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Age and reproduction in Savannah sparrows and tree swallows

NATHANIEL T. WHEELWRIGHT and CHERYL B. SCHULTZ*

Department of Biology, Bowdoin College, Brunswick, ME 04011, USA

Summary

1. Compared to older females, 1-year-old Savannah sparrows (*Passerculus sandwichensis*) and tree swallows (*Tachycineta bicolor*), studied over seven breeding seasons on Kent Island, New Brunswick, Canada, laid eggs later in the season, had smaller clutches, and produced fewer surviving offspring.

2. To determine why young birds have lower reproductive success than older birds, we induced birds of different ages to replace clutches under the same conditions by removing clutches in an experiment simulating nest predation.

3. In both species, yearlings produced eggs similar in size to those of older females, but they laid fewer eggs per clutch in both first and replacement clutches than older birds. Yearling Savannah sparrows took more time to replace their clutches and lost more mass than older females. Differences were not significant in tree swallows because only three 1-year-old experimental females replaced their clutches.

4. Replacement clutches were larger than first clutches in Savannah sparrows and mean egg size increased between clutches, outcomes not expected had there been a major physiological cost of reproduction. Tree swallows showed a decline in clutch size and no change in mean egg size between clutches. Possibly Savannah sparrows lay their first clutch earlier than optimal in terms of clutch and egg size in order to leave time to replace failed clutches, to lay a second clutch after their first brood fledges, or to coordinate fledging (rather than egg-laying) with periods of food abundance.

5. The results of this experiment suggest that the higher reproductive success of older birds is due to improvement of reproductive performance with age and experience, rather than higher survivorship of successful breeders or increased reproductive effort. Age-specific reproduction was not an artefact of differential mortality of inferior breeders: birds that laid early in the season or produced large clutches were no more likely to survive than less successful breeders. Yearlings did not appear to withhold reproductive effort nor did older birds seem to invest more in reproduction, although the failure of some yearling tree swallows to replace their lost clutches provided some support for age-specific differences in reproductive effort. Constraint, rather than restraint, most probably explains the relatively poor reproductive success of yearlings.

Key-words: age, life-history evolution, cost of reproduction, *Passerculus sandwichensis*; reproduction, Savannah sparrow, *Tachycineta bicolor*, tree swallow, Kent Island, New Brunswick.

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Introduction

In numerous animal species young individuals or individuals breeding for the first time produce fewer offspring than older or more experienced individuals

(Tinkle, Wilbur & Tilley 1970; Clutton-Brock 1988). The phenomenon of age-specific reproductive success is perhaps best documented in birds, where long-term studies have highlighted various aspects of breeding in which young individuals are less successful than older individuals (Nolan 1978; Perrins 1979; Rockwell, Findlay & Cooke 1983; Newton 1986; Wooler, Bradley & Croxall 1992).

*Present address: Department of Zoology, University of Washington, Seattle, WA 98195, USA.

Birds attempting to breed for the first time may have problems finding a mate or suitable habitat, for example, or they may forego breeding altogether (Blus & Keahey 1978; Reese & Kadlec 1985; Lessels & Krebs 1989; Moser & Rusch 1989). Compared to older birds, young females may lay smaller eggs, eggs provisioned with lower levels of lipid or protein, or fewer eggs per clutch (Crawford 1977; Gratto, Cooke & Morrison 1983; Afton 1984; Askenmo & Unger 1986; Ollason & Dunnet 1986; Fleischer, Smyth & Rothstein 1987; Forslund & Larsson 1992). Typically, young birds are slow to begin nesting at the start of the breeding season (Middleton 1979; Harvey, Stenning & Campbell 1985; Perrins & McCleery 1985; Murphy 1986; Reid 1987; Stutchbury & Robertson 1988; Perdeck & Cave 1992). Because of their delay in breeding or because of insufficient nutrient reserves, they may be less likely than older birds to replace a clutch destroyed by predators (Hund & Prinzing 1985). In double-brooded species, young females are often less likely to lay a second clutch after their first fledges, and the interval between clutches may be longer than in older females (Nol & Smith 1987; de Laet & Dhondt 1988). In some cases even offspring sex ratio may be age-dependent, with young females producing mostly daughters (Blank & Nolan 1983). Even when yearlings produce as many offspring on average as older birds, they may have a higher variance in reproductive success (De Steven 1980).

As a consequence, the number of offspring that fledge and ultimately become recruited into the breeding population tends to increase with a parent bird's age, at least until senescence begins (Leionen 1973; Hannon & Smith 1984; Perrins & McCleery 1985; Dhondt 1989). Such age-specific reproductive success would presumably make young females less attractive mates to established males and may partly explain age-assortative mating.

Three hypotheses have been proposed to explain the positive correlation between age and reproductive success in natural populations: (i) improvement in intrinsic reproductive abilities with age and experience; (ii) increasing reproductive effort with age; and (iii) greater survival of successful breeders. The hypotheses are not necessarily mutually exclusive, but they stress different factors and levels of analysis.

The first hypothesis attributes the greater reproductive success of older birds to characteristics that change with age, such as larger body size, higher social status, or more extensive experience. Such factors may themselves be correlated. Older males are often more successful than young birds in attracting and maintaining mates, for example, because they are physically dominant, hold better territories, have more complex song repertoires, or arrive earlier at the breeding grounds (Cosens & Sealy 1986; Stutchbury & Robertson 1988; Arcese 1989; Catterall, Kikkawa & Gray 1989). Because of their experience, older birds may be skilled in foraging or avoiding predators (Ori-

ans 1969; Quinney & Smith 1980; Sullivan 1988; Hesp & Barnard 1989; Desrochers 1992a; although see Smith, Arcese & McLean 1984), which may enable them to produce more or larger eggs, or feed young at a faster rate. Traits such as superior foraging abilities can indirectly aid reproductive success by freeing time that can be used to attract or guard mates, or satisfy individual maintenance requirements (De Steven 1980; Catterall *et al.* 1989). Food supplement experiments that advance the date of egg-laying in yearlings more than in older females highlight the fact that reproduction by young adults may be limited by their rate of food acquisition (Ewald & Rohwer 1982; Desrochers 1992a; see also Duncan 1987). Previous breeding experience and familiarity with the same mate may in themselves improve subsequent reproductive success (Perrins & McCleery 1985; Ollason & Dunnet 1986).

The second hypothesis, which originates from life-history theory, predicts that individuals should scale their investment in reproduction according to their age-specific probability of reproductive success and mortality, or residual reproductive value (Williams 1966; Pianka & Parker 1975; Stearns 1976; Charlesworth 1980; Pugesek 1981). If young birds have little chance of breeding successfully, perhaps because of some of the factors discussed above, and if attempts to raise young incur a cost in terms of diminished survival or future fecundity (Bryant 1979; Nur 1988; although see Wheelwright, Leary & Fitzgerald 1991), young birds should withhold reproductive effort until they have achieved the size, status or experience necessary for successful reproduction. Faced with constraints, young birds should show restraint (Curio 1983). Furthermore, if the probability of becoming reproductively senescent or dying increases at some age (Collias *et al.* 1986; Curio 1988), individuals should invest relatively heavily in reproduction as they approach that point. Note that the first hypothesis ('age-specific abilities') and second hypothesis ('life-history theory') may be interrelated because natural selection for elevating reproductive effort with age would reinforce the pattern of relatively poor reproductive performance in young birds initially caused by their inferior breeding skills (Pugesek 1987).

The third hypothesis proposes that the commonly documented correlation between age and reproductive success in bird populations is merely an artefact of differential survival: older birds represent a non-random subset of the original cohort. A bird's ability to survive may be positively correlated with its reproductive performance, given that survival and breeding skills are likely to be governed by similar traits, such as body size, vigour and perceptual abilities (Smith 1981; Nol & Smith 1987). In such a case, differential survival of successful breeders would increase the mean reproductive success of a cohort, giving the appearance that individuals improve their reproductive performance with age, even if they do not.

Age-related increases in reproductive success in populations could possibly result if some individuals chose not to (or were unable to) breed in their first year but, when they finally did breed, had above-average reproductive success in subsequent years (Pyle *et al.* 1991). Conceivably, delaying reproduction could improve an individual's reproductive success compared to birds that had bred as yearlings; this would be especially likely if the costs of premature reproduction diminished subsequent reproductive success. As above, even if individuals themselves did not show an improvement between successive seasons, older cohorts in a population would have a higher mean reproductive success because of the inclusion of birds that had delayed reproduction.

Despite a rich literature demonstrating correlations between age and reproductive success, there have been almost no experimental demonstrations of age-specific reproductive performance in birds (De Steven 1980; Reid 1987; Desrochers 1992b). Direct tests of the phenomenon are critical because various factors may co-vary with age; disentangling life-history trade-offs, habitat variation, age and experience can be problematical (Hochachka 1992). For instance, young birds tend to arrive at the breeding grounds later than older birds, perhaps because they have shorter wings, winter farther from the breeding grounds, or are socially subordinate on the wintering grounds and leave for migration in poorer condition (Ketterson & Nolan 1983; Bédard & LaPointe 1984; Frances & Cooke 1986). However, if superior territories or mates have already been claimed or food is less abundant by the time they arrive, age-related reproductive differences would not necessarily be due to intrinsic factors, such as inferior parental abilities or reproductive effort withheld, but instead would be imposed indirectly by arrival time. Correlations of age and reproductive success alone cannot satisfactorily control for the fact that birds of different ages typically breed under different environmental conditions. Another problem is isolating the breeding performance of females from that of their mates in species with biparental care (Smith & Roff 1980; Perrins & McCleery 1985).

We investigated age-specific reproduction in females of two taxonomically and ecologically dissimilar species, Savannah sparrows (*Passerculus sandwichensis* Wilson) and tree swallows (*Tachycineta bicolor* Vieillot), using observational and experimental approaches. Previous studies of age-specific reproductive performance in Savannah sparrows presented contradictory results. Ross (1980) maintained that yearling Savannah sparrows laid fewer eggs per season than older females, but Bédard & LaPointe (1985) were unable to find any relationship between age and reproductive success in that species. In tree swallows, DeSteven (1978) documented that yearlings had smaller clutches than older females. Stutchbury & Robertson (1988) found the relation to be true only early in the breeding season.

In this study we simulated nest predation to test whether females of different ages were equally capable of replacing lost clutches. In addition, we investigated which aspects of breeding performance varied with age. By performing the same manipulation simultaneously on all females (and therefore under similar environmental conditions), we eliminated the confounding seasonal effects on clutch size. By inducing females to lay replacement clutches, we could reduce the influence of male parental care on a female's reproductive success (Røskoft 1983). Although a female's ability to replace a lost clutch could in theory depend partially on the quality of her mate's territory or his behaviour, in both study species the majority of foraging occurs away from the nest and courtship-feeding has not been observed. By focusing on a female's age-related abilities to replace her clutch after she had already laid one previously, we could also discount the role of energetic reserves stored before migration (Murphy & Boag 1989).

We also present data on associations between age and reproductive performance based on observations of unmanipulated Savannah sparrows and tree swallows over a 7-year period as an independent test of the predictions outlined above.

Study site and methods

This study was conducted during the late spring and summer of 1987–93 at the Bowdoin Scientific Station on Kent Island, an 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W). The Labrador Current's cool waters create dense fog and low temperatures in summer, making the island a metabolically demanding habitat for small land birds (Williams 1987). A series of parallel trails divides the study area into 50-m square quadrats used for mapping territories and nests, and for quantifying behaviour. For a more complete description of the site, see McCain (1975) and Wheelwright, Schultz & Hodum (1992).

We refer to 1-year-old females as 'yearlings'; females known to be at least 2 years old are termed 'older females.' The first clutch laid by a female in a season is called her 'first clutch' in Savannah sparrows, which may raise two broods, or 'original clutch' in tree swallows, which are single-brooded. If her first brood successfully fledges, a female Savannah sparrow may lay a 'second clutch.' For both species, 'replacement clutch' refers to a clutch laid after the first or original was destroyed or abandoned.

SAVANNAH SPARROWS

Savannah sparrows nest at densities of 10–30 individuals ha⁻¹ throughout the open areas of Kent Island. They forage for small invertebrates in the fields as well as along the upper shore, in the intertidal zone at low tide, and in white spruce (*Picea glauca*) trees;

late in the breeding season their diet shifts to seeds. Their biology has been described in detail by Stobo & McLaren (1975), Bédard & LaPointe (1985), Wheelwright *et al.* (1992), and Wheelwright & Rising (1993). Annual return rates of adults and nestlings to Kent Island are about 45% and 11%, respectively, which enabled us to establish a large known-age population of marked birds. Birds arrive from their southerly wintering grounds in late April or early May. They lay 1–2 (very rarely 3) clutches per summer in grass-covered nests on the ground. All yearling or older females attempt to breed. Predation by ravens (*Corvus corax*), common crows (*C. brachyrhynchos*), and herring gulls (*Larus argentatus*) claims up to 90% of Savannah sparrow nests in some years and habitats (Dixon 1972, 1978); in 1987–93 about 20% of nests were destroyed by predators (N. Wheelwright, unpublished data).

In addition to Canadian Wildlife Service aluminium bands, every adult in the study area was ringed with a unique, randomly determined combination of three plastic colour-bands; nestlings were marked with a single colour-band. As a measure of female reproductive success, we measured unflattened wing chord (to 1 mm), tarsus length (to 0.1 mm), and mass (to 0.1 g) of 7-day-old nestlings. (Savannah sparrow nestlings normally fledge at 9–11 days of age; weighing them at 8 days of age runs the risk of causing premature fledging: Dixon 1972; N. Wheelwright, personal observations.) In total, 2965 Savannah sparrows were banded during the study, including 368 females banded or recaptured as adults and 2493 birds banded as nestlings or juveniles.

Depending upon the year of the study, an average of 73% of individuals we considered to be yearlings had been banded as nestlings or fledglings; thus, their age was known precisely. After observing the population for 7 years we are confident that almost all newly arriving unbanded birds are also yearlings because marked adult females show extremely high fidelity to their nesting sites between years (Wheelwright & Mauck, unpublished). Distances between nests in successive years average less than 40 m, and no female has moved more than 0.5 km. Of more than 5000 sparrows banded on Kent Island since 1963, only one has been recovered breeding more than 1 km from where it had been banded (that individual, banded as a nestling, established a territory as a yearling 3 km away; cf. Dixon 1972, Bédard & LaPointe 1985). The assumption that recruits are yearlings is supported by the similarity in wing length between known (banded as nestlings or fledglings) and presumed (newly arriving) yearling females in the population as a whole, measured early in the season (known yearlings: 64.9 ± 1.9 mm, $n = 50$; presumed yearlings: 64.6 ± 1.8 , $n = 55$; two-tailed t -test: $P > 0.30$). In contrast, known yearlings had significantly shorter wings than older females (65.9 ± 1.4 mm, $n = 71$; $P < 0.0001$) and individuals' wing length increased between 1 and 2

years of age (N. Wheelwright, unpublished data). In the analyses presented below, there were no differences in clutch size ($P > 0.90$) or date of hatching ($P > 0.19$) in any year between known and presumed yearlings, so samples were combined.

In 1989, we randomly selected eight yearlings and 16 older females whose clutches had been initiated within 2–3 days of each other and had been completed by 2 June. The yearling group included six birds banded at Kent Island as nestlings the previous year and two individuals presumed to be yearlings because they first appeared at the study site in 1989 as unbanded adults. Both presumed yearlings had wing lengths of 62 mm, which was almost 4 mm shorter than that of the average older female. All the older females had been banded as nestlings in 1987 or earlier, or had been captured as adults before 1989. None of the yearlings, but all of the older females, were known to have nested at least once before 1989.

We captured and measured a subsample of experimental females at the beginning of the nest-predation experiment (not all were captured in order to minimize disturbance that might have caused desertion). Eight yearlings and five older experimental females were mist-netted and weighed between 5 May and 10 June 1989. Their masses did not differ significantly (yearlings: 19.2 ± 1.6 g; older females: 18.2 ± 1.4 g; one-tailed t -test: $P = 0.32$). In the population as a whole, yearling females weighed as much or more than older females (known yearlings vs. older females, both measured early in the season: 19.4 ± 1.8 g, $n = 47$, vs. 18.9 ± 1.9 g, $n = 68$; two-tailed t -test: $P = 0.14$). Yearlings nested among older birds, with no apparent age-related differences in habitat.

On 4 June 1989 we removed eggs from all experimental nests, alternating the order of removal between age classes. The length and diameter of each egg were measured with dial calipers to 0.1 mm and weighed to 0.1 g. Predators had already removed eggs from three experimental nests (two older females and one yearling) during the previous 2 days; these nests were included in the experiment. To evaluate the insulative value of nests, we heated a 25 cc plastic vial of water to 38 °C (normal incubation temperature for Savannah sparrows: Davis *et al.* 1986), laid it in the centre of each nest, and recorded the temperature of the water in the vial after 5 min. During the thermal measurements there was little variation in windspeed ($c. 15$ km h⁻¹), cloud cover (100%), and temperature (11 °C). We have never seen Savannah sparrows reuse a nest after eggs or nestlings have been preyed upon or after the first brood has fledged (see also Dixon 1972), so, after noting the compass orientation that nest entrances faced, we removed all nests, dried them to constant mass over low heat, and weighed them to 0.1 g. Experimental females were subsequently observed to determine when or if they replaced their clutches.

Twenty-three of the 24 experimental females replaced their nests. One older female was never seen again and was believed to have been preyed upon. We found 22 replacement nests during incubation, but the 23rd female's nest was found only after it had been destroyed by a predator during incubation. Based on observations of 733 nests, Savannah sparrows almost never lose just part of the clutch due to partial predation or other causes (see also Ross 1980), so the maximum number of eggs in a nest was considered the clutch size. Replacement clutches destroyed by predators before they hatched were excluded from certain analyses, and hence sample sizes vary. Replacement eggs were counted, measured and weighed as above. All females were captured in mist-nets and weighed to 0.1 g within 24 h after the first nestlings in their replacement clutch had hatched. Nestlings were weighed and measured 7 days after hatching. As soon as the nestlings had fledged, nests were removed, dried and weighed as above.

TREE SWALLOWS

Tree swallows breed in nest boxes in a field in the centre of the island; the colony has been occupied for more than a half century. Unlike ground-nesting Savannah sparrows, tree swallow numbers can be limited by nest site availability, and young or socially subordinate individuals are less likely to obtain nests. Some non-breeding yearlings are seen each year, especially late in the season. Another important difference between the species is that as aerial insect-feeders, tree swallows are strongly influenced by weather. The natural history of tree swallows at Kent Island has been described in detail by Paynter (1954) and Wheelwright, Leary & Fitzgerald (1991). Each summer breeding females lay a clutch of 3–8 eggs. Incubation normally takes 15–16 days, and most nestlings fledge 21–22 days after hatching (Paynter 1954; Robertson & Stutchbury 1992).

Virtually all adult female tree swallows, about three-quarters of the males, and all nestlings have been banded annually on Kent Island since 1966. In contrast to Savannah sparrows, few tree swallows banded as nestlings return to Kent Island (<2%). However, yearling females can be aged with confidence because of their characteristic brownish plumage (Hussell 1983). Once females begin to breed at the site, they are relatively philopatric; c. 45% of adult females return to the colony between years (Wheelwright *et al.* 1991).

Our observations and experiments with tree swallows were similar to those described for Savannah sparrows except as noted below. Tree swallow nestlings were measured at age 11–12 days after hatching. In the nest predation experiment, seven yearlings and 14 older females were randomly selected from females incubating complete clutches on 13 June 1990. All females were weighed that afternoon. The following

morning their eggs were removed, counted and measured. Nest depth and the relative amount of feathers incorporated in the nest were determined but the nest was left undisturbed. Only three of seven yearlings, and three of seven 2- and 3-year-old females replaced their clutches; seven of seven females older than 3 years old relaid. Otherwise, as with Savannah sparrows, we found no difference in reproductive performance between 2-, 3-, and 4-year-old or older tree swallows, so we combined them into one group (hereafter referred to as 'older females') for comparison with yearlings.

Associations between age and reproductive performance were examined for data that were normally distributed with ANOVA and *t*-tests (paired and unpaired, where appropriate) using Statview (Abacus Concepts 1992); one-tailed tests were used to test the hypothesis of less successful reproduction in young birds. We also used combined probabilities for determination of the overall significance of trends in observations from different years where data were sometimes taken using slightly different methods (Sokal & Rolf 1981, p. 780). About 40% of individuals were measured in more than one breeding season. Because some samples were not strictly independent, we also present *P*-values for each year separately. Summary data are presented as $\bar{x} \pm 1$ SD, except where noted otherwise.

Results

ASSOCIATIONS BETWEEN AGE AND REPRODUCTIVE PERFORMANCE: SAVANNAH SPARROWS

Yearling Savannah sparrows laid fewer eggs per clutch than older females, all clutches combined (one-tailed *t*-test: $P < 0.05$). However, age-related reproductive performance can be confounded with seasonal trends because younger females generally began their first clutches later in the breeding season than older birds (see below), clutch size declined with laying date (Spearman rank: $P < 0.03$, $n = 166$ nests), and older females were more likely than yearlings to lay second clutches (see below). Therefore, we analysed first and second clutches separately.

Yearlings tended to lay smaller first clutches than older females (Fig. 1; combined probabilities for 1988–93, excluding 1990: $\chi^2 = 22.5$, $df = 10$, $P < 0.02$). Age-related differences in the mean size of the first clutch were relatively small, on the order of 0.2–0.3 eggs, or about 5% of clutch size. Yearling females were slower to begin breeding, hatching their clutches an average of about 4 days later than older females (Fig. 2; combined probabilities for 1988–93: $\chi^2 = 47.4$, $df = 12$, $P < 0.001$). For second clutches, older females laid no more eggs per clutch than yearling females (Table 1).

The mean time between hatching of the first and

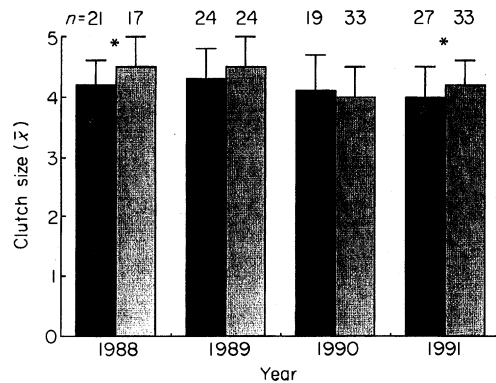


Fig. 1. Age and mean size of the first clutch in Savannah sparrows, 1988–91. Yearling females (black bars) laid significantly fewer eggs than older females (stippled bars) in 2 of 6 years, as indicated by asterisks ($*P < 0.05$). Yearlings also had smaller first clutch sizes in 1992 and 1993, although differences were not significant. Overall, combining probabilities for all years, yearlings had significantly smaller first clutch sizes than older birds ($P < 0.02$). Vertical lines denote ± 1 SD with sample sizes above.

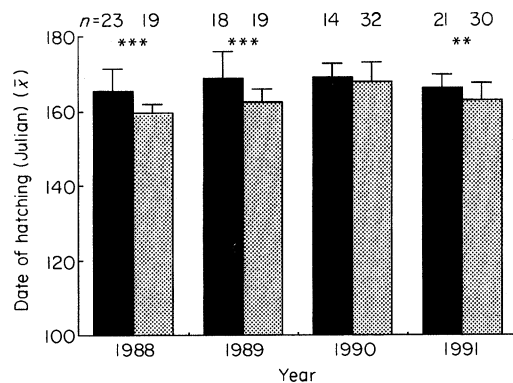


Fig. 2. Age and mean hatching date of the first clutch in Savannah sparrows. Yearling females (black bars) reproduced significantly later in the season than older females (stippled bars) in 3 of 4 years, as indicated by asterisks ($**P < 0.01$; $***P < 0.001$). Yearlings also initiated their first clutches later in 1992 and 1993, although differences were not significant. Overall, combining probabilities for all years, yearlings reproduced significantly later in the season than older females ($P < 0.001$). Vertical lines denote ± 1 SD with sample sizes above. Julian date of 152 = 1 June.

second clutches (interclutch interval) for females that laid a second clutch after successfully fledging young from the first clutch differed by less than 1 day between yearlings and older females in most years (Table 1).

In about half of the years of the study nestlings raised by yearling females were lighter and had shorter tarsi and wings than those raised by older females; the reverse was the case in other years, although differences were generally not significant (Table 1). Thus, yearlings were evidently as capable as older females in provisioning their offspring. In all years of the study, mean fledging success (fledglings per egg) was lower for yearling females than older females for first clutches, although combined probabilities were not significant (Table 1; $\chi^2 = 17.2$, $df = 12$, $P > 0.05$). For second clutches, yearlings had lower mean fledg-

ing success in 4 of 6 years but differences were not significant (Table 1). Older females produced more successful clutches (clutches fledging at least one young) than yearlings (Table 1; combined probabilities: $\chi^2 = 28.4$, $df = 8$, $P < 0.001$) and had greater success in recruiting offspring into the breeding population (one-tailed t -test: $P = 0.04$).

For individuals whose reproductive success as yearlings could be compared to that as 2-year-olds, there was a clear trend towards an increase in clutch size and a seasonal acceleration in the timing of egg-laying. Fourteen individuals showed an increase in first clutch size between age 1 and 2 years, 40 laid the same number of eggs, and 4 showed a decrease in clutch size. Mean clutch size increased between age 1 and 2 years for all years combined (paired t -test: $P = 0.03$). Hatching date of first clutch nests was earlier in their second year (compared to their first year of breeding, standardized by the yearly mean) for 43 individuals; two females laid on the same relative date, and 18 laid relatively later in their second year.

Although the emphasis of this study was a comparison of yearlings with older females collectively, we looked at mean clutch size and timing of hatching of the first clutch of individual females as a function of age. Because of sample size limitations, samples were pooled across years. The results suggest that the size of the first clutch increases between age 1 and 2 years, after which it decreases monotonically each year to age 6 years (Fig. 3). Egg-laying, on the other hand, appears to be initiated progressively earlier in the season as Savannah sparrows age (Fig. 4).

CLUTCH REMOVAL EXPERIMENT: SAVANNAH SPARROWS

First clutches

One-year-old experimental female Savannah sparrows laid smaller first clutches than older females nesting at the same time (Table 2). Although clutch size

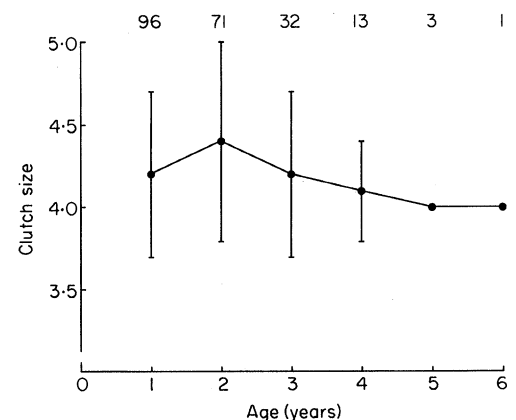


Fig. 3. Age and mean size of the first clutch in Savannah sparrows, combining data from 1988–91. Clutch size is greatest in 2-year-olds. Vertical lines denote ± 1 SD with sample sizes above.

Table 1. Reproductive performance of yearling vs. older female Savannah sparrows at Kent Island, New Brunswick. Values are means (± 1 SD), followed by sample sizes (number of clutches or broods). Egg and nestling dimensions are means of clutch or brood averages within nests. Nestlings were measured at 7 days of age. Replacement clutches (laid after the loss of the first clutch) and data from experimental females are excluded (experimental females included in first clutch size); the exclusion of 24 females involved in the clutch removal experiment explain the small (and possibly biased) samples in 1989. Interclutch interval = time between hatching of the first clutch (if it was successful) and that of the second clutch. Successful clutches = clutches in which at least one offspring fledged

	Year	1-year-old females	Older females	<i>P</i>
Second clutch size (number of eggs)	1988	3.7 (0.6), 21	3.9 (0.5), 22	0.11
	1989	4.2 (0.5), 4	3.6 (0.8), 12	0.07
	1990	3.9 (1.0), 12	3.8 (0.7), 16	0.53
	1991	3.5 (0.5), 6	3.8 (0.5), 17	0.11
	1992	3.8 (0.4), 6	4.3 (0.6), 16	0.09
	1993	4.1 (0.7), 7	4.6 (0.7), 9	0.29
Interclutch interval (days)	1988	37.1 (5.0), 11	36.7 (6.3), 15	0.44
	1989	23 (0), 1	35.6 (6.6), 10	0.04
	1990	32.0 (5.0), 6	31.2 (5.5), 15	0.76
	1991	26.9 (3.7), 7	29.4 (5.1), 14	0.13
Nestling mass (g): first brood	1988	15.4 (1.2), 12	15.9 (1.2), 11	0.11
	1989	15.1 (1.8), 16	15.8 (1.2), 18	0.11
	1990	15.0 (1.2), 14	14.7 (1.5), 27	0.56
	1991	15.8 (1.1), 14	15.3 (1.7), 21	0.18
	1992	15.1 (1.8), 14	15.9 (1.0), 19	0.10
	1993	16.2 (1.1), 6	15.6 (1.5), 8	0.42
Nestling tarsus (mm): first brood	1988*	20.2 (0.8), 13	20.7 (0.4), 13	0.02
	1989	18.9 (0.7), 16	19.1 (0.7), 18	0.33
	1990	17.6 (1.1), 14	17.4 (0.7), 27	0.35
	1991	21.0 (0.6), 14	20.9 (0.8), 21	0.41
	1992	20.3 (0.9), 14	20.8 (0.6), 19	0.05
	1993	20.3 (0.5), 6	20.2 (1.1), 8	0.90
Nestling wing (mm): first brood	1988	29.9 (3.2), 13	31.4 (9.7), 14	0.30
	1989	30.5 (4.8), 16	32.3 (4.0), 18	0.11
	1990	28.4 (3.1), 14	28.5 (3.0), 26	0.90
	1991	29.1 (2.6), 14	29.8 (3.6), 21	0.27
	1992	29.4 (2.9), 14	30.6 (2.0), 19	0.19
	1993	31.4 (3.5), 6	30.8 (3.4), 8	0.74
Nestling mass (g): second brood	1988	13.2 (1.8), 15	13.6 (1.8), 20	0.26
	1989*	13.0 (1.0), 3	14.7 (1.5), 12	0.04
	1990	14.3 (1.5), 12	14.7 (2.0), 13	0.54
	1991	16.8 (1.7), 4	15.1 (1.7), 10	0.06
	1992	14.6 (1.0), 5	13.9 (2.6), 13	0.55
	1993	14.8 (1.5), 4	15.2 (1.6), 8	0.70
Nestling tarsus (mm): second brood	1988	19.1 (1.2), 15	19.6 (1.2), 20	0.15
	1989	18.3 (1.4), 3	19.0 (1.1), 12	0.18
	1990	17.4 (1.0), 10	17.1 (1.6), 11	0.71
	1991	20.6 (1.5), 3	20.6 (1.0), 10	0.48
	1992	20.4 (0.4), 5	19.4 (1.5), 13	0.19
	1993	20.2 (0.3), 4	20.1 (0.8), 8	0.84
Nestling wing (mm): second brood	1988	26.7 (3.3), 15	27.8 (3.2), 20	0.16
	1989	28.3 (6.3), 3	29.1 (2.3), 12	0.36
	1990	27.5 (5.0), 10	28.2 (5.5), 11	0.76
	1991	31.0 (4.8), 4	28.7 (2.8), 11	0.13
	1992	31.4 (3.3), 5	27.9 (5.7), 13	0.22
	1993	30.0 (2.3), 4	30.2 (2.4), 8	0.87
Fledging success (fledglings per egg): first clutch	1988	0.57 (0.44), 21	0.69 (0.42), 17	0.21
	1989	0.67 (0.46), 23	0.70 (0.39), 24	0.39
	1990	0.64 (0.45), 18	0.86 (0.33), 33	0.06
	1991	0.54 (0.46), 27	0.68 (0.39), 33	0.09
	1992	0.54 (0.48), 24	0.64 (0.46), 28	0.45
	1993	0.29 (0.47), 17	0.31 (0.46), 24	0.89

Table 1—(continued)

	Year	1-year-old females	Older females	P
Fledging success	1988	0.71 (0.43), 20	0.82 (0.23), 22	0.16
(fledglings per egg):	1989	0.75 (0.50), 4	0.83 (0.21), 12	0.33
second clutch	1990	0.88 (0.17), 12	0.85 (0.26), 17	0.72
	1991	0.63 (0.39), 6	0.66 (0.36), 17	0.42
	1992	0.78 (0.19), 6	0.85 (0.19), 16	0.43
	1993	0.96 (0.09), 7	0.82 (0.34), 9	0.30
Number of	1988**	1.2 (0.4), 37	1.5 (0.5), 27	<0.01
successful clutches	1989***	0.8 (0.4), 5	1.8 (0.4), 12	<0.001
per season	1990	1.3 (0.5), 27	1.3 (0.5), 37	0.76
	1991	1.1 (0.4), 32	1.3 (0.6), 39	0.09

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.001$ (results of one-tailed *t*-tests).

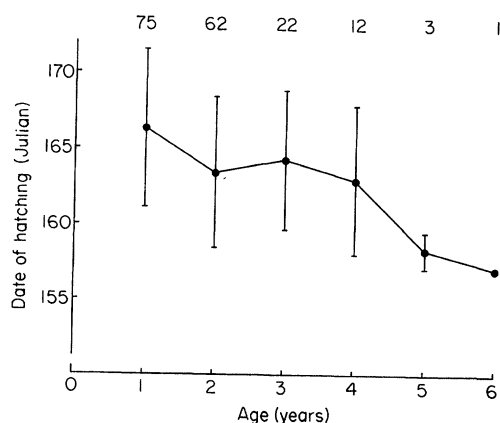


Fig. 4. Age and mean hatching date of the first clutch in Savannah sparrows, combining data from 1988–91. The initiation of breeding becomes progressively earlier with age. Vertical lines denote ± 1 SD with sample sizes above.

varied among age groups, the size of the eggs themselves (mass, length, and diameter) was unrelated to maternal age (Table 2).

Yearlings built flimsier-looking nests which weighed less than those of older birds, although not quite significantly so (Table 2). However, we found no correlation between the mass of a nest and its insulative value as estimated by short-term cooling rates (Spearman rank: $P = 0.91$, $n = 21$ nests), nor did cooling rates differ between age groups (Table 2). Yearlings may have incurred additional physiological costs during incubation by orienting their nests less appropriately than older birds. Despite cold, wet prevailing winds blowing off the ocean from the exposed south and east of the study site, the nests of yearlings was randomly oriented. In contrast, older females preferentially constructed their nests entrances facing towards the protected north or west (Table 3).

Replacement clutches

Within 2–8 days after removal of the first nest, most experimental female Savannah sparrows had already

constructed new nests and begun to lay replacement clutches. Yearlings took an average of 2 days longer to replace their lost clutches than older birds (Table 2). They also laid fewer eggs than older birds in their replacement clutches. As in the first clutch, egg size was independent of female age (Table 2). Yearlings lost significantly more mass than older birds between May and the time their replacement clutches had hatched (yearlings: loss of 0.8 ± 1.3 g, $n = 7$; older females: gain of 1.3 ± 0.9 g, $n = 5$; one-tailed *t*-test: $P < 0.01$).

There were no significant differences between age classes in the mass of the replacement nest (Table 2). All but the one female that disappeared retained the same mate between clutches and re-nested in the same area. The distance between the first nest built by a female and her replacement nest averaged 17 m (± 7 m, range = 3–31 m, $n = 23$ pairs of nests) and did not differ between yearlings and older females (two-tailed *t*-test: $P = 0.14$). Under normal conditions females build replacement or second clutch nests at a distance of 15–20 m from their original nest (Wheelwright & Mauck, unpublished, see also Stobo & McLaren 1975).

Experimental yearlings were just as successful at raising their offspring as older birds. Furthermore, their nestlings were no different in size at 7 days of age than those of older females (Table 2). Four of the eight experimental yearlings returned the following year, compared to eight of the 16 older females (Fisher Exact Test: $P > 0.70$).

First clutch vs. replacement clutch

Surprisingly, replacement clutches in Savannah sparrows were significantly larger than original clutches (Table 4). Twelve females laid replacement clutches that were identical in size to their first clutches, whereas 10 females increased their clutch size by one egg; in no case was a female's replacement clutch smaller than her original clutch (Binomial test:

Table 2. Characteristics of the first and replacement clutches of yearling vs. older female Savannah sparrows involved in the clutch removal experiment. Values are means (± 1 SD). Egg dimensions are means of clutch averages within nests. Successful clutches = clutches in which at least one offspring fledged

	1-year-old females	Older females	<i>P</i>
First clutches			
Clutch size (number of eggs)*	4.0 (0)	4.3 (0.5)	0.04
Egg mass (g)	2.1 (0.2)	2.0 (0.1)	0.41
Egg length (mm)	19.2 (0.1)	19.4 (0.8)	0.31
Egg diameter (mm)	14.5 (0.4)	14.6 (0.3)	0.33
Nest mass (g)	6.6 (1.0)	8.0 (2.0)	0.06
Thermal loss ($^{\circ}$ C)	5.3 (1.3)	4.9 (0.7)	0.15
Number of nests	7	14	
Replacement clutches			
Time to replace clutch (days)**	4.9 (1.6)	3.0 (1.2)	<0.01
Clutch size (number of eggs)*	4.4 (0.5)	4.8 (0.4)	0.03
Egg mass (g)	2.3 (0.2)	2.2 (0.2)	0.42
Egg length (mm)	19.6 (0.1)	19.5 (0.1)	0.27
Egg diameter (mm)	14.8 (0)	14.7 (0.1)	0.40
Nestling mass (g)	14.4 (1.0)	14.4 (1.4)	0.48
Nestling tarsus (mm)	18.7 (1.3)	19.0 (1.3)	0.31
Nestling wing (mm)	29.0 (4.2)	29.1 (2.9)	0.48
Successful clutches	88%	79%	0.40
Nest mass (g)	6.6 (1.1)	6.1 (1.3)	0.31
Number of nests	7	12	

* $P < 0.05$; ** $P < 0.01$ (results of one-tailed *t*-test and Fisher's exact test).

Table 3. Number of first clutch nest entrances, according to compass orientation, in the south field study site. The site is sheltered from N and W winds by forest, but exposed to cool winds and fog coming off the ocean from the E and S. Orientations are given for all yearling and older Savannah sparrows as well as those involved in the clutch removal experiment. Nests that were not covered and hence lacked a particular entrance orientation were excluded. Differences between age groups were significant (χ^2 test: $P = 0.004$)

	Nest orientation				Total
	N	E	S	W	
1-year-old females					
Experimental females	1	2	2	2	7
All yearlings	62	52	48	46	208
Older females					
Experimental females	11	1	1	1	14
All older females	57	45	30	79	211

$P < 0.001$). On average, replacement clutches were about 10% bigger than original clutches.

Replacement eggs were longer, wider and heavier than eggs of the first clutch (Table 4). Females that originally laid large eggs tended to replace them with large eggs (Spearman rank comparing mean egg sizes for first and replacement clutches: mass: $r_s = 0.65$, $P < 0.01$; length: $r_s = 0.89$, $P < 0.001$; diameter: $r_s = 0.78$, $P < 0.001$; $n = 18$ paired clutches). Egg shape (length/diameter) remained constant between nests of the same female (Table 4). Replacement nests tended to weigh about 20% less than original nests

(Table 4), but this may have been because replacement nests were not weighed until after the young had fledged, whereas original nests were weighed soon after the clutch had been completed (see Methods). There was no correlation between the mass of a female's first nest and that of her replacement nest (Spearman rank: $P = 0.55$).

REPRODUCTIVE SUCCESS AND SURVIVAL: SAVANNAH SPARROWS

In the population as a whole, yearling Savannah sparrows that survived to age 2 years had been no more successful as breeders during their first nesting season than yearlings that did not survive to age 2 years. Specifically, there was no difference between survivors and non-survivors in first clutch size (birds that returned: 4.1 ± 0.9 , $n = 84$; birds that did not return: 4.1 ± 0.8 , $n = 74$; $P = 0.85$), date of hatching (Julian date: 165.0 ± 6.6 , $n = 67$ vs. 165.2 ± 4.8 , $n = 57$; $P > 0.50$), or fledging success (0.61 ± 0.44 , $n = 84$ vs. 0.52 ± 0.46 , $n = 74$; $P = 0.16$).

ASSOCIATIONS BETWEEN AGE AND REPRODUCTIVE PERFORMANCE: TREE SWALLOWS

Yearling tree swallows typically laid clutches that were about 10% smaller than those of older females (Fig. 5; combined probabilities: $\chi^2 = 48.0$, $df = 14$, $P < 0.001$). The eggs of yearlings tended to hatch 2–6

Table 4. Characteristics of first vs. replacement clutches laid by all Savannah sparrows involved in the clutch removal experiment. Values are means (± 1 SD). Egg dimensions are means of clutch averages within nests

	Clutch		<i>P</i>
	First	Replacement	
Clutch size (number of eggs)**	4.2 (0.4)	4.6 (0.5)	<0.01
Egg mass (g)**	2.0 (0.1)	2.2 (0.2)	<0.01
Egg length (mm)**	19.3 (0.1)	19.5 (0.1)	<0.01
Egg diameter (mm)**	14.5 (0.3)	14.7 (0.4)	<0.01
Length/diameter	1.3 (0.6)	1.3 (0.6)	0.55
Nest mass (g)	7.5 (1.8)	6.2 (1.2)	0.12
Number of nests	20-24	22	

***P* < 0.01 (results of paired *t*-tests).

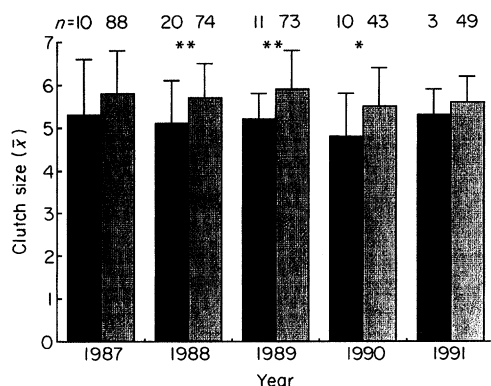


Fig. 5. Age and mean clutch size in tree swallows. Yearling females (black bars) laid significantly fewer eggs than older females (stippled bars) in 2 of the 5 years, as indicated by asterisks (**P* < 0.05; ***P* < 0.01). Yearlings also had significantly smaller first clutch sizes in 1992 and 1993. Vertical lines denote ± 1 SD with sample sizes above.

days later than those of older females (Fig. 6; combined probabilities: $\chi^2 = 36.5$, *df* = 14, *P* < 0.001). Given the smaller clutch size of yearlings (and the facts that a single egg is laid per day and regular

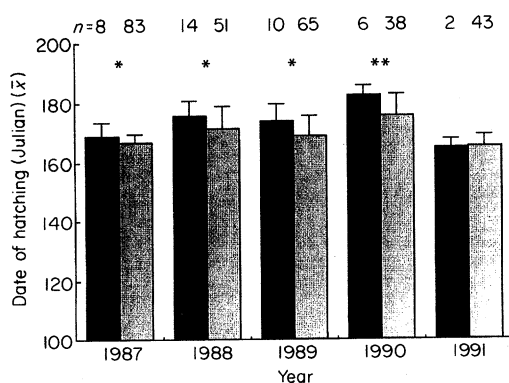


Fig. 6. Age and mean hatching date in tree swallows. Yearling females (black bars) reproduced significantly later in the season than older females (stippled bars) in 4 of 5 years, as indicated by asterisks (**P* < 0.05; ***P* < 0.01). Yearlings also reproduced significantly later in the season in 1992 and 1993. Vertical lines denote ± 1 SD with sample sizes above. Julian date of 152 = 1 June.

incubation usually begins with the penultimate egg: Paynter 1954), the delay in initiating clutches must have been even greater for yearlings.

Although the mean size of nestlings raised by yearling females was less than that of older females in most years, differences were not significant within years (except for tarsus in 1990; Table 5; one-tailed *t*-test: *P* > 0.10) or in all years combined (combined probabilities: *P* > 0.10). Likewise, there was no obvious age-related difference in fledging success (Table 5). Return rates of tree swallows banded as nestlings on Kent Island are too low to draw any conclusions about long-term survival (Wheelwright *et al.* 1992).

As in Savannah sparrows, there was a trend towards an increase in clutch size and earlier egg-laying in the relatively few tree swallows that we were able to observe in both their first and second years of breeding. Eight individuals showed an increase in first clutch size between age 1 and 2 years, eight showed no change in clutch size, and three showed a decrease in clutch size. Six females hatched their clutch earlier in the second year, six at about the same time, and two later.

Clutch size in tree swallows tended to increase until at least age 4 years, after which there was a suggestion of a decline (Fig. 7; sample sizes for 7- and 8-year-old females were too small to justify much confidence in the increase in clutch size late in life). Similarly, the timing of breeding showed a progressive trend towards earlier breeding with age until at least 4 years old (Fig. 8).

CLUTCH REMOVAL EXPERIMENT: TREE SWALLOWS

Original clutches

There were few differences between age groups in the size of the original clutch laid by experimental female tree swallows. Although the mean clutch size of yearlings was smaller than that of older females, the difference was not significant (one-tailed *t*-test: *P* = 0.10; Table 6). Egg dimensions did not differ between age groups. Older females built deeper (Table 6) and heavier (*P* < 0.05) nests than yearlings, however.

Table 5. Reproductive performance of yearling vs. older female tree swallows at Kent Island, New Brunswick. Values are means (\pm 1SD), followed by sample sizes (number of clutches or broods). Egg and nestling dimensions are means of clutch or brood averages within nests. Nestlings were measured at 11–12 days of age. Replacement clutches (laid after the loss of the first clutch) and data from experimental females are excluded (except that experimental females are included in clutch size); the exclusion of 24 females involved in the clutch removal experiment explains the small (and possibly biased) samples in 1990

	Year	1-year-old females	Older females	P
Nestling mass (g)	1988	20.2 (2.4), 9	20.4 (3.2), 25	0.43
	1989	22.1 (2.9), 5	22.7 (2.4), 48	0.28
	1990	19.7 (2.0), 5	21.0 (2.3), 16	0.13
	1991	21.0 (2.0), 2	22.5 (3.8), 39	0.13
	1992	21.5 (2.9), 10	22.5 (3.4), 24	0.46
Nestling tarsus (mm)	1988	12.3 (0.3), 9	12.2 (0.3), 25	0.18
	1989	11.1 (0.4), 5	11.1 (0.4), 48	0.46
	1990**	11.9 (0.2), 5	12.2 (0.2), 16	0.01
	1991	11.1 (0.5), 2	11.3 (0.4), 39	0.30
Nestling wing (mm)	1988	41.8 (5.1), 9	43.7 (6.7), 25	0.25
	1989	55.0 (3.2), 5	52.5 (5.2), 48	0.16
	1990	41.1 (7.2), 5	43.7 (3.6), 16	0.14
	1991	67.6 (0.6), 2	67.8 (6.5), 39	0.48
	1992	64.2 (4.6), 10	66.1 (5.1), 24	0.33
Fledging success (fledglings per egg)	1987	0.69 (0.48), 10	0.76 (0.34), 87	0.38
	1988	0.59 (0.35), 12	0.72 (0.35), 34	0.15
	1989	0.61 (0.44), 10	0.77 (0.34), 57	0.09
	1990	0.74 (0.30), 6	0.76 (0.31), 17	0.45
	1991	1.00 (0), 3	0.77 (0.30), 49	0.15
	1992	0.57 (0.42), 14	0.62 (0.40), 19	0.71

* $P < 0.05$; ** $P < 0.01$ (results of one-tailed t -tests).

Replacement clutches

Female tree swallows began laying replacement clutches as quickly as 6 days after their original clutch was removed. Because only three yearlings replaced their clutches, the difference between yearlings and older birds in the time between removal of the original clutch and completion of the replacement clutch was not significant (Table 6). Ten of 14 older females replaced their clutches (including one of four 2-year-olds, two of three 3-year-olds, and all seven birds that

were at least 4 years old). As in the first clutch, egg dimensions in the replacement clutch did not differ between age groups. However, yearlings that did replace their clutch laid fewer eggs than older females (one-tailed t -test: $P = 0.03$; Table 6). Females of both age groups lost mass in replacing clutches, but there were no significant differences in mass between experimental yearlings and older females at the time of clutch removal (23.3 ± 0.6 g, $n = 3$ vs. 23.9 ± 1.2 g, $n = 10$, respectively) or by the time their replacement clutches hatched (19.6 ± 0.4 g vs. 20.5 ± 1.4 g; one-tailed t -test: $P > 0.16$).

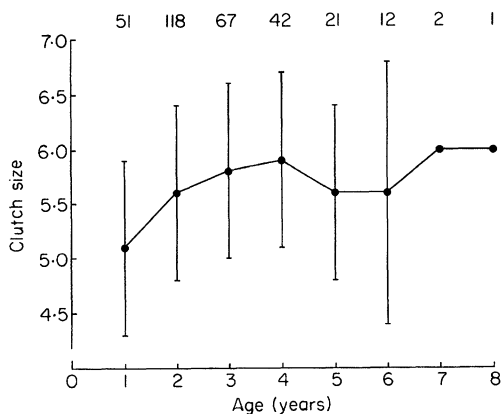


Fig. 7. Age and mean clutch size in tree swallows, combining data from 1988–91. Clutch size increases with age, at least until 4 years of age. Vertical lines denote \pm 1 SD with sample sizes above.

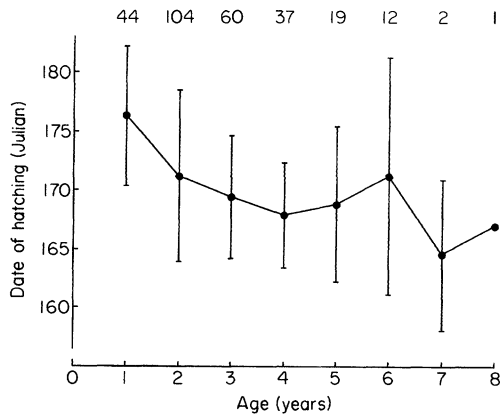


Fig. 8. Age and mean hatching date in tree swallows, combining data from 1988–91. The initiation of breeding becomes progressively earlier with age, at least until 4 years of age. Vertical lines denote \pm 1 SD with sample sizes above.

Table 6. Characteristics of the original and replacement clutches of yearling vs. older female tree swallows involved in the clutch removal experiment. Values are means (± 1 SD). Egg dimensions are means of clutch averages within nests. Successful clutches = clutches in which at least one offspring fledged

	Original clutches		P
	1-year-old females	Older females	
Original clutches			
Clutch size (number of eggs)	5.3 (0.5)	5.6 (0.6)	0.10
Egg mass (g)	1.7 (0.1)	1.7 (0.2)	0.34
Egg length (mm)	18.6 (0.9)	18.8 (0.8)	0.37
Egg diameter (mm)	13.3 (0.3)	13.2 (0.4)	0.45
Nest depth (cm)*	5.2 (1.0)	6.9 (1.8)	0.02
Number of nests	7	14	
Replacement clutches			
Time to replace clutch (days)	8.3 (0.6)	7.8 (1.6)	0.30
Clutch size (number of eggs)*	4.3 (0.58)	5.1 (0.57)	0.03
Egg mass (g)	1.6 (0.06)	1.7 (0.13)	0.19
Egg length (mm)	18.5 (0.19)	18.6 (0.81)	0.38
Egg diameter (mm)	13.2 (0.30)	13.4 (0.35)	0.17
Nestling mass (g)**	17.4 (0.2)	19.7 (0.7)	<0.01
Nestling tarsus (mm)	12.0 (0.2)	12.1 (0.2)	0.21
Nestling wing (mm)	59.5 (2.1)	63.9 (3.9)	0.09
Successful clutches	66%	60%	>0.10
Number of nests	3	10	

* $P < 0.05$; ** $P < 0.01$ (results of one-tailed t -tests and Fisher's exact test).

Yearling females fed their nestlings at a slower rate than older females (7.0 ± 2.1 trips h⁻¹ vs. 14.5 ± 5.3 trips h⁻¹; $P = 0.05$). At 12 days of age, the nestlings of yearling females weighed significantly less than those of older females (Table 6). Three of the seven experimental yearlings returned the following year, compared to four of the 14 older females (Fisher Exact Test: $P = 0.87$).

Original clutch vs. replacement clutch

Female tree swallows of both age classes laid fewer eggs, on average, in the replacement clutch (one-tailed t -test: $P < 0.01$), but replacement eggs were not smaller in size (Table 7; $P > 0.10$; cf. Table 4). The size of a female's original and replacement clutch was positively correlated, as were egg dimensions in the original and replacement clutch (Spearman rank: $P < 0.01$, $n = 13$).

REPRODUCTIVE SUCCESS AND SURVIVAL: TREE SWALLOWS

In tree swallows, as in Savannah sparrows, the probability of surviving to age 2 years was unrelated to an individual's reproductive success as a yearling. There was no difference in clutch size (birds that returned: 5.1 ± 0.9 , $n = 25$; birds that did not return: 5.0 ± 1.1 , $n = 52$; $P = 0.68$) or date of hatching ($P = 0.29$).

Fledging success, in contrast, was significantly greater in birds that returned the following year (0.71 ± 0.41 , $n = 25$ vs. 0.40 ± 0.45 , $n = 52$; $P < 0.005$). However, the lower mean fledging success for non-returning birds may have largely been a result of herring gull predation on breeding adults during the breeding season (Wheelwright & Dorsey 1991) and hence not necessarily due to inferior reproductive performance *per se*.

Discussion

Savannah sparrows and tree swallows, although unlike ecologically and phylogenetically, showed similar age-related patterns of reproduction over a 7-year period. Compared to older females, yearlings typically laid fewer eggs per clutch; they began to lay eggs later in the season; and their fledging success tended to be lower. In addition, in the case of Savannah sparrows, yearlings were less likely than older females to lay a second clutch after fledging the first brood.

In other aspects of reproduction, however, yearlings were the equal of their elders: neither egg size (mass, length, diameter) nor nestling body size (mass, tarsus, wing) varied as a function of the age of the female parent in Savannah sparrows or tree swallows (cf. DeSteven 1978). In Savannah sparrows, age-related differences were less pronounced or were absent altogether in second broods, perhaps because yearlings capable of laying a second clutch were a non-random

Table 7. Characteristics of original vs. replacement clutches laid by all tree swallows involved in the clutch removal experiment. Values are means (± 1 SD). Egg dimensions are means of clutch averages within nests

	Clutch		<i>P</i>
	Original	Replacement	
Clutch size (number of eggs)**	5.4 (0.6)	4.9 (0.6)	<0.01
Egg mass (g)	1.7 (0.2)	1.7 (0.1)	0.46
Egg length (mm)	18.7 (0.2)	18.5 (0.7)	0.42
Egg diameter (mm)	13.2 (0.4)	13.3 (0.3)	0.11
Length/diameter	1.4 (0.1)	1.4 (0.1)	0.55
Number of nests	21	13	

** $P < 0.01$ (results of paired *t*-tests).

subset of yearlings. For example, the interval between successive clutches, potentially a measure of the physiological strain caused by rearing young (McGillivray 1983), was no longer for yearling Savannah sparrows that laid a second clutch than for older birds. Moreover, mean nestling size and fledging success of second clutches produced by Savannah sparrows did not differ between age classes.

Similarly, age-related differences in reproduction tend to disappear later in the season in tree swallows (Stutchbury & Robertson 1988). In tree swallows, which are single-brooded and potentially limited by the availability of cavity nest sites, late breeders may represent socially subordinate or inexperienced birds, regardless of their age, which could explain the lack of differences between yearlings and older females late in the season. In general, our observations of age-specific reproduction at Kent Island are similar to those reported by Ross (1980) for Savannah sparrows (but see Bédard & LaPointe 1985) and DeSteven (1978) and Stutchbury & Robertson (1988) for tree swallows.

The magnitude (and in some comparisons, direction) of differences in reproduction between yearlings and older females varied between years (cf. Rockwell, Findlay & Cooke 1985; Sydeman *et al.* 1992). Year-to-year differences may have been influenced by the fact that insect prey abundance varied among years, judging from samples of midges (Diptera: Chironomidae) and other insects eaten by Savannah sparrows and tree swallows (Wheelwright *et al.* 1991). It may be that age-specific differences in reproductive performance are more likely to be exposed in years or habitats when environmental conditions are stressful (De Steven 1980; Hannon & Smith 1984; Bédard & LaPointe 1985; Hussell & Quinney 1987; Winkel & Winkel 1987; Stutchbury & Robertson 1988). The only aspects of reproductive performance that consistently differed between yearlings and older females were clutch size and time of laying. Nestling body size, in contrast, was in some years greater in broods cared for by yearlings and some years the reverse in both Savannah sparrows and tree swallows. The reason may be that success in feeding nestlings depends upon

the vagaries of the current weather, which could by chance favour late-breeding yearlings in some years. Clutch size and time of laying, in contrast, depend largely on age-related features such as female body condition or more predictable cues such as day length.

The clutch-removal experiments provided the strongest evidence for age-specific reproductive performance. Yearlings of both species laid smaller original clutches than older experimental females nesting at the same time. Their replacement clutches were also smaller than those of older birds. There was little indication in Savannah sparrows that age-specific differences in reproductive abilities were exacerbated by the extra challenge of having to replace a clutch. For instance, yearling Savannah sparrows were just as likely as older females to replace experimentally destroyed clutches. In tree swallows, on the other hand, fewer than half of the yearlings replaced their clutch versus 10 of 14 older females (including 100% of the birds that were at least 4 years old), suggesting age-specific differences in the likelihood of replacing lost clutches.

Yearling Savannah sparrows took more time to replace their clutch, and they lost more mass in the process than older females. Female sparrows and swallows building a nest for the first time in their lives seemed less adept than experienced females, constructing small and inappropriately oriented nests. In the case of tree swallows, there were no age-related differences in the time it took to replace lost clutches or in mass lost in the effort. To summarize the results of our observations and experiments, yearling female Savannah sparrows and tree swallows were clearly less successful than older females in some but not all aspects of reproduction.

Of the three major hypotheses put forth to explain positive correlations between age and reproductive success—improvement in an individual's intrinsic reproductive abilities with age, increasing reproductive effort with age, and greater survival of successful breeders—the results of this study are most consistent with the first, although we are unable to rule out the second hypothesis. The proposition that the reproductive performance of young birds is con-

strained by lack of experience is supported by various studies of age-specific foraging skills and vigilance against predators (Orians 1969; De Steven 1980; Quinney & Smith 1980; Ewald & Rohwer 1982; Duncan 1987; Sullivan 1988; Desrochers 1992a, b). In this study experimental yearling female Savannah sparrows improved with experience (relative to older females) in at least one component of reproduction, nest construction. A longitudinal (cohort) analysis of marked individual Savannah sparrows and tree swallows demonstrated that females increased their clutch size and accelerated the timing of breeding between age 1 and 2 years of age.

The second hypothesis—that young birds withhold reproductive effort or that older birds invest disproportionately heavily in reproduction—seems inadequate to explain the results of this study. First, both Savannah sparrows and tree swallows have high annual mortality rates. With life expectancies of two breeding seasons or less, natural selection would favour withholding present reproductive effort only if reproduction had a drastic negative effect on survival and future fecundity (Murray 1984). A detailed study of tree swallows at Kent Island found no cost of reproduction within the range of naturally occurring clutch sizes, even when females' broods were experimentally augmented by two nestlings for up to three consecutive seasons (Wheelwright *et al.* 1991). Observational data in both species showed no obvious relationship between clutch size and future fecundity or survival (Wheelwright *et al.* 1991; N. Wheelwright, unpublished data). Nor did yearling Savannah sparrows in this study appear to show reproductive 'restraint' (Curio 1983): all experimental females replaced their lost clutches with even larger clutches and bigger eggs, losing appreciable mass in the process. Our study offers some support for the second hypothesis through the observation that clutch sizes increased steadily with age in tree swallows, although not in Savannah sparrows.

The third hypothesis—differential survival of successful breeders—was not supported by this study. In both species, surviving yearlings had laid no more eggs per clutch and had reproduced no earlier than yearlings that did not return the next year. In Savannah sparrows, there was also no difference in the number of successful clutches produced between survivors and non-survivors.

An important implication of a positive correlation between age and reproductive success is that males should prefer older females where they have a choice, especially in species where biparental care is essential and males can only attend a limited number of nests. Assortative mating by age is known in various bird species (Hund & Prinzing 1985; Shaw 1985), including Savannah sparrows (N. Wheelwright, unpublished data). Our demonstration of the 'ecological constraint' of age-specific reproduction also has implications for understanding 'helping' in birds (Emlen 1982).

The clutch removal experiments provided some insights about the physiological cost of reproduction. As predicted, females of both species, and yearlings in particular, lost mass after laying a replacement clutch, which suggests that yearlings pay a disproportionate metabolic cost in producing eggs. But females of all ages were surprisingly quick to respond to the loss of their first nest, initiating a clutch weighing more than 50% of their body mass, in just over 1 week in the case of tree swallows, and within several days in Savannah sparrows, which also had to construct new nests.

Unexpectedly, instead of responding to the strain of a lost first clutch by producing fewer eggs or smaller eggs in their replacement clutch (cf. Middleton 1979), the majority of female Savannah sparrows increased the number and size of their eggs. The increase in clutch size between first and replacement clutches was also unanticipated because of the commonly found negative correlation between hatching date and clutch size (Harvey, Stenning & Campbell 1985; Duncan 1987; Finke, Milinkovitch & Thompson 1987; Stutchbury & Robertson 1988; Perrins & McCleery 1989; see Table 1). Other studies have demonstrated brief periods early in breeding where clutch size and egg size actually increased as the season progressed (Stobo & McLaren 1975; Weatherhead 1979; Ross 1980; Askenmo & Unger 1986). The early-season increase in clutch size could have been caused by several factors. To reach Kent Island at the beginning of the breeding season, Savannah sparrows must migrate several hundred km from their winter habitats and cross the Bay of Fundy. When females arrive to lay their first clutch, their fat reserves depleted by the trip, they face May storms, temperatures just above freezing, a paucity of insects, and a month's wait until plants begin to leaf out. In contrast, by the time experimental females laid their replacement clutches, they had had the opportunity to recover from the trip, and even though they had to duplicate the effort of laying a clutch, the weather when they laid their replacement clutch was less stressful and insects were more abundant. Clutch size and egg size are positively correlated with food availability in several passerine species (Otto 1979; Murphy 1986; Hussell & Quinney 1987). An alternative hypothesis is suggested by Ekman & Askenmo's (1986) proposition that clutch size should be adjusted to the probability that mature offspring will be produced. Savannah sparrows may hold back on reproductive effort until the likelihood of escaping predators improves later in the season. Nest predation is relatively high until late June, when the vegetation grows tall enough to make it difficult for predators to find nests (Dixon 1972, 1978; Bédard & LaPointe 1984; N. Wheelwright, unpublished data). Despite the high risk of nest predation the constraints of producing reduced clutch sizes and small eggs, early nesting may increase the probability that a female can fledge young from the first nest and undertake a second clutch (Askenmo & Unger 1986), provide

insurance against nest predation by allowing time to replace a lost first clutch (Bédard & LaPointe 1984), or enhance the survival of fledglings, which become independent when insects are most available, temperatures mildest, and time maximal for learning to forage before conditions worsen at the end of the breeding season (Bédard & LaPointe 1985; Askenmo & Unger 1986; Nilsson & Smith 1988; Matthysen 1989). Finally, birds that complete reproduction early benefit by having more time to moult and deposit fat before undertaking migration.

In conclusion, Savannah sparrows and tree swallows at Kent Island show an improvement in reproductive performance between age 1 and 2 years, but the pattern is apparently not merely due to age-specific allocation of reproductive effort, as predicted by life-history models. Nor does it appear to result from selective mortality of inferior breeders, since successful breeders were no more likely to survive than less successful breeders. Instead, the reduced reproductive success of young birds seems mainly to be constrained by their inexperience.

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