

INFLUENCE OF PARENTAL AGE AND SEASON ON SAVANNAH SPARROW REPRODUCTIVE SUCCESS

JEAN BÉDARD

AND

GISÈLE LAPOINTE

ABSTRACT.—The age of Savannah Sparrow parents had no clear influence on nesting phenology, clutch size, or net reproductive output (number of young fledged) at Isle Verte, Québec, Canada. Older females started nesting earlier in one of two study years which had complete data. Nestlings reared in the second half of the season spent about one day less in the nest and gained weight significantly faster than those reared during the first half.

Breeding success has been found to be positively correlated with age in a number of passerines (Crawford 1977, De Steven 1978, Harvey et al. 1979, Ross 1980b, and others). In the Savannah Sparrow (*Passerculus sandwichensis*), older males settle earlier in the spring on their former breeding territories (Bédard and LaPointe 1984a) while their mates begin nesting faster and also re-nest more rapidly after each brood than mates of yearling males (Ross 1980a). The ability to make an earlier start, along with a tendency to lay larger clutches and/or to be more efficient at rearing nestlings (Ross 1980a, b) could account for improved breeding performance with age.

As part of a larger study of Savannah Sparrow biology in eastern Québec (Bédard and Meunier 1983; Bédard and LaPointe 1984a, b; Meunier and Bédard 1984), we gathered standard information on reproductive effort and breeding phenology in a population in which most birds were individually marked and aged. Our objectives were to verify whether or not breeding performance improves with age in this short-lived species and to see if there is an advantage to early breeding. More specifically, we attempted to answer the following questions:

- (1) Does age of the pair members influence initiation date?
- (2) Does the age of the female influence the size of the clutch laid?
- (3) Does the age of either parent influence net breeding output (number of young fledged)?
- (4) Does early breeding insure optimal nestling growth rate and/or fledging weight?

METHODS

The study was conducted from 1976 to 1980 in the Isle Verte National Wildlife Area, 225 km northeast of Québec City, Canada. The 20-ha area (10 ha in 1976), staked at 30-m inter-

vals, straddled several distinctive belts of vegetation from the upper levels of a strongly tidal salt marsh to abandoned agricultural fields (see Bédard and LaPointe 1984b for a more complete description). The number of territorial males settling in the study site was 43, 66, and 63 in 1977, 1978, and 1980, respectively. Of these males, 9, 26, and 22 failed to attract a mate in those three years. We mist-netted all males within a few days of arrival (one in 1978 and five in 1980 resisted capture), often luring them with a recording of Savannah Sparrow song. Females were captured while either incubating or feeding young. In 1977, 21 (including 5 returning birds) out of 34 breeding females were banded; in 1978, 39 (11 returning) out of 40 were banded; in 1979, 32 (16 returning) out of 32; and in 1980, 32 (12 returning) out of 41. The birds were individually marked with colored plastic leg-bands, and sexed by the presence or absence of a cloacal protuberance, and by subsequent behavior. Commencing with the second year of the study, all unbanded birds settling in the study area were assumed to be yearlings. This assumption was made on the following basis (from Bédard and LaPointe 1984a): (1) individuals of both sexes are strongly site-faithful; (2) wing-length increases with age (investigated in males only) and unbanded birds of that sex had significantly shorter wings than banded, returning individuals. Given these two age-classes for each sex, we established four pair-bond types: older male and older female, older male and yearling female, yearling male and older female, and yearling male and yearling female. Observations were not equally intensive in all years of the study. We visited the entire grid daily, however, from mid-April (18 May in 1979) until early August (late June in 1979), and our effort to observe nesting was very intensive and fairly even between years 1977, 1978, and 1980 (about 1,000 man-hours/year).

We made daily records of the space used by all birds on maps of the study area (scale: 1 cm = 5 m) by noting the position of aggressive encounters between neighbors, the perches on which the birds sang, and their foraging and other movements.

Each year we systematically searched the study grid for nests. We found most (161/214) during laying or during the first half of incubation. Although the remaining 53 nests were found during the nestling stage, daily monitoring of parental behavior had revealed their presence beforehand. We have excluded these 53 cases from calculations of nesting phenology.

We marked eggs and nestlings individually, and weighed the latter daily to the nearest 0.1 g with a Pesola scale, except during cold and/or rainy weather. Since hatching was often asynchronous, nests sometimes contained nestlings of different ages.

Our statistical tests followed the procedures described in Sokal and Rohlf (1981) and in Siegel (1956). All Mann-Whitney U-tests are for large samples and are one-tailed. Throughout the analyses, mean values are accompanied by the standard error of the mean (SE). Statistical packages used for computer analysis include SAS (SAS Institute 1982) and SPSS (Nie et al. 1975).

RESULTS

OVERALL NESTING PHENOLOGY

The onset of laying varied little among years. The earliest first clutch was started on 20 May 1980, and the latest first clutch was started on 26 May 1977. We also noted slight variability in other phases of the breeding cycle. The duration of the nest initiation period was 50, 46, 53, and 58 days for 1976, 1977, 1978, and 1980, respectively, while the duration of the nesting season (number of days between the onset of laying and the last day of fledging) was 68, 61, 77, and 76 days for the same respective years.

AGE AND BREEDING PHENOLOGY

We collected enough information in 1978 and 1980 to examine the relation between initiation date and parental age by pair-bond type. Using one-way analysis of variance, we found that initiation date did not vary among the four pair-bond types (in 1978: $F = 2.76$, $df = 3,26$, $P = 0.06$; in 1980: $F = 1.15$, $df = 3,30$, $P = 0.35$). However, in 1978, female age alone did affect initiation date. In that year, nine returning females laid their first egg 4.2 ± 3.4 (SE) days after the first egg was laid (taken as day 0), while 22 yearling females laid 9.7 ± 5.1

days after day 0 (Mann-Whitney U-test, $z = 2.81$, $P < 0.0025$).

PARENTAL AGE AND CLUTCH SIZE

Before attempting to isolate the influence of age on clutch size, we ascertained that year, habitat, and date of laying did not affect this value. We found no difference in the mean clutch size of first nesting attempts among years (Kruskal-Wallis ANOVA, $P = 0.41$) for 1976 (4.1 ± 0.1 , $n = 23$), 1977 (4.0 ± 0.1 , $n = 43$), 1978 (4.1 ± 0.1 , $n = 30$) and 1980 (3.9 ± 0.1 , $n = 45$). We were also unable to detect consistent differences in clutch size among birds in the marsh versus those in the agricultural habitat during any of the years of the study (Mann-Whitney U-test, marsh vs. field, $P > 0.05$). Birds occupying a mosaic of habitat types were excluded from this analysis. Finally, the date of initiation (first attempts of individually-marked females only) for clutches of 3 eggs or less, 4 eggs, and 5 eggs did not differ significantly from each other (Kruskal-Wallis ANOVA, $df = 113$, $P = 0.605$).

The size of first replacement clutches was significantly smaller (3.8 ± 0.1) than that of first clutches of the same females (4.1 ± 0.1 , Student's t -test for paired samples, all years, $t = 2.63$, $n = 45$, $P = 0.006$). Unfortunately, the small sample size in some year classes prevented us from establishing the effect of age on this reduction.

We compared the clutch size (first attempts only) of 19 marked females between the year they were banded as yearlings and one ($n = 14$) or two ($n = 5$) years later so as to detect possible individual variation in clutch size with age. Clutch size averaged 4.2 ± 0.1 in the year of banding, 4.2 ± 0.2 one year after, and 3.8 ± 0.3 two years after banding (t -test for paired values, $P > 0.05$ in all comparisons). We also failed to find an influence of age on clutch size between the categories of returning and yearling females (first attempts only) in 1977 ($z = 0.98$, $P = 0.16$), 1978 ($z = 1.58$, $P = 0.057$), and in 1980 ($z = 1.25$, $P = 0.10$). Furthermore, one-way analysis of variance on clutch size did not reveal any differences among the four pair-bond types (Table 1) in 1977 ($F = 0.36$, $df = 3,39$, $P = 0.78$), in 1978 ($F = 0.80$, $df = 3,35$, $P = 0.50$), or in 1980 ($F = 0.18$, $df = 3,41$, $P = 0.91$).

PARENTAL AGE AND NET REPRODUCTIVE OUTPUT

Older females consistently fledged more young than yearlings in all years of the study, but the differences are not statistically significant (t -tests, $P > 0.05$). The mean output for older and yearling age classes are, respectively: $1.4 \pm$

TABLE 1. Mean clutch size of first nesting attempts according to the age of both parents (pair bond type) at Isle Verte, Québec (sample sizes are in parentheses).

Year	Pair bond type			
	Older male Older female	Older male Yearling female	Yearling male Older female	Yearling male Yearling female
1977	4.0 ± 0 (1)	3.7 ± 0.6 (6)	3.8 ± 0.6 (4)	4.0 ± 0.1 (32)
1978	4.5 ± 0.2 (6)	4.0 ± 0.3 (8)	4.0 ± 0.4 (4)	4.1 ± 0.1 (21)
1980	3.8 ± 0.3 (6)	4.0 ± 0.2 (9)	3.9 ± 0.1 (8)	4.0 ± 0.1 (22)

0.6 ($n = 5$) and 1.2 ± 0.3 ($n = 39$) in 1977; 3.3 ± 0.6 ($n = 10$) and 2.8 ± 0.4 ($n = 30$) in 1978; 2.8 ± 0.6 ($n = 14$) and 2.1 ± 0.4 ($n = 31$) in 1980. This trend does not hold, however, when male age is considered.

Pair-bond type did not influence the number of young fledged in 1977 (one-way ANOVA; $F = 0.33$, $df = 3,39$, $P = 0.80$) or in 1980 ($F = 1.14$, $df = 3,42$, $P = 0.34$). However, net output did vary with pair-bond type in 1978 (one-way ANOVA; $F = 3.08$, $df = 3,35$, $P = 0.04$). Pairs composed of older males and yearling females enjoyed the highest reproductive success (Table 2), while pairs composed of two yearling individuals fared the worst.

NESTLING GROWTH

Heavy nest losses due to predation and inclement weather forced us to discard the incomplete 1977 data set from this analysis. Ross (1980b) found that nestling growth in the Ipswich Sparrow (*P. s. princeps*) is maximal (with respect to growth rate) towards the middle of the nesting season, while nestling weight gain is least in mid-summer (see also Weatherhead 1979 for Savannah Sparrow nestling weight gain). First, we examined whether or not such tendencies existed at Isle Verte by comparing nestling weight among "early-season," "mid-season," and "late-season" cohorts for age-classes of 1 to 9 days. We found significant variation in nestling weight among these three cohorts for five different age-classes in 1978

and for four age-classes in 1980 (Kruskal-Wallis ANOVA, $P < 0.05$). "Early-season" nestlings were consistently lightest in weight, while "late-season" nestlings were the heaviest on days 3, 4, 5, 6, and 9 in 1978, and on days 5, 6, 7, and 9 in 1980. Therefore, we adopted a two-category breakdown ("early" vs. "late"). We used 12 June to divide the nesting season in approximately equal halves and considered all nests that were started on or before that date as containing "early" nestlings.

In 1978, early broods required 10.4 ± 0.2 days of rearing ($n = 19$) while late ones stayed in the nest only 9.8 ± 0.2 days ($n = 13$). In 1980, the respective values were 10.0 ± 0.2 days ($n = 21$) and 9.0 ± 0.3 days ($n = 11$). The difference is significant in both cases (Mann-Whitney U-test; $z = 1.84$, $P = 0.03$ in 1978 and $z = 2.10$, $P = 0.02$ in 1980). Average nestling weight did not differ significantly between early and late broods until day 6 in 1978 and day 5 in 1980 (Table 3). Afterwards, late-reared nestlings were generally heavier than early-reared ones. We calculated growth curves for early- and late-hatched nestlings using Ricklefs' (1967) logistic model and asymptotes of 16.5 g for 1978 and of 15.8 g for 1980. The regression equations are $y = 0.12x - 0.53$ and $y = 0.14x - 0.54$ for early and late nestlings, respectively, in 1978. For the same categories in 1980, the respective equations are $y = 0.14x - 0.55$ and $y = 0.16x - 0.57$. Comparison of these equations revealed that the error variances were not significantly different ($F_{7,7} = 3.24$, $P > 0.05$ for 1978; $F_{7,7} = 2.59$, $P > 0.05$ for 1980). Therefore, the slopes of these lines could be compared using standard statistical tests. In both years, late-hatched nestlings grew at a much faster rate than early-hatched ones ($t = 3.91$, $P = 0.0008$, one-tailed, for 1978; $t = 4.11$, $P = 0.0005$, one-tailed, for 1980).

DISCUSSION

We found that differences in Savannah Sparrow nesting phenology could not be explained by the age of the parents. From our earlier

TABLE 2. Net reproductive output (mean number of young fledged ± SE) according to the age of both parents (pair bond type) for years 1977, 1978, and 1980 (sample sizes are in parentheses).

Year	Pair bond type			
	Older male Older female	Older male Yearling female	Yearling male Older female	Yearling male Yearling female
1977	2.0 ± 0 (1)	1.2 ± 0.8 (6)	0.5 ± 0.5 (4)	1.1 ± 0.3 (32)
1978*	2.5 ± 0.7 ^{a,b} (6)	4.6 ± 0.9 ^b (8)	2.8 ± 1.0 ^{a,b} (4)	2.0 ± 0.4 ^a (21)
1980	2.7 ± 1.1 (6)	1.1 ± 0.5 (9)	2.5 ± 0.6 (8)	2.4 ± 0.4 (23)

* Means followed by the same letter are not significantly different (Student-Newman-Keuls multiple range test; $P > 0.05$).

TABLE 3. Mean nestling weight with age according to clutch initiation date (Early = on or before 12 June; Late = after 12 June).

Year	Clutch initiation category	Age (days from hatch)									
		1	2	3	4	5	6	7	8	9	
1978	Early	$\bar{x} \pm SE$ (27)	1.83 ± 0.06 (39)	2.85 ± 0.10 (45)	4.17 ± 0.12 (50)	5.89 ± 0.15 (36)	8.38 ± 0.20 (31)	10.13 ± 0.27 (39)	12.43 ± 0.20 (46)	13.50 ± 0.33 (23)	13.88 ± 0.43 (12)
	Late	$\bar{x} \pm SE$ (15)	2.04 ± 0.09 (28)	2.78 ± 0.10 (31)	4.31 ± 0.16 (31)	6.35 ± 0.20 (31)	8.72 ± 0.25 (31)	11.31 ± 0.24 (31)	13.18 ± 0.25 (29)	14.50 ± 0.22 (23)	15.22 ± 0.23 (18)
	<i>P</i> *	0.046	0.784	0.540	0.062	0.294	0.011	0.057	0.012	0.012	0.012
1980	Early	$\bar{x} \pm SE$ (56)	1.60 ± 0.06 (67)	2.50 ± 0.08 (68)	4.07 ± 0.11 (67)	5.96 ± 0.17 (59)	8.20 ± 0.18 (52)	10.35 ± 0.17 (52)	12.04 ± 0.20 (47)	13.20 ± 0.23 (50)	14.30 ± 0.27 (40)
	Late	$\bar{x} \pm SE$ (29)	1.53 ± 0.05 (51)	2.58 ± 0.09 (44)	4.20 ± 0.13 (43)	6.18 ± 0.17 (41)	8.94 ± 0.35 (42)	11.08 ± 0.28 (41)	13.21 ± 0.31 (38)	14.29 ± 0.39 (28)	14.60 ± 0.42 (21)
	<i>P</i> *	0.576	0.500	0.485	0.351	0.024	0.006	0.002	0.010	0.010	0.703

* *P* is the significance level of Mann-Whitney U tests between early- and late-hatched nestlings at each age.

results (Bédard and LaPointe 1984a) and from a number of published studies, we predicted that pairs composed of returning individuals would begin nesting earlier. We found, however, that only female age influenced initiation date, and only in one of the two years for which we had complete data.

A strong tendency towards early initiation by the older Savannah Sparrows at Isle Verte could be absent for several reasons. First, the species may be too short-lived (survival rate 0.38, Bédard and LaPointe 1984a) to allow marked age-specific differences in phenology to develop. Secondly, there may be environmental constraints at Isle Verte that counteract such a tendency; the slower growth rate of early-reared nestlings (see below) may be a reflection of this.

We did not obtain a clear answer to our search for a relation between parental age and clutch size. Although several workers have detected slight, albeit statistically significant, differences in clutch size due to habitat, year, and date (Stobo and McLaren 1975, Welsh 1975, Dixon 1978), we were unable to do so at Isle Verte. Perhaps such differences, which are viewed as parental responses to incumbent difficulties in obtaining food or in rearing the progeny, are offset in our case by the great richness of the habitat. One could also argue that the presence of 14 unbanded females in 1977 could have masked an age/clutch-size relationship in 1978. Only five or six of these females, however, could have re-appeared in 1978 to be misclassified as yearlings, considering a survival rate of 0.38. Furthermore, evidence of the relationship did not emerge in 1980 when all returning females were banded.

We also failed to find a clear influence of age on net reproductive output, noting only a statistically unsubstantiated tendency for older individuals to produce more young. Since initial clutches do not differ in size between the two age classes, increased reproductive output, if present, would be due more to improved parental efficiency than to an increase in the number of eggs laid.

The effects of phenology on nestling growth are explicit. Faster growth of late-reared nestlings could be related to warmer conditions and more available food as the summer progresses. Mean air temperatures in this estuarine site averaged 3.0°C greater in July than in June (16.7°C versus 13.8°C in 1978 and 15.3°C versus 12.2°C in 1980). Moreover, weekly sampling of arthropods showed that prey abundance more than doubled between early June and late July (Meunier and Bédard 1984). Both Dixon (1972) and Ross (1980b) also worked in coastal sites, yet they found that

early broods received *more* food than late ones. The fact that early-reared nestlings at Isle Verte spend more time in the nest, gain weight more slowly, and leave weighing less than late-reared ones would be difficult to reconcile with a tendency in this population to breed as early as possible. Even though early-reared nestlings are lighter at Isle Verte, it is possible that their survival will not necessarily be adversely affected. Once autonomous, they could further benefit from the improved thermal and trophic conditions in July and August. On the whole, birds of this early cohort might have more time than late-reared ones to complete growth and to prepare for the fall migration (see also Ross 1980b). The results published by Perrins (1965), Dawson (1972), Dolbeer (1976) and Garson et al. (1981) showed that early nesting could be positively related to nesting success and that weight at fledging is positively related to subsequent survival. Ross and McLaren (1981), however, were unable to link fledging weight and survival to breeding age in the Sable Island Ipswich Sparrow.

ACKNOWLEDGMENTS

We thank the following persons for assistance with the field work: Esther Bonneau, Danielle Brazeau, Marie Deslauriers, Georges Gilbert, Serge Higgins, Michelle Languedoc, Yves Lauziere, Luc Major, Marie Meunier, André Nadeau, Isabelle Ringuet and Gaétan Rochette. We extend special thanks to Sylvie Michaud for her statistical advice. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada in the form of an operating grant to the senior author. We also thank the Canadian Wildlife Service for their cooperation and understanding while we worked in the Isle Verte National Wildlife Area. We sincerely appreciate the helpful suggestions made on early drafts of this article by Louis Best, Howard Ross and Reto Zach.

LITERATURE CITED

- BÉDARD, J., AND G. LAPOINTE. 1984a. Banding returns, arrival times and site fidelity in the Savannah Sparrow (*Passerculus sandwichensis*). *Wilson Bull.* 96:196–205.
- BÉDARD, J., AND G. LAPOINTE. 1984b. The Savannah Sparrow territorial system: can habitat features be related to breeding success? *Can. J. Zool.* 62:1819–1828.
- BÉDARD, J., AND M. MEUNIER. 1983. Parental care in the Savannah Sparrow. *Can. J. Zool.* 61:2836–2843.
- CRAWFORD, R. D. 1977. Breeding biology of year-old and older female Red-winged Blackbirds. *Wilson Bull.* 89:73–80.
- DE STEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow, *Iridoprocne bicolor*. *Ibis* 120:516–523.
- DAWSON, D. G. 1972. The breeding ecology of House Sparrows. Ph.D. diss., Oxford University.
- DIXON, C. L. 1972. A population study of Savannah Sparrows on Kent Island in the Bay of Fundy. Ph.D. diss., University of Michigan.
- DIXON, C. L. 1978. Breeding biology of the Savannah Sparrow on Kent Island. *Auk* 95:235–246.
- DOLBEER, R. A. 1976. Reproductive rate and temporal spacing of nesting Red-winged Blackbirds in upland habitat. *Auk* 93:343–355.
- GARSON, P. J., W. K. PLESZCZYNSKA, AND C. H. HOLM. 1981. The "polygyny threshold" model: a reassessment. *Can. J. Zool.* 59:902–910.
- HARVEY, P. H., P. J. GREENWOOD, C. M. PERRINS, AND A. R. MARTIN. 1979. Breeding success of Great Tits, *Parus major*, in relation to age of male and female parent. *Ibis* 121:216–219.
- MEUNIER, M., AND J. BÉDARD. 1984. Nestling foods of the Savannah Sparrow. *Can. J. Zool.* 62:23–27.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT [EDS.]. 1975. *Statistical Package for the Social Sciences*. 2nd ed. McGraw-Hill Book Co., New York.
- PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major*. *L. J. Anim. Ecol.* 34:601–647.
- RICKLEFS, R. E. 1967. A graphical model of fitting equations to growth curves. *Ecology* 48:978–983.
- ROSS, H. A. 1980a. The reproductive rates of yearling and older Ipswich sparrows, *Passerculus sandwichensis princeps*. *Can. J. Zool.* 58:1557–1563.
- ROSS, H. A. 1980b. Growth of nestling Ipswich Sparrows in relation to season, habitat, brood size, and parental age. *Auk* 97:721–732.
- ROSS, H. A. AND I. A. MCLAREN. 1981. Lack of differential survival among young Ipswich Sparrows. *Auk* 98:495–502.
- SAS INSTITUTE. 1982. *SAS User's Guide*. SAS Institute, Inc., Cary, NC.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Co., New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Co., San Francisco.
- STOBO, W. T., AND I. A. MCLAREN. 1975. The Ipswich Sparrow. *Proc. N.S. Inst. Sci. Suppl.* 2, 27:1–105.
- WEATHERHEAD, P. J. 1979. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. *Auk* 96:391–401.
- WELSH, D. A. 1975. Savannah Sparrow breeding and territoriality on a Nova Scotia dune beach. *Auk* 92:235–251.

Département de Biologie, Faculté des sciences et de génie, Université Laval, Ste-Foy, Québec G1K 7P4, Canada. Received 30 June 1983. Final acceptance 3 July 1984.