2 yr old (see Methods, for determination of minimum age). For both males and females, however, mean minimum age appears to equilibrate at 3.5–3.7 in later years. By looking only at those birds that appear to be site attached, we estimate that the average successful, site-attached bird on LPI lives for about 2.6 yr after the onset of breeding. This figure agrees closely with the figure of 2.7 yr calculated for successful, experienced females above.

Three birds in the study were 8 yr old or older: 1 female and 1 male banded as breeding adults in 1973 bred through 1980, and 1 male banded as a chick in 1973 bred through 1981.

#### DISCUSSION

*Breeding success, return rates, and population dynamics.*—Spotted Sandpipers return to a breeding area more often after nesting success than failure (Oring and Lank 1982, Fig. 2), and the young are somewhat philopatric. These trends result in a rapid increase of local populations during periods of high breeding success until density limits settlement, success, or both. On a small, isolated island such as LPI, the impact of such density-limiting factors is potentially great. The constancy of the LPI breeding population size, the behavioral exclusion of females and males, and the attacks by adults on neighboring chicks indicate that population density limits local population size and productivity, with space being available for approximately 20 females and 30 males. Density effects are closely intertwined with the degree of breeding synchrony in the population, however, a factor we have not yet analyzed in detail.

Widespread reproductive failure, as occurred in 1975, led to emigration of males and inexperienced females and to the low population of 1976. For unknown reasons, despite the low density, there also was no immigration of new females. Several successive failures may lead to local population extinction and to the absence of Spotted Sandpipers in areas that appear suitable for breeding. The degree to which a single poor year, like 1975, leads to population decline is related to the age structure of the population. When the population is com-

prised of a relatively large number of experienced birds, most of which were successful there in previous years, it is resilient to failure. On the other hand, when most birds are naive breeders, failure may lead to emigration by both sexes and, eventually, to local extinction.

Although most successful males and females show breeding-site fidelity, some do not. Successful females probably return except in the case of a major habitat change. Successful males in their first and second breeding seasons return at lower rates than females and older males, implying higher mortality, weaker site fidelity, or both. One logical explanation of high mortality of young males would be that extensive male incubation and brood rearing has high costs in terms of predation or body condition. This was not found to be the case on LPI (males had no significant weight loss during incubation and only three males were depredated in 200 male breeding years), making this explanation of non-return unlikely. We conclude that young males are somewhat less site faithful than young females, even following success.

Greater female site fidelity may be due to the fact that among females, but not males, experience resulted in higher hatching and fledging success (Tables 3, 4, and 5). Males are limited to one successful reproductive effort per season, and most males that persist on the island eventually are able to enter the breeding population, thus limiting variability in male reproductive success, regardless of experience. At the behavioral level, the fact that females migrate north in advance of males may be important. Females return and reclaim territories with an expectation, but no certainty, that males also will return. Later migrating males may be actively recruited *en route* by females with suitable territories. As experience with a territory does not appear to provide a substantial advantage to males, breeding with a new female may be a more productive strategy than returning home with the expectation, but not the certainty, of a mate's returning and suitable breeding habitat remaining.

*Spotted Sandpipers at other localities.*—Spotted Sandpipers have been carefully studied at several localities (Table 8). At each site, polyandry was found, and females laid more eggs on average than is typical for monogamous sandpipers. These studies revealed considerable variation between sites in polyandry incidence, predation, and eggs laid and hatched

TABLE 8. Comparison of reproduction in three Spotted Sandpiper populations.

	LPI, Minnesota 144 ♀ yr	Lake Itasca, Minnesota 12 ♀ yr	Gull Island, New York 11 ♀ yr
Polyandry (♂ ♂/♀)	1.66	1.17	1.86
Eggs per female	8.17	6.33	8.00
Eggs hatching per female	3.07	2.33	7.64
Percentage hatching nests	44	37	86

per female. The between-site variation in these short-term studies of small populations, however, was not greater than the interyear variation observed on LPI.

*Population biology and the incidence of polyandry.*—Over the course of this study, the breeding sex ratio on LPI averaged 1.39 males per female and varied from 1.11 to 2.00. From banding data (159 ♀♀, 162 ♂♂; Oring 1982) we believe the adult sex ratio is near unity. Skewed breeding sex ratios, as are found in the Spotted Sandpiper, may result from any of several demographic features of a population: differential fledging rates, juvenile mortality, age at first breeding, recruitment, or adult mortality. We believe that the skewed sex ratio witnessed in our population was due to a higher mean age at first breeding of females and greater male recruitment. This conclusion is based upon: (1) lack of evidence for differential juvenile or adult mortality, (2) direct observations of marked individuals showing that females are socially excluded from breeding at 2+ times the rate of males, and (3) although males often are prevented by other males from settling on particular sites, in contrast to females, males that persist gain access to breeding females and territories when primary mates can no longer exclude them following the onset of incubation. In summary, polyandry in Spotted Sandpipers, while somewhat facultative (Oring and Knudson 1972, Jenni 1974, Maynard Smith 1977), is not merely facultative, for in large part the skewed sex ratio of breeding birds results directly from the behavior of males and females.

Asynchronous male arrival and low density reduce competition among males and hence increase the potential for polyandry. In 1976 we recorded the lowest density of both sexes and the greatest asynchrony in male arrival of the study. Consequently, no males were excluded from the population by male-male behavioral

interactions, and the incidence of polyandry was unusually high.

If we accept the ages at which birds banded on LPI as chicks first returned to breed as indicating *age at first breeding*, females first breed at approximately 1.4 yr; males at 2.5. These figures are highly biased, however, due to sexual differences in philopatry (Oring and Lank 1982). We believe 1.4 yr approximates reality for females, based upon our frequent observations of inexperienced females being excluded from the breeding population. Due to evidence for low male natal philopatry (Oring and Lank 1982), however, and our observation that essentially all males that persist are able to enter the breeding population, we believe the *age at first breeding* for males approximates 1.0 yr. Given our lack of evidence for differential mortality and the fact that the differences between age at first breeding for males and females is inadequate to account for the observed breeding sex ratio, we consider the figure of 1.4 yr for females to be conservative.

Just as sex ratio and synchrony influence the incidence of polyandry, so does the level of nest predation. Although predation, as an ultimate factor, may have played a key role in the development of male incubation patterns (Emlen and Oring 1977, Oring 1982), today predation may either limit or facilitate *resource-defense polyandry*. If predation occurs while the initial pair-bond is intact, polyandry may be limited, because: (1) exclusion of secondary males may increase, as nonincubating males are free to defend territories; and (2) the courting of secondary males by females may decrease during reneating. On the other hand, when nest destruction occurs after the severing of the pair-bond, predation may facilitate polyandry in that: (1) males may vacate territories, enhancing settlement of secondary males; or (2) there may be a recycling of males (e.g. 1975) such that a male mates with 2+ females. In the

TABLE 9. Summary of life history characteristics of scolopacids.

Variable	Spotted Sandpiper	Temminck's Stint	Dunlin
$\bar{x}$ age of first breeding <sup>a</sup>	1.0/♂, 1.4/♀	1.8/♂, 1.0/♀	1.8/♂, 1.8/♀
$\bar{x}$ eggs parented/year	5.7/♂, 7.9/♀	6.9/adult	4.5/♂, 4.5/♀
$\bar{x}$ clutch size	3.6	3.9	3.9
Percentage nests hatching eggs	44	52	59
Presence of biparental care	+ to -	-	+
$\bar{x}$ annual return rate (%)	54/♂, 58/♀	79/♂, 71/♀	77/♂, 72/♀
$\bar{x}$ longevity (yr) <sup>a</sup>	3.5/♂, 3.7/♀	7.0/adult	5.3/adult
Oldest known individual	8	11	14
Years studied	9	10	8
Source	This study, Oring and Lank (1982)	Hildén (1978)	Soikelli (1967, 1970)

<sup>a</sup> See text for assumptions involved in estimating  $\bar{x}$  age of first breeding and mean longevity.

latter case, both polyandry and polygyny are facilitated.

The nature of the Spotted Sandpiper polyandrous system is such that the *operational sex ratio* (Emlen and Oring 1977) is skewed in favor of females, there is greater intrasexual competition among females than among males, and the variance in annual female reproductive success is greater than that among males (Oring et al. unpubl. data). Increased competition among females places a premium on females to be on familiar ground, and thus experience is a greater asset to females than to males in terms of relative reproductive success. This scenario accounts for many of the differences in female and male population biology. (1) Females breed at a 28% lower density than males. (2) Females are behaviorally excluded from the breeding habitat at 2+ times the rate of males. Conversely, some males persist until they enter the breeding population in mid-season, whereas essentially all females unsuccessful at acquiring territories early in the season are unsuccessful for the season. (3) Females exhibit greater natal philopatry than do males (Oring and Lank 1982). Chicks hatched on LPI accounted for up to 40% of the annual female breeding population but only 20% of the males (Table 1). Returning females first breed on LPI at an age of 1.4 yr whereas males first breed locally at an average age of 2.5 yr. (4) Successful females may exhibit greater site tenacity than successful males following their first year of breeding ( $P = 0.08$ ). This reduced site tenacity of young successful males accounts for the greater fluctuation in the age structure of males as opposed to females. In short, males have

more options open to them than do females in terms of where and when they breed.

*Population biology and life history strategies.*—All of the basic features of Spotted Sandpiper populations, including age structure, sex ratio, rates of immigration and emigration, reproductive effort and success, and mortality are best viewed as the result of individual bird strategies characterized by extreme lability. Relative to other scolopacids with multi-purpose breeding territories, Spotted Sandpipers are generalists occupying a wide temperate distribution in early successional habitat. Nesting and chick-rearing normally occur in semi-open areas near the water's edge. Periodic extinction of Spotted Sandpiper populations occurs due to: (1) plant succession proceeding to the point where semi-open areas become overgrown, (2) flooding, and (3) nest and chick predation. On the other hand, new areas become suitable for colonization through the regular scouring action of water and ice, as well as through the activities of humans. Often such newly created areas are initially occupied by less than a full complement of the many predators typical of the temperate zone. Thus, there is relatively frequent change in the suitability of Spotted Sandpiper breeding habitat.

Turnover in suitable habitat may have enhanced selection for the active dispersal of young as well as for the dispersal of adults following catastrophes (Oring and Lank 1982). Compared to other multi-purpose, territorial scolopacids, only three species, Spotted Sandpipers, Temminck's Stint, and Dunlin, are known well enough to allow satisfactory comparison of natural history features related to

pioneering behavior. Table 9 compares life history features of those three species. Because substantial variation in the population biology of these species doubtless occurs between geographic areas as well as over time, such comparisons must be considered as tentative.

The Spotted Sandpiper appears to be the most pioneering of the three species. Spotted Sandpipers breed first at an earlier age, lay more eggs per breeding female per year, probably live shorter lives, and have lower per nest success. Dunlin, by contrast, breed initially at a relatively old age, lay relatively few eggs per female per year, may continue to breed over a greater number of years, and have greater nest success. Temminck's Stints are intermediate with regard to pioneering features. The Common Sandpiper (*Actitis hypoleucos*), a close relative of the Spotted Sandpiper, is characterized by very low annual mortality (19%) and high site fidelity (85%) (Holland et al. 1982). Thus it appears similar to the Dunlin in life-history features.

Today, Spotted Sandpipers occupy by far the largest geographical range of any of the 30+ species of North American sandpipers. This broad distribution is a result of the widespread availability of semi-open areas in proximity to water, a dispersal system that enhances colonization of these areas, the high reproductive rates of polyandrous females, and the generalized behavior patterns that allow breeding success under a wide range of ecological conditions.

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