

BANDING RETURNS, ARRIVAL TIMES, AND SITE FIDELITY IN THE SAVANNAH SPARROW

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The breeding biology of the Savannah Sparrow (*Passerculus sandwichensis*) has been studied from numerous angles (Dixon 1972, 1978; Stobo and McLaren 1975; Welsh 1975; Weatherhead 1979a, b; Weatherhead and Robertson 1980; Bédard and Meunier 1983). Little attention has been devoted, however, to the temporal pattern of arrival on the breeding grounds, the attachment to specific breeding sites, or the effects of age upon these aspects of reproduction. Patterns such as these have a direct bearing on site and mate selection, processes which are central to current theories of avian mating systems (see Oring 1982 for a recent review). The aim of this study is to summarize and interpret our observations on the biology of the Savannah Sparrow in the context of social organization.

STUDY AREA AND METHODS

The study was conducted from 1976 – 1981 in the Isle Verte National Wildlife Area, 225 km NE of Québec City, Québec, Canada. The 20-ha rectangular study area (10 ha in 1976) consisted of a *Spartina* salt marsh and abandoned field ecotone marked with wooden stakes at 30-m intervals. The two long sides of the rectangle were bound by habitats inhospitable to sparrows (flooded marsh and a highway bordering built-up areas). The study area was used by about 55 breeding pairs and a variable number of bachelor males every year. All males were mist-netted within a few days of arrival, often having been lured to the net by a recording of Savannah Sparrow songs. Over half of the females were also captured, most while incubating or feeding young. The birds were individually marked with colored plastic leg-bands, sexed by the presence or absence of a cloacal protuberance, and weighed. Measurements of wing-length (flattened) were also obtained in 1978 and 1980. Between 1976 and 1980, 281 nestlings were banded at 6 days of age with distinctive “wide-striped” color bands, but none were ever resighted on the study area.

Observations were not equally intensive in all years of the study. Arrival dates were thoroughly monitored in 1978, 1980, and 1981 only. Site fidelity data and banding returns for both sexes, however, are available for all years of the study. Every year, a 100-m-wide band outside each end of the study grid was surveyed occasionally to check for the possible presence of individuals banded within our study area.

The entire grid was visited daily from mid-April (18 May in 1979) until early August (late June in 1979 and late May in 1981). The locations of all activities performed by males (singing, agonistic encounters, foraging, movements, etc.) were recorded on a map of the area (1 cm = 5 m), while the activity patterns of females were mapped in a less detailed fashion. This mapping enabled us to delineate an “activity space” for each individual, the center of which was subjectively determined after excluding the outermost 5% of observation points. Site fidelity of males was determined by comparing the center of the activity space during territory establishment (1–15 May) in one year with that used at the same stage in the following year. Fidelity was measured in terms of the distance (m) between two such

TABLE 1
RETURN RATES OF ADULT MALE AND FEMALE SAVANNAH SPARROWS KNOWN TO BE AT
LEAST 1 YEAR OLD WHEN BANDED DURING THIS STUDY

Year banded	No. banded		No. returning 1-4 years after banding							
	M*	F*	1		2		3		4	
			M	F	M	F	M	F	M	F
1976	24	11	11	5	9	1	4	1	1	0
1977	59	33	19	10	9	2	6	0	1	0
1978	61	34	21	13	14	7	6	3	—	—
1979	25	22	9	5	4	2	—	—	—	—
1980	53	22	26	5	—	—	—	—	—	—
Total	222	122	86	38	36	12	16	4	2	0
% returning			38.7	31.2	21.6	12.0	11.4	5.1	2.5	0

* M = males; F = females.

points from successive years for a given individual. For females, nest location (and exceptionally, the center of the activity space) was used to assess site fidelity between successive years. Statistical procedures followed Siegel (1956), and Sokal and Rohlf (1981).

RESULTS

Banding returns.—Of 344 breeding adults banded during the study, 167 returned for at least one (and a maximum of four) additional breeding season(s). The slight tendency for males to return at a higher rate than females the year following banding (Table 1) was not statistically significant, whether using a conventional frequency analysis ($\chi^2 = 1.65$, $df = 1$, $P = 0.20$, all years combined) or a multivariate log-linear model (Bishop et al. 1975). In the latter analysis, we found no interaction between year, sex, and status (returns at least 1 year or does not return) ($\chi^2 = 4.9$, $df = 4$, $P = 0.30$).

Since observations were not conducted after 1981, only the cohorts banded in 1976 and 1977 can be used to obtain a complete estimate of adult mortality. Assuming that all this cohort had disappeared by 1982, the weighted annual mortality rates (Farner 1955) are 0.55 and 0.69 for 1976 and 1977, respectively. Therefore, in any given year, first-year birds made up the highest proportion of the breeding population. No bird banded either as a nestling or as an adult was ever observed settling in the 100-m band at either end of the study area.

Arrival dates.—The first male Savannah Sparrows arrived between 19 and 24 April. In 1978, the arrival period was protracted, with an average of 4.4 new males appearing in the study grid each day from 23 April until

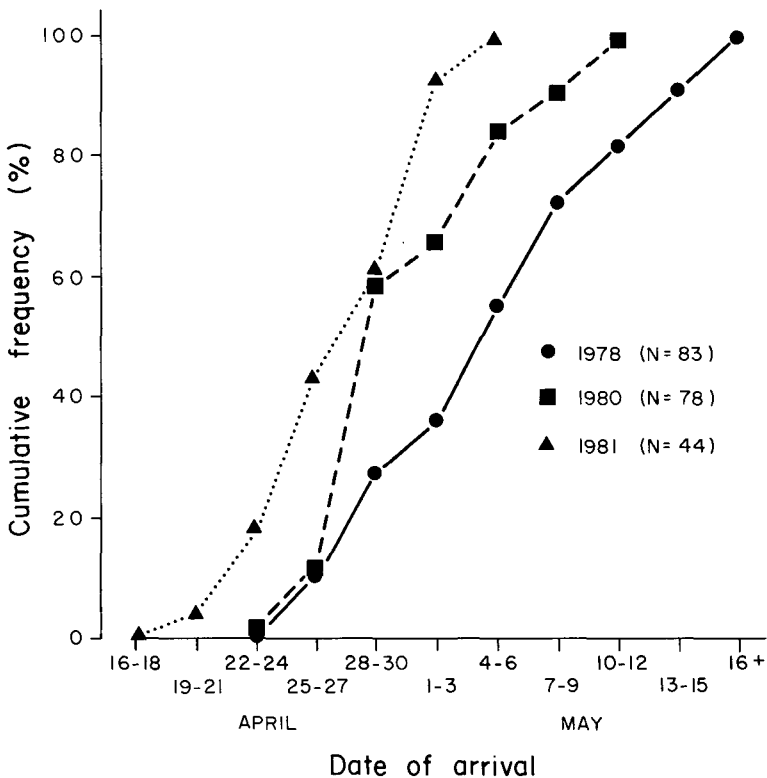


FIG. 1. Cumulative number of male Savannah Sparrows arriving at Isle Verte from mid-April–mid-May for 3 years in which the study area was surveyed daily during the settlement phase.

16 May. By then, all males had established a territory (Fig. 1). The 1980 season showed a different temporal pattern of male arrival: a sudden wave of 27 individuals arrived 29 April, accounting for 35% of all the territorial males that year. In 1981, the daily flow of incoming males was steadier than in 1980, except for a wave of 13 birds that appeared on 1 May. The population build-up of males in 1981 spanned 16 days, as opposed to 19 days in 1980 and 24 days in 1978. The Kolmogorov-Smirnov two-sample test (Siegel 1956) was used to examine differences in the distributions of arrival dates. The pattern of arrival was significantly more protracted in 1978 than in 1980 ($D = 0.313$, $N = 83,78$, $P < 0.001$) and more spread out in 1980 than in 1981 ($D = 0.329$, $N = 78,44$, $P < 0.01$).

The arrival dates of females were difficult to record as they were se-

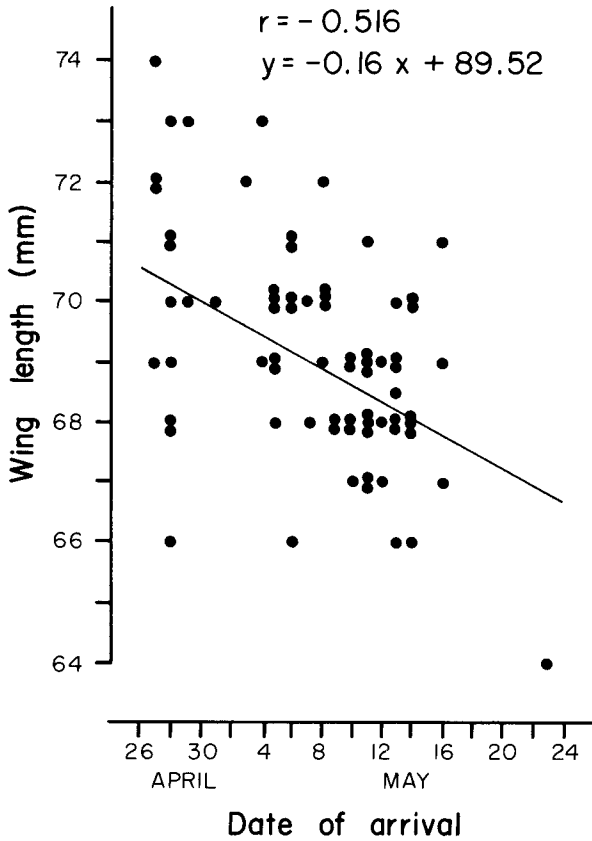


FIG. 2. Wing-length in relation to date of arrival for male Savannah Sparrows at Isle Verte during 1978 (includes 66 first-year males and 12 previously-banded older males).

cretive and frequently escaped notice. Females were first seen 18, 12, and 20 days after the first males in 1978, 1980, and 1981, respectively.

To establish whether wing-length increases with age, we examined a sample of 15 males that had been recaptured over a period of 1–3 years. Twelve individuals were re-measured the year after banding and three others were re-measured 2 years after banding. Wing-length increased significantly between captures by an average of 1.7 mm ($t = 3.9$, $N = 15$, $P < 0.0025$, one-tailed t -test for paired comparisons, Sokal and Rohlf 1981).

This indicator of age was thereby used in testing the effect of age on

TABLE 2
AVERAGE WING LENGTH (MM) OF UNBANDED MALES AND OF RETURNING BIRDS FOR 1978
AND 1980

Year	Previously-banded returning males $\bar{x} \pm SE$	Unbanded males $\bar{x} \pm SE$	Student's <i>t</i> (one-tailed)
1978	70.8 \pm 0.5 (N = 12)	68.9 \pm 0.2 (N = 62)	2.85 ^a
1980	71.4 \pm 0.8 (N = 7)	69.5 \pm 0.2 (N = 51)	3.46 ^b

^a $P < 0.005$.

^b $P < 0.0005$.

male arrival dates. In 1978, earlier-arriving males had longer wings ($r = -0.516$, $N = 72$, $P < 0.01$, Fig. 2), i.e., older males arrived earlier that year. The significance of this correlation remained unaffected following removal of the particularly short-winged individual from the analysis (without outlier, $r = -0.456$, $N = 71$, $P < 0.01$). In 1980, we obtained accurate arrival dates for 78 males (unbanded and returning), but only seven of the 34 older banded males were recaptured for wing measurement. Therefore, we could not expect to detect a significant correlation between wing-length and arrival date for that year ($r = -0.095$, $N = 58$, $P > 0.05$).

The wing-length data also suggested that unbanded newcomers were, on the average, smaller (thereby younger, see above) birds and thus probably first-year males. In both 1978 and 1980, these birds had a significantly shorter average wing-length than the previously-banded returning males (Table 2). Therefore, we grouped arrival dates according to these two size/age categories (unbanded vs banded) and calculated two frequency distributions as in Fig. 1. The span of arrivals of the unbanded first-year males was significantly longer than that of older returning birds in 1978 (Kolmogorov-Smirnov test, $D = 0.3$, $N = 55,28$, $P < 0.05$). Again, no significant difference emerged in 1980 ($D = 0.12$, $N = 5,28$, $P > 0.05$) or in 1981 ($D = 0.20$, $N = 12,33$, $P > 0.05$). The average arrival date was significantly earlier for banded males in 1978 (3 May vs 7 May, $t = 2.82$, $df = 81$, $P < 0.01$), but not in 1980 ($t = 1.60$, $df = 76$, $P > 0.05$), nor in 1981 ($t = 0.36$, $df = 47$, $P > 0.05$).

Site fidelity.—Of 344 banded sparrows, 167 settled in the study area for two or more successive breeding seasons. The distance moved by these individuals between successive seasons was small; 80% of all the moves were less than 60 m, which represents the average diameter of territories

TABLE 3
THE NUMBER OF BANDED SAVANNAH SPARROWS MOVING DIFFERENT DISTANCE
CATEGORIES BETWEEN SUCCESSIVE BREEDING SEASONS^a

	Distance (m)														Total			
	0-20		21-40		41-60		61-80		81-100		101-120		121-140		141+		M	F
	M	F	M	F	M	F	M	F	M	F	M	F	M	F				
First move after banding	24	5	29	13	10	9	3	2	4	1	2	1	2	0	11	1	85	32
All subsequent moves	12	2	18	1	5	3	2	0	3	1	0	1	0	0	1	1	41	9
Total	36	7	27	14	15	12	5	2	7	2	2	2	2	0	12	2	126	41

^a Data are combined for all years of the study (1976-1981).

in our study area (Bédard and LaPointe, unpubl.). No difference was found between the sexes (Kolmogorov-Smirnov two-sample test; $D = 0.20$, $N = 126$ males, 41 females, $P > 0.05$, Table 3). There was no significant difference between first moves after banding and all moves in subsequent years for either males or females (Table 3, males: $D = 0.15$, $N = 85,41$, $P > 0.05$; females: $D = 0.24$, $N = 32,9$, $P > 0.05$).

Social context and breeding success may also influence site fidelity. However, the presence or absence of a nesting attempt in a given year did not influence the distance moved in the following season by males or females (Kolmogorov-Smirnov test; males: $D = 0.16$, $N = 74,52$, $P > 0.05$; females: $D = 0.09$, $N = 32,9$, $P > 0.05$). Likewise, males or females with breeding failures did not move farther the next year than those who succeeded in fledging young (males: $D = 0.15$, $N = 18,52$, $P > 0.05$; females: $D = 0.05$, $N = 10,20$, $P > 0.05$). Finally, both males and females remained just as attached to their site following a change of mate than if they had remained with the same partner in the succeeding year (males: $D = 0.26$, $N = 17,12$, $P > 0.05$; females: $D = 0.33$, $N = 9,15$, $P > 0.05$). In contrast, moves that took place between two successive nesting attempts within the same breeding season were always shorter than moves between seasons (males: $D = 0.22$, $N = 48,126$, $P < 0.05$; females: $D = 0.40$, $N = 35,41$, $P < 0.01$).

DISCUSSION

The lack of differential return rates between male and female Savannah Sparrows in this population agrees with Dixon's (1972) observations on Kent Island for the same species. This contrasts with the significantly lower female return rate in a number of monogamous passerines that nest

in open-ground habitats, such as the Clay-colored Sparrow (*Spizella pallida*) (Walkinshaw 1968, Knapton 1979), the Field Sparrow (*S. pusilla*) (Best 1977), the Seaside Sparrow (*Ammospiza maritima*) (Post 1974), and the Song Sparrow (*Melospiza melodia*) (Nice 1937).

More perplexing than differences in average arrival date for the population as a whole are differences in the temporal pattern of arrivals among years. In boreal latitudes, there should exist a premium on early spring arrival. This does in fact seem to be a fairly universal trait in passerines (Nice 1937, Walkinshaw 1968, Best 1977), generally seen as a result of intrasexual selection. Therefore, one would have predicted that the delayed arrivals in the late 1978 season would have been accompanied by influxes of males compensating for the delay in the migration. To the contrary, this pattern of arrival was exhibited in the 2 early years.

The significant correlation between wing-length and arrival date was based only on the 1978 data, when a high proportion of older males were recaptured and when arrivals were spread out. In 1980 and 1981, there was less effort to recapture returning males; this and the short time-span of male arrivals prevented us from detecting any such trend.

The effect of age on arrival date has been examined in other passerines. Walkinshaw (1968) concluded that "older" male Field Sparrows returned earlier in the spring, but Best (1977) was unable to substantiate this finding in the same species. Catchpole (1972) also found that older male *Acrocephalus* warblers were always the first to settle back on their territories in the spring, although they were not necessarily the first to attract a mate (Catchpole 1980).

Males arriving earlier might increase their chances of obtaining a better territory. Since returning Savannah Sparrows are remarkably site faithful (see also Dixon 1972, Stobo and McLaren 1975), this can obviously not work. The premium on early spring arrival, if it exists at all at Isle Verte, must therefore serve an alternative purpose, such as to extend the breeding season. This would be advantageous in an area where half of the first nesting attempts end in failure (during the years 1977, 1978, and 1980, 66 of 133 [49.4%] first attempts failed [Bédard and LaPointe, unpubl.]).

The existence of site fidelity raises the question of whether the birds are optimizing their choice of breeding location. If such optimization were occurring, then we should witness individual movements towards new sites in successive years, at least by birds that were forced to occupy "poor" locations during a given season (where nesting attempts failed). For instance, late-arriving first-year males are known to squeeze between already established birds (Bédard and LaPointe, unpubl.). In the following year, they should try to improve their situation by choosing a more favorable location, perhaps following an earlier arrival. The results shown

here indicate that this does not occur and Oring (1982) offers an explanation for this phenomenon. Under conditions of low environmental stability, lack of ability to assess habitat quality, or short life expectancy, "the advantages of site fidelity may more than compensate for possible advantages of moving to territories of apparently higher quality," (Oring 1982:35). The Savannah Sparrows we studied appear to adopt this alternative strategy. As an example, the late-arriving (20 May 1977) male 065 returned to the same site for 5 years in a row, despite the fact that he never even managed to attract a female. Several males also remained faithful to the same location despite a string of successive breeding failures within and between seasons. Both Searcy (1979) and Best (1977) have noted instances of passerine males similarly passing up opportunities of moving to "better" territories.

Therefore, site selection by male Savannah Sparrows after their arrival on the breeding grounds at Isle Verte appears to be influenced primarily by previous occupancy. The same seems to apply to females, although our sample sizes are smaller. Female site fidelity is further supported by the fact that female return rates equal those of males. This site fidelity feature is, of course, not a new finding (e.g., Darley et al. 1977, Freer 1979, Harvey et al. 1979, and others); in the Field Sparrow, Walkinshaw (1968) and Best (1977) found likewise. Even in polygynous Red-winged Blackbird (*Agelaius phoeniceus*), Nero (1956) made a strong case for site fidelity, but, except for Searcy (1979), few others have associated this characteristic with Red-winged Blackbirds.

SUMMARY

The Savannah Sparrow (*Passerculus sandwichensis*) was studied at Isle Verte, Québec, during the breeding season from 1976–1981. The temporal arrival pattern of males varied markedly between the 3 years of the study for which we had complete data: the time-span of arrivals diminished from 24–19–16 days for 1978, 1980, and 1981, respectively. Wing-length was found to be an indicator of age. During the only year with complete data we found that older (longer-winged) males arrived earlier. Birds banded as nestlings (N = 281) never returned to the study area to settle as breeders. Birds having bred once in the study area were never found to settle elsewhere (i.e., in a 100-m belt adjacent to the area). Site fidelity was evaluated by comparing the position of the activity spaces occupied by known individuals at equivalent periods of successive seasons; 80% of all moves were less than the average diameter of a territory at Isle Verte (60 m). The distance moved did not vary between sexes, nor did it differ when nesting was not attempted, when nesting failed, or, when change of mate occurred. Strong site fidelity in this population of Savannah Sparrows is viewed as an alternative strategy to habitat quality re-assessment upon spring arrival.

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