Age and Reproduction in Savannah Sparrows and Tree Swallows

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The Journal of Animal Ecology, Vol. 63, No. 3 (Jul., 1994), 686-702.

Journal of Animal Ecology 1994, **63**, 686–702

Age and reproduction in Savannah sparrows and tree swallows

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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

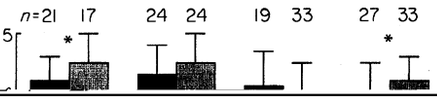
have problems finding a mate or suitable habitat, for example, or they may forego breeding altogether (Blus

Hesp & Barnard 1989; Desrochers 1992a; although see Smith, Arcese & McLean 1984), which may enable

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

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 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



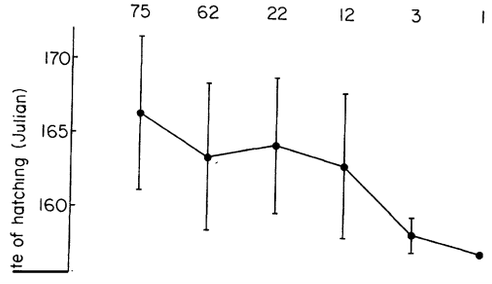
ing success in 4 of 6 years but differences were not significant (Table 1). Older females produced more successful clutches (clutches fledging at least one

Table 1. Reproductive performance of yearling vs. older female Savannah sparrows at Kent Island, New Brunswick. Values

Table 1—(*continued*)

	Year	1-year-old females	Older females	*P*
Fledging success (fledglings per egg): second clutch	1988	0·71 (0·43), 20	0·82 (0·23), 22	0·16
	1989	0·75 (0·50), 4	0·83 (0·21), 12	0·33
	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 successful clutches per season	1988**	1·2 (0·4), 37	1·5 (0·5), 27	<0·01
	1989***	0·8 (0·4), 5	1·8 (0·4), 12	<0·001
	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).



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

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

	1-year-old females	Older females	*P*
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 (°C)	5·3 (1·3)	4·9 (0·7)	0·15
Number of nests	7	14	

experiment. Values are means (±1 SD). Egg dimensions are means of clutch averages within nests

	Clutch		
	First	Replacement	*P*
[illegible]**	4.2 (0.4)	4.6 (0.5)	<0.01

Table 5. Reproductive performance of yearling vs. older female tree swallows at Kent Island, New Brunswick. Values are

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		
	1-year-old females	Older females	*P*
Original clutches			
[redacted]			
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
[redacted]			
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
[redacted]			
Nestling wing (mm)	59·5 (2·1)	63·9 (3·9)	0·09
Successful clutches	66%	60%	>0·10
Number of nests	3	10	

$*P<0{\cdot}05$; $**P<0{\cdot}01$ (results of one-tailed *t*-tests and Fisher's exact test).

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		
	Original	Replacement	*P*
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	

successive clutches, potentially a measure of the

chance favour late-breeding yearlings in some years.

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

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

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 predators migrate 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

and season on Savannah sparrow reproductive success. *Condor*, **87**, 106–110.
Blank, J. L. & Nolan, V. Jr (1983) Offspring sex ratio in red-winged blackbirds is dependent on maternal age. *Proceedings of the National Academy of Sciences USA*, **80**, 6141–6145.
Blus, L. J. & Keahey, L. A. (1978) Variation in reproductivity with age in the brown pelican. *Auk*, **95**, 128–134.
Bryant, D. M. (1979) Reproductive costs in the house martin (*Delichon urbica*). *Journal of Animal Ecology*, **48**, 655–675.
Catterall, C.P., Kikkawa, J. & Gray, C. (1989) Inter-related age-dependent patterns of ecology and behaviour in a

feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds *Agelaius phoeniceus*. *Journal of Animal Ecology* **51**, 429–450.

Finke, M.A., Milinkovich, D.J. & Thompson, C.F. (1987) Evolution of clutch size: an experimental test in the house wren (*Troglodytes aedon*). *Journal of Animal Ecology*, **56**, 99–114.

Murphy, M.T. (1986) Temporal components of reproductive variability in Eastern kingbirds (*Tyrannus tyrannus*). *Ecology*, **67**, 1483–1492.

Murray, B.G. (1984) A demographic theory on the evolution of mating systems as exemplified by birds. *Evolutionary Biology*, **18**, 71–140.

Newton, I. (1986) *The Sparrowhawk*. T. and A.D. Poyser,

poral and age-related variation in the laying rate of the parasitic brown-headed cowbird in the eastern Sierra

Nilsson, J.-A. & Smith, H.G. (1988) Effects of dispersal date on winter flock establishment and social dominance in

2724–2730.

Forslund, P. & Larsson, K. (1992) Age-related reproductive

917–928.

Nol, E. & Smith, J.N.M. (1987) Effects of age and breeding

Rockwell, R.F., Findlay, C.S. & Cooke, F. (1985) Life history studies of the Lesser Snow Goose (*Anser caerulescens caerulescens*). V. Temporal effects on age-specific fecundity. *Condor*, **87**, 142–143.

Rϕskaft, E. (1983) Sex-role partitioning and parental care by the rook *Corvus frugilegus*. *Ornis Scandinavica*, **14**, 180–187.

Ross, H.A. (1980) The reproductive rates of yearling and older Ipswich sparrows, *Passerculus sandwichensis prin-*

gull: effects of parental age, timing of breeding and year in relation to food availability. *Journal of Animal Ecology*, **60**, 135–150.

Tinkle, D.W., Wilbur, H.M. & Tilley, S.G. (1970) Evolutionary strategies in lizard reproduction. *Evolution*, **24**, 55–74.

Weatherhead, P.J. (1979) Ecological correlates of monogamy in tundra-breeding Savannah sparrows. *Auk*, **96**, 391–401.

Wheelwright, N.T. & Dorsey, F.B. (1991) Avoiding pred-