LACK OF DIFFERENTIAL SURVIVAL AMONG
YOUNG IPSWICH SPARROWS

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ABSTRACT.—The rate at which "Ipswich Sparrows" (*Passerculus sandwichensis princeps*) returned to their place of birth on Sable Island, Nova Scotia was determined by extensive banding and recapturing during 1976–1979. Low first-year survival rates of 2–4% (from the egg) coincided with a large decline in the size of the breeding population. Survival was statistically independent of brood size, the habitat and month when nestlings were raised, and the age or longevity of parents. Nestling survival was also unrelated to indices of nutritional well-being: weight, tarsus length, maximum growth rate, and the rate at which early growth decelerated. There was weak evidence that surviving juveniles had slightly longer tarsi than average. Natural selection for attributes expected to be important for overwinter survival seems to have been in abeyance or to have been obscured by the high rates of mortality. *Received 5 May 1980, accepted 20 February 1981.*

THE success of a particular reproductive pattern by a bird (frequency and size of clutches, habitat, and season of laying) in a given year is the product of the number of offspring produced and their probability of survival to maturity. It has frequently been argued that clutches of restricted size or frequency will evolve when offspring survival rates are inversely related to numbers of nestlings in the brood because of finite limits to parental care. Empirical evidence, however, is sometimes contrary and more often inadequate (review in Klomp 1970). The age of parents has been suggested as another influence on the quality of offspring (Lack 1968: 297) and has been correlated with postnestling survival rates (e.g. Perrins and Moss 1975). Body size, as affected for example by brood size, has been found to influence some passerine survival rates (e.g. De Steven 1978). The date of hatching may determine the amount of food and time available to young birds to prepare for migration and may influence social rank at winter food sources (Fretwell 1972). Finally, natal habitat is also an obvious determinant of fitness in a bird.

Generally, the most difficult variable to measure in testing this nexus of hypotheses has been the survival rate of offspring. Here we examine the survival of young Ipswich Sparrows (*Passerculus sandwichensis princeps*) in relation to measurements of size, growth, and some features of their upbringing. [See Ross (1980a) for an analysis of the variation of size and growth of nestlings with respect to conditions of their upbringing.] This race of the Savannah Sparrow is well suited for such studies, because virtually all individuals each spring return to Sable Island, Nova Scotia (Stobo and McLaren 1975). On the island the open terrain and relative tameness of the birds allow large segments of the population to be searched for leg bands. Nest disturbances by humans do not result in significant breeding losses because of the tenacity of the sparrow and the absence of terrestrial predators.

METHODS

The rate of return by young Ipswich Sparrows to Sable Island was measured for birds hatching in 1976, 1977, and 1978 as part of a larger study of factors influencing individual fitness. Each year large numbers of nestlings were banded, and in subsequent years the returning birds were recaptured and identified.

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Ipswich Sparrows have a long breeding season, raising up to four broods between May and September (Stobo and McLaren 1975). Nestlings were studied throughout the breeding season, in all habitats and from all brood sizes. Sometimes the age of at least one parent was known from banding records to be either SY (second year) or ASY (after second year). Adults of unknown age were designated AHY (after hatching year). Nests were discovered by accidentally flushing incubating females or by watching parents return to the nest to incubate eggs or feed nestlings.

Nestlings were banded in the western part of the island in two major habitats, here called Sparse and Dense, that cover the vegetated parts of the island. Dense habitat (called "Dense Mixed" by Stobo and McLaren 1975) comprised grassy or heathy areas of well-consolidated terrain and enclosed numerous small freshwater ponds. Sparse habitat ("Sparse Marram" in Stobo and McLaren 1975) comprised the less-consolidated dune areas, which were vegetated by various densities of marram grass (*Ammophila breviligulata*) and beach pea (*Lathyrus japonicus*).

Nestlings were weighed daily between 1000 and 1400 with a spring scale to the nearest 0.5 g from hatching (day 0) until they were 7 days old. When 7 days old, the nestlings were given an aluminum band, and the length of the right tarsus was measured with a vernier caliper to the nearest 0.1 mm. Nestlings discovered after hatching were weighed and measured when estimated by size and plumage to be 7 days old. Shortly after this, the young leave the nest and hide in the grass for about 2 weeks. They fledge and begin to disperse from the male territory when about 3 weeks old.

The trajectory of weight gain by nestlings was summarized by the two coefficients of the polynomial

$$\frac{\Delta W_i}{\Delta T_i} = r_a W_i - r_b W_i^2,$$

which is an approximation of the logistic equation (Ricklefs 1967, Ross 1980a). The rate of proportional weight gain is r_a (with units of time^{-1}), and the rate at which the absolute weight gain is damped as the asymptote is approached is r_b (with units of weight$^{-1} \cdot$ time^{-1}). W_i is the nestling weight on day i, and ΔW_i is the incremental change in weight ($W_{i+1} - W_i$) over the time interval ΔT_i, which in this study was always 1 day. A fuller discussion of this analysis is given in Ross (1980a).

A few undiscovered nests with eggs could have suffered gull predation, so our estimates of hatching success may be slightly high. Because almost all nestlings were monitored from hatching, there were no complications in estimating their survival rates in the nest (cf. Johnson 1979).

Independent, fledged juveniles were mist-netted and banded at a number of locations throughout the section of the island where nestlings were banded. Juveniles flew widely in late summer, so conditions of their upbringing were unknown.

Returning banded birds were discovered by thoroughly searching large areas of the island in May and June 1977, 1978, and 1979. Because the vegetation is sparse at that time of year and Ipswich Sparrows allow close approach by humans, it was possible to scrutinize systematically all birds in an area for leg bands. Banded individuals were recaptured by mist-netting and so identified. Their sex was determined by the presence or absence of a cloacal protuberance (see Stobo and McLaren 1975). A small number of banded individuals eluded capture and identification; their sex was inferred from territorial or nesting behavior.

Tests were made for heterogeneity in overwinter survival of nestlings with respect to natal habitat, month, brood size, and parental age and longevity, using the log likelihood ratio test, or G-test (Sokal and Rohlf 1969). The significance of the G-statistic is determined from tables of χ^2, but the test has advantages over the χ^2 test. Component G values are precisely additive in multiway tests, in the manner of mean squares in analysis of variance. The G-statistic is a sum of $f \ln f$ terms, so very small cell frequencies (f) make little contribution to the value of G. They do inflate the degrees of freedom, which increases the probability of making a type II error. Exact binomial probabilities were calculated in analyzing the sex ratio of survivors because of small samples.

Measurements of body weight, tarsus length, wing chord, growth rate, and damping rate were treated by analysis of variance. For each variable, the scores for the entire cohort of nestlings or fledged juveniles were compared with the scores of that subset that was recaptured in subsequent years on Sable Island. The technique for measuring tarsus length was inadvertently changed between 1976 and 1977. Consequently, all tarsus lengths were transformed to z-scores using the annual means and standard deviations (Sokal and Rohlf 1969, Ross 1980a).

RESULTS

Only small numbers (3–6%) of the nestlings banded during 1976–1978 were re-encountered as adults on the island (Table 1). A higher proportion of the indepen-

TABLE 1. The rate of return and sex ratio of returning cohorts of Ipswich Sparrows banded in their hatching year, 1976–1978, on Sable Island.

	Nestlings banded	Number recaptured	Number males recaptured[a]	Juveniles banded	Number recaptured	Number males recaptured[a]
1976[b]	455	18 (+1.75)[b]	5	187	23 (+2.25)[b]	13
1977[c]	376	11 (+0.6)[c]	7	38	3 (+1.4)[c]	2
1978	282	16	9	2	0	—

[a] Exact 2-tailed probabilities under H_0: $p(\male) = p(\female)$, $P > 0.05$ in all years.

[b] Three unidentified banded males and one unidentified banded female prorated among recaptured nestlings and juveniles to estimate overall survival (see Table 8).

[c] Three unidentified banded females (one thought to be ASY). Two were prorated among recaptured nestlings and juveniles as above.

dent, fledged juveniles returned as adults. The sex ratio of the returning birds did not deviate significantly from 1:1, although the small sample makes this test rather weak.

Survival rate appeared to be higher among birds from larger broods, among those born earlier in the season, and among birds reared in Dense habitat (Table 2). In the G-tests of these results (Table 3), each of the independence terms is equal to the sum of the associated interaction term, the interaction terms at lower levels, and the component 2-way independence terms. Nestling survival (S) had no significant interaction with month (M), habitat (H), or brood size (B) when taken singly. Survival was involved on three higher order independence terms: $M \times B \times S$, $H \times B \times S$, and $M \times B \times H \times S$. In each of these, when the overall value of G was partitioned, the two significant terms, $M \times B$ and $H \times B$, accounted for most of the deviations, leaving nonsignificant residual interaction terms. The $M \times B$ and $H \times B$ terms reflect seasonal and habitat variations in clutch size (Stobo and McLaren 1975, Ross 1979). All interaction terms involving S had nonsignificant G values. Overall, therefore, the rate of return was statistically independent of any combination of natal month, habitat, and brood size.

There was significant heterogeneity among clutch sizes in the successful hatching of eggs and rearing of offspring until they quit the nest (Table 4), deriving largely from the low rate of success among clutches of four eggs. This significance was obliterated among overwinter survivors, however, as already demonstrated for brood size.

TABLE 2. The breakdown of overwinter survival of Ipswich Sparrows (R = Returned, NR = Not Returned) subdivided according to natal brood size (b/n), habitat, and month when 7 days old of nestlings banded during 1976–1978 on Sable Island. These data are analyzed by the G-statistic in Table 3.

		Brood size					
		b/2 + b/3		b/4		b/5 + b/6	
		Survivorship					
Habitat	Month	R	NR	R	NR	R	NR
Sparse	June	1	21	3	68	0	10
	July	1	23	0	70	6	64
	August	0	23	4	34	0	5
Dense	June	3	47	5	91	6	97
	July	2	49	3	122	6	167
	August	1	73	2	63	1	29

TABLE 3. Analysis of the independence of the probability of return (S) to Sable Island with respect to natal month (M), habitat (H), and brood size (B) of Ipswich Sparrows banded as nestlings during 1976–1978.

Source	df	G-statistic[a]
Independence:		
$M \times S$	2	1.612 ns
$H \times S$	1	0.310 ns
$B \times S$	2	1.204 ns
$M \times H$	2	1.404 ns
$M \times B$	4	106.460 ***
$H \times B$	2	29.082 ***
Interaction:		
$M \times B \times S$	4	6.869 ns
$M \times H \times S$	2	2.340 ns
$H \times B \times S$	2	0.830 ns
$M \times B \times H$	4	23.465 ***
Independence:		
$M \times B \times S$	12	116.146 ***
$M \times H \times S$	7	5.666 ns
$H \times B \times S$	7	31.427 ***
$M \times B \times H$	12	160.409 ***
Interaction:		
$M \times B \times H \times S$	4	6.207 ns
Independence:		
$M \times B \times H \times S$	29	179.783 ***

[a] ns = $P > 0.05$, *** = $P < 0.001$.

The offspring of known-age adults were banded in 1977 and 1978. Usually the age of only one member of a pair was known, and we assumed that ages of members of a pair were uncorrelated. Offspring of SY adults were banded in both 1977 and 1978. There was no significant difference between years in the proportion of offspring surviving for SY parents of either sex (males: $G = 0.03$, df $= 1$, $P > 0.05$; females: $G = 0.50$, df $= 1$, $P > 0.05$). Offspring of ASY adults were banded in 1978. Although the rate of return was approximately twice as large for the offspring of ASY adults as for those of SY adults, the difference was not significant for either parental sex or when the age of either one of the parents was known (Table 5).

The rate of return of nestlings was also considered with respect to parental longevity. Adults were separated into those known to have lived at least 2 yr, and so to have become at least ASY in age, and those encountered for only one breeding season. In the latter group were individuals that were known to be SY but that failed to return in their third year and individuals banded as adults of unknown age

TABLE 4. Variation among clutch sizes in hatching and rearing success and in overwinter survival of Ipswich Sparrows banded as nestlings during 1976–1978 on Sable Island.

	Clutch size					
	c/1	c/2	c/3	c/4	c/5	c/6
Number of eggs	1	18	144	620	665	48
Number of 7–10-day-old nestlings raised[a]	0	13	113	434	527	35
Number surviving to SY[b]	0	0	5	14	22	3

[a] Heterogeneity of survival rate among clutch sizes (excluding c/1): $G = 15.74$, df $= 4$, $P < 0.01$.
[b] Heterogeneity of survival rate among clutch sizes (excluding c/1, c/2), per egg: $G = 2.93$, df $= 3$, $P > 0.05$; per nestling: $G = 2.26$, df $= 3$, $P > 0.05$.

TABLE 5. The rate of return of Ipswich Sparrows banded as nestlings during 1976–1978 with respect to the known age of at least one parent.

Parental		Offspring		
Sex	Age	Recaptured when SY or older	Not recaptured	Contingency G, df = 1[a]
Male	ASY	6	76	
	SY	6	162	1.59 ns
Female	ASY	5	71	
	SY	6	157	0.94 ns
Either	ASY	9	139	
	SY	11	291	1.33 ns

[a] ns = $P > 0.05$.

(AHY). If an AHY individual returned the next year it became ASY. The nestling return rates of the two groups, regardless of whether individual adults had mated more than once (thus producing half-sib families), did not differ significantly (Table 6).

The morphological differences between the surviving groups and the original cohorts of nestlings or fledged juveniles were very slight and nonsignificant (Table 7). For each character except juvenile wing chord, the frequency distribution was unimodal, sometimes with a slightly longer tail at lower values. Only juvenile wing chord departed significantly from normality (tests for skew and kurtosis, Sokal and Rohlf 1969). Juvenile wing chord was significantly platykurtotic ($t_s = 2.22$, $P < 0.05$), clearly because it was bimodal, with modes at 70 mm and 75 mm. The male and female segments of the surviving groups were more divergent in wing chord (SE difference between means, $t_s = 7.96$, df = 25, $P < 0.001$) than in weight ($t_s = 3.80$, $P < 0.001$), or tarsus length ($t_s = 0.031$, n.s.). Clearly, the bimodality in juvenile wing chord represents an early expression of sexual dimorphism.

DISCUSSION

A common difficulty in studies of this sort is to distinguish whether failure of a bird to return to the area of its birth is because of death or dispersal elsewhere. During the breeding season, Ipswich Sparrows only rarely occur off Sable Island; a few have been found mated with mainland Savannah Sparrows on coastal beaches

TABLE 6. The rate of return of Ipswich Sparrows banded as nestlings during 1976–1978 with respect to the longevity of either parent. Adults were subdivided into those that were known to reach ASY (>1 yr) and those not encountered beyond SY or AHY (1 yr).

Parental		Offspring		
Sex	Longevity	Recaptured when SY or older	Not recaptured	Contingency G, df = 1[a]
Male	>1 yr	8	154	
	1 yr	7	172	0.21 ns
Female	>1 yr	8	108	
	1 yr	7	170	1.22 ns
Either	>1 yr	13	237	
	both 1 yr	8	194	0.39 ns

[a] ns = $P > 0.05$.

TABLE 7. The mean, (n), and variance of body characters for the whole nestling or juvenile cohort banded during 1976–1978 and for the subset that returned to Sable Island in subsequent years. Means were compared by univariate analysis of variance. Variances were compared by the F-ratio test.

			Mean		Variance	
Age when measured		Character	Original cohort	Returning subset[a]	Original cohort	Returning subset[a]
Nestling	7 days	Weight	20.20 g (917)	19.94 ns (35)	3.301	4.276 ns
	7–10 days	Weight	20.36 g (1,106)	20.12 ns (46)	3.996	4.535 ns
	7 days	Tarsus length	0.000 (917)	−0.108 ns (35)	0.998[b]	0.899 ns
	7–10 days	Tarsus length	0.001[c] (1,104)	−0.026 ns (46)	0.998[b]	0.946 ns
	0–7 days	Growth rate (r_a)	0.642 (596)	0.635 ns (25)	0.007	0.006 ns
	0–7 days	Damping rate (r_b)	0.0298 (596)	0.0292 ns (25)	4.3×10^{-5}	4.2×10^{-5} ns
Juvenile		Weight	24.26 g (220)	24.37 ns (27)	3.693	3.915 ns
		Tarsus length	−0.004[c] (223)	0.339 ns (27)	1.000	0.641 ns
		Wing chord	72.64 mm (223)	73.04 ns (27)	8.635	9.186 ns

[a] ns = $P > 0.05$.
[b] Differ from 1.000 because of rounding error.
[c] Differ from 0.000 because of rounding error.

in Nova Scotia (Stobo and McLaren 1975). On Sable Island, which is long and narrow (vegetated terrain at most about 1 km wide), most yearlings settled 500–1,000 m from where they were raised (Ross 1979). The longest displacement recorded was 7.5 km. A much longer section of the island was searched annually for banded birds, and we are confident that virtually all survivors were discovered.

Between 1976 and 1978 the rates of returns of young Ipswich Sparrows were much lower than during 1968–1970 (Table 8). Because both nestling and juvenile survival rates have been calculated as the proportion reaching their first breeding season, then in 1976 (Table 1) the ratio (18/455) ÷ (23/187), or 0.325, was the probability of surviving from the 7-day-old nestling stage until the late-summer juvenile stage. In that year, at least, the survival rate of young birds on the island

TABLE 8. Survivorship (l_x) table for Ipswich Sparrow cohorts during 1968–1970 (after data in Stobo and McLaren 1975) and during the present study.

	Birth year of cohort					
Stage	1968	1969	1970	1976	1977	1978
Eggs	1.00	1.00	1.00	1.00	1.00	1.00
Leaving nest (7–10 days)	0.84	0.78	0.79	0.84	0.79	0.72
Late-summer juveniles	0.50[a]	0.25[a]	0.71[a]	0.25[c]	0.19[c]	—
First spring (SY)	0.14[b]	0.05[b]	0.14[b]	0.03[d]	0.02[d]	0.04

[a] Based on spring and late-summer censuses.
[b] Based on spring and late-summer censuses and return rates of banded adults.
[c] Based on ratio of juveniles and nestlings returning in 1977 and 1978 (see text).
[d] Four unidentified banded birds in 1977 and two in 1978 (a third assumed to be ASY) prorated among recaptured juveniles and nestlings to estimate overall survival rate (see Table 1).

was very low. In all 3 yr, however, the survival rate during migration and over-wintering was much below those of earlier years. This coincided with a sharp decline in the estimated sizes of the sparrow populations in spring from 2,000–3,000 in the late 1960s and early 1970s to 1,250 in 1978 (Stobo and McLaren 1975 and unpubl. data). Harsh winters in 1976–1977 and 1977–1978 are suspected to have been involved in the decline (the spring population was again near 2,000 in 1979).

It might be thought that selection would have been particularly intense during such a period of population decline. Survival rates of young birds proved to be unrelated, however, to a variety of circumstances of upbringing or to various measures of their growth rate or size, all of which have been hypothesized in the literature to affect fitness of young birds.

The small sizes of the returning nestling cohorts of course weakens the power of the various statistical tests used. The observed effects of month and brood size (Table 3) would have been significant if the same survival rates had obtained and about 4 or 5 times as many nestlings had been banded and recaptured. Such an "explanation," however, cannot be offered seriously, because survival rate (Table 2) was as high among August as among July young and increased with (grouped) brood size. Neither of these situations conforms with the usual *a priori* hypotheses that large and late broods should prove inferior. The effects of parental age and longevity are in the "right" direction, but again would have been significant only if the original cohort had been at least 3 or 4 times as large.

The significance of the interaction term $M \times B \times H$ (Table 3) reflects the complexity of interaction among these variables. Individual females tend to lay their largest clutches in late June and early July (Stobo and McLaren 1975, Ross 1979). In Dense habitat, laying is begun about 2 weeks earlier, and peak clutches are reached earlier than in Sparse habitat (Ross 1979). To the extent that these represent adaptive adjustments by parent birds, they may tend to eliminate differences in offspring fitness that might otherwise be imposed by season or habitat.

The differences between nestling traits in the original and returning cohorts are strikingly small (Table 7), a result hardly attributable to small sample sizes. The damping rate, r_b, which is strongly correlated with r_a, measures the abruptness with which weight gain declines near the asymptote and may indicate the rate at which differentiation supplants growth in the developing nestling. It is therefore of interest that in the Ipswich Sparrow the greater production of young by older birds (Stobo and McLaren 1975, Ross 1980a) consists of offspring that average lighter in weight and show a more abrupt reduction of growth at the end of the nestling period (Ross 1980a). These older parents presumably rear more nestlings partly by reducing the amount of food they devote to each. Some compensation could occur after the young leave the nest to hide in the grass, where they are fed by parents, especially the male (Stobo and McLaren 1975). At any rate, older or longer-lived parents did not produce young with significantly better prospects for survival, nor did the attenuated growth of their young carry a selective penalty.

The banded juveniles, compared with nestlings, suffered more of their mortality and potentially more selection on their migration and winter ranges. There is no firm evidence, however, of changes in mean or variance in the returning fraction of the cohort (Table 7). The mean changes in juvenile traits are in the "right" direction for selection for most robust individuals, but only tarsus length reached a P level as low as 0.09. Similarly, variance of tarsus length was reduced, consistent with stabilizing selection, at $P = 0.10$. Such levels of probability, however, even assum-

ing one-tailed tests of hypotheses, are hardly adequate considering the array of tests on Table 7.

Again it is possible that variances of the traits were too great and returning cohorts too small to detect possible real changes. Variances, especially of wing chord, were certainly inflated by the presence of both sexes among banded juveniles. Average variance of juvenile wing chord in the separate sexes of the surviving cohort was only 2.664 mm, consistent with the estimate of 2.190 mm in adults (Stobo and McLaren 1975: Table XIX). Even if sexes had been separable among juveniles and if such small variances had accordingly been obtainable, the increased wing chord in the surviving groups would have been significant only if about four times as many juveniles had been banded and recaptured. Although tarsus length did not differ significantly between sexes in the surviving cohort, average variance in the separate sexes was only 0.364 units, substantially smaller than for the whole cohort (Table 7). If sexes had been separable in the original cohort, the slight increase in tarsus length in the surviving cohort may well have been highly significant.

It must be concluded in general, however, that there was very little, if any, differential survival of young Ipswich Sparrows with respect to the conditions or attributes measured. It may be that survival depended on unidentified attributes. It is also possible that the most fit adults were those that produced the most young, not the "best" young by any reasonable measure. The advantage would then have gone to older adults (Ross 1980b) and perhaps to those that nested in Dense habitat (Ross 1979).

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