BREEDING BIOLOGY OF THE SAVANNAH SPARROW ON KENT ISLAND

CLARA L. DIXON
Department of Biology, Albion College, Albion, Michigan 49224 USA

ABSTRACT.—I studied the breeding biology of the Savannah Sparrow (*Passerculus sandwichensis*) on Kent Island, New Brunswick, Canada from 1964 through 1968. I estimated the breeding population to be 125–135 pairs (412–445 individuals/km^2). The mean number of nests produced per female, including those destroyed by predators, was 2.97. Clutch size ranged from 2 to 5. The mean clutch size based on 1,142 eggs in 284 nests of known clutch size was 4.02. Not only was the four-egg clutch most numerous but a greater percentage of eggs in the four-egg clutches hatched and the mean number of young fledged per nest was also highest. The mean incubation period was 12.2 days, the mean duration of nestling life was 9 days, and the approximate length of the breeding season as 52 days. The daily mortality rate of eggs was 11.9% and of nestlings 2.1%. Predation was the major factor affecting reproductive success; 50.5% of all nests located were destroyed by predators. The main nest predators were Common Crows and Herring Gulls. Of the nests destroyed by predators, 87.8% contained eggs rather than nestlings. The intense predation necessitated high nest replacement. The mean interval between the termination of one nest and the appearance of the first egg in the succeeding nest was 6.3 days. If successive nests are destroyed on the day incubation begins, it is hypothetically possible for a pair to produce four nests during a single breeding season; many birds in the population produce at least three. Although enough time was available for birds to fledge two broods in a season, few of them fledged more than one. Thus, the nesting success was low (success from egg to hatching 18.1%). High nest replacement compensated for high egg mortality, and an average of 2.16 young per pair were fledged per season.
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KENT Island, New Brunswick, Canada (66°46′W, 44°35′N) is the outermost island in the Grand Manan archipelago, on the eastern edge of the Gulf of Maine at the entrance of the Bay of Fundy. The greatest length of this 60.7 ha island is 2.8 km and its width varies from 0.2 to 0.8 km. In the central part of the island there are approximately 10.7 ha of open grassy meadow which constitute the primary nesting area of Savannah Sparrows (*Passerculus sandwichensis*). This paper, based on field data obtained during five breeding seasons (1964 through 1968), describes the clutch size and its variations, incubation, mortality, and breeding success of this population.

METHODS

I relied primarily on direct observation of birds in this study. Daily nest checks provided information from 398 nests containing 1,514 eggs. A nest was considered complete when an inner lining of fine grass was present. Color banding individualized 741 adults and flying fledglings, and 491 nestlings were given year-specific color bands. In order to understand the pattern of nest replacement, nests in a portion of the study area were systematically destroyed in 1968. My assistants and I then attempted to locate successive nests produced by identified pairs. Population size was estimated by counting singing males plus extrapolations from known numbers of birds nesting in restricted portions of the study area.

RESULTS AND DISCUSSION

POPULATION SIZE

I have estimated the total breeding population on Kent Island to be between 125 and 135 pairs (412–445 individuals/km^2). Although Savannah Sparrows have been

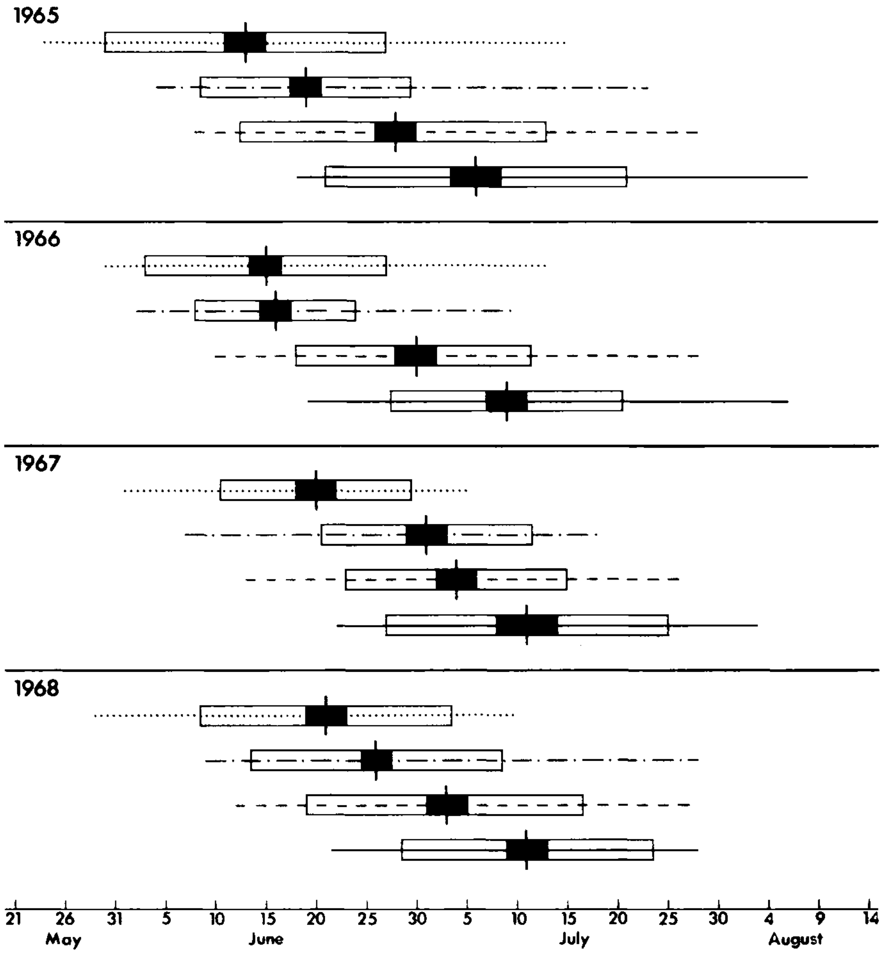

Fig. 1. Breeding phenology of Savannah Sparrows on Kent Island, 1965–1968. Horizontal lines indicate range of dates; (. . . . . . . = onset of laying; –·– = predation; – – – = hatching; ——— = fledging); vertical line = sample mean; open rectangle = one standard deviation on each side of mean; solid rectangle = one standard error on each side of sample mean.

reported from all nonwooded areas of the island, they nest primarily in 10.7 ha of centrally-located open fields. An estimated 100 pairs nested in this central area. A 1.38 ha portion of the breeding area supported 12 pairs of breeding birds (8.7 pairs/ha). This density is high as compared with 3.7 pairs/ha reported by Potter (1972) in a mainland population near Ann Arbor, Michigan and 5.4 pairs/ha reported by Welsh (1975) for birds nesting in a beach dune area in Nova Scotia.

BREEDING SEASON

I used the date of the laying of the first egg to describe the timing of the breeding, and where necessary I extrapolated using a mean incubation period of 12 days and a mean nestling period of 9 days. Critical dates in the breeding season are presented in Fig. 1.

On Kent Island the first egg was laid as early as 24 May and as late as 15 June, giving a 52-day period during which onset of laying occurred. The mean time be-

TABLE 1. Laying of first egg in relation to nest completion

Date found	Nest condition	Date of first egg	Minimum time between completion of nest and laying of first egg
25 May	Complete	1 June	7 days
25 May	Complete	31 May	6 days
30 May	Complete	31 May	1 day
3 June	Partial	7 June	4 days
3 June	Partial	6 June	3 days
3 June	Complete	4 June	1 day
4 June	Complete	6 June	2 days
6 June	Partial	9 June	3 days
19 June	Complete	20 June	1 day

tween the completion of the nest and the appearance of the first egg was 3 days (Table 1). Based on 27 nest replacements, not all of which were successful, the mean time interval between the termination of one nest and the appearance of the first egg in the next nest was 6.3 days. Assuming incubation begins a day before the last egg is laid, as is evidenced by the general asynchrony of hatching, the time from the appearance of the first egg to the fledging of young is 23 days. Allowing 6 days for nest replacement activities and the laying of the first egg in the succeeding nest, a minimum of 29 days is required for renesting. Hence it is theoretically possible for the Savannah Sparrows on Kent Island to fledge young from two nests but not from three during a single breeding season. However, I found only five instances of two successful nests from a pair during a breeding season. Between 1965–68, 60% of all nests found were destroyed or deserted, and as after the nest is destroyed or deserted the birds build a new nest, many pairs produce three or more nests during the breeding season in order to fledge young from one of them.

CLUTCH SIZE AND VARIATIONS

A clutch was considered complete when the number of eggs remained unchanged for 2 or more days. Clutch size varied from 2 to 5 with 63% of the nests containing 4 eggs; 20% had 5 eggs, 15% had 3 eggs and only 1% contained 2 eggs. The mean clutch size based on 1,142 eggs in 284 nests of known clutch size was 4.02 (SD = 0.546).

For 168 nests of known clutch size I also know the week of onset of laying. These clutches showed a seasonal reduction in size. Table 2, modeled after Stokes (1950), analyzes variation in relation to the week of the onset of laying. The coefficient of

TABLE 2. Seasonal variations in clutch size in relation to the week of onset of laying

Date of onset of laying	Number of nests by clutch size				Mean	SD
	2	3	4	5		
24–30 May	0	1	11	1	4.00	0.408
31 May–6 June	0	2	28	2	4.00	0.359
7–13 June	0	2	16	6	4.17	0.565
14–20 June	0	2	23	9	4.21	0.538
21–27 June	0	2	13	5	4.15	0.587
28 June–4 July	0	5	21	1	3.85	0.456
5–11 July	2	7	5	1	3.33	0.817
12–18 July	0	2	1	0	3.33	0.577
Totals	2	23	118	25	3.99	0.579

TABLE 3. Relative success of various clutch sizes

	Clutch size			
	2	3	4	5
Number of clutches	4	43	180	57
Number of egg days	48	722	4,431	1,033
Number of eggs destroyed	2	42	228	150
Number of eggs deserted	0	6	36	20
Number of eggs unhatched	1	14	48	13
Number of eggs hatched	5	61	404	99
Percentage of eggs hatched	62.5	48.4	56.1	34.7
Number of eggs of unknown outcome	0	3	4	3
Number of nestling days	35	451	3,179	645
Number of nestlings destroyed	0	14	59	14
Number nestlings deserted	0	0	0	4
Number nestlings died	1	5	41	10
Number nestlings fledged	2	41	291	56
Percentage of hatched eggs that fledged	40	67	72	57
Percentage of total eggs that fledged	25	32.5	40.4	19.7
Mean number of young fledged per nest	0.5	.98	1.62	.98
Number of nestlings unknown fate	2	2	10	5

correlation between the individual clutch size and the date of onset of laying was −0.589 ($P < .05$, t-test).

Most clutches contained four eggs. Not only were the four-egg clutches most numerous but a greater percentage of eggs in four-egg clutches hatched than in three-egg or five-egg clutches and a greater percentage of nestlings fledged (Table 3). In only 21% of the five-egg clutches were five eggs hatched, and in only four nests (7%) were five young fledged. In normal food years adults may be unable to feed five nestlings adequately.

If the number of young fledged per nest is used as a criterion for reproductive success, the four-egg clutch was significantly more successful. During the 4 years of this study the mean number of young fledged from four-egg clutches was 1.62 as compared with 0.98 from five-egg clutches, 0.95 from three-egg clutches, and 0.50 from two-egg clutches.

The 1967 breeding season was hampered by prolonged cold, foggy, rainy weather. During that breeding season the three-egg clutch was more successful than either the four-egg or five-egg clutches; 58% of the three-egg clutches survived as compared with 28% of the four-egg clutches and 22% of the five-egg clutches. Thus, it seems that under duress of extremes in fog and rainfall the birds are less successful in rearing four or five young.

INCUBATION

Incubation has been defined by Nice (1954) as "the time from the laying of the last egg to the hatching of the last young . . . where all eggs hatch." In six clutches for which I have this information, the length of incubation ranged from 11 to 13 days with a mean of 11.8 days. Mayfield (1961) calculates incubation periods for individual eggs in clutches for which he knows both the day the last egg was laid and the date each young hatched. He makes two assumptions: (1) incubation begins the day prior to the laying of the last egg (the pattern in the Savannah Sparrow is in agree-

TABLE 4. Causes of mortality in the Savannah Sparrow

	1965	1966	1967	1968	1965–68	Percent of individuals	Percent of losses
Eggs laid	413	308	202	591	1,514		
Losses due to:							
Predation	152	115	71	327	665	43.9	76.8
Desertion	51	25	20	35	131	8.7	15.1
Failure to hatch	27	14	12	17	70	4.6	8.1
Total losses	230	154	103	379	866	57.2	
Unknown outcome			3	7	10	0.7	
Young hatched	183	154	96	205	638	42.1	
Losses due to:							
Predation	22	8	12	52	94	14.7	59.1
Desertion	0	0	0	4	4	0.6	2.5
Dead in nest	18	20	8	15	61	9.6	38.4
Total losses	40	28	20	71	159	25.0	
Unknown			9	7	16	2.5	

ment with this assumption), and (2) the last egg hatched was the last egg laid even though all eggs were not hatched. Applying these assumptions to 28 eggs from 7 nests for which I know both the day the last egg was laid and the day each young hatched, the mean length of incubation was 12.2 days. Of the eggs for which I have data, 43% had an 11-day incubation period.

The mean duration of nestling life was 9 days. This is short as compared with the average 11-day nestling period that Nice (1957) reports for 11 species of altricial birds with open nests.

Although both the incubation period and the nestling period are comparatively short, only two successful broods are possible in the short (52 day) breeding period on Kent Island.

MORTALITY IN THE NEST

Three general categories of mortality factors operate in the nest: (1) predation and parasitism, which represent a balance between two adapted systems, those of predator and prey; (2) adaptations based upon selected genetic variables within the population, such as egg fertility, that affect hatching success (or failure); and (3) various behavioral attributes of adult birds that affect mortality. These causes of mortality are summarized on Table 4.

Predation.—By far the most important factor responsible for mortality of Savannah Sparrow eggs and young is predation. Thus, 50.5% of the nests found containing at least one egg were lost to predators either as eggs or as nestlings. The nest loss is

TABLE 5. Critical dates in the breeding season of the Savannah Sparrow

Year	Mean date onset of laying	Mean date hatching	Mean date fledging	Mean date predation
1965	13 June	28 June	6 July	19 June
1966	15 June	30 June	9 July	16 June
1967	20 June	2 July	11 July	1 July
1968	21 June	3 July	11 July	26 June
1965–68	17 June	30 June	9 July	23 June

TABLE 6. Predation of eggs and nestlings based on egg-days and nestling-days of exposure[a]

Year	Number of egg days	Number of eggs lost to predators	Daily mortality	Number of nestling days	Number of nestlings lost to predators	Daily mortality
1965	2,260	152	0.0672	1,489	22	0.0147
1966	1,415	115	0.0812	1,237	8	0.0064
1967	864	71	0.0821	680	12	0.0176
1968	2,087	327	0.1566	1,170	52	0.0440
1965–68	6,626	665	0.1003	4,576	94	0.0205

[a] Survival is calculated by days of nest exposure. For explanation of method see text

less than the two-thirds loss to predation reported for the Kirtland's Warbler (*Dendroica kirtlandii*) by Mayfield (1960), but considerably higher than the 36.7% of Song Sparrow (*Melospiza melodia*) eggs and nestlings taken by predators (Nice 1937) and the 42.9% loss to predation that Ricklefs (1969) reported for six passerine species.

The most important nest predators were Common Crows (*Corvus brachyrhynchos*) and Herring Gulls (*Larus argentatus*). The only mammals on the island, the snowshoe rabbit (*Lepus americanus*) and the muskrat (*Ondatra zibethica*), could not be considered nest predators.

During the breeding season there is an increasing intensity of predation that reaches a peak during the last week in June. At peak intensity 89% of the nests located were destroyed by predators. This increase in predation may be density dependent. In many instances animals concentrate on a source of food that is relatively abundant and then move on to something else when this source declines. It may also be affected by increasing predator skill, by nest disturbance caused by daily nest checks, and by the fact that nest replacements may not have been as well concealed as initial nesting attempts.

Immediately following the June peak, predation dropped approximately 40%, and during the first 3 weeks in July 50% of the rather small number of available nests were destroyed by predators. The decline coincides with the mean date of hatching, 30 June. Although it is difficult to explain, crows appear to prefer eggs. Table 5, tabulating the critical mean dates in the nest life of the Savannah Sparrow, shows that the mean date of predation always falls between the mean date of onset of laying and the mean date of hatching. Furthermore, 87% of the nests lost to predators contained eggs rather than nestlings. Table 6, which shows predatory losses calculated from egg-days or nestling-days of exposure, indicates that the daily mortality rate of eggs due exclusively to predation was approximately five times the daily mortality rate of nestlings lost to predators. This differs from the results reported by Nice (1937) for the Song Sparrow; its eggs and nestlings were taken with equal frequency. A similarly high egg loss as compared with nestling loss was reported by Murton and Isaacson (1964) in their study of the Woodpigeon (*Columba palumbus*) in Carlton, England. Their study is of particular interest as the major nest predators were Corvids. The Woodpigeons lost their eggs to jays (*Garrulus glandarius*) and magpies (*Pica pica*). I am reasonably sure that the Common Crow is the major predator of Savannah Sparrow nests on Kent Island. This high egg loss as compared with nestling loss is puzzling since one would think the larger more nutritious nestlings would be more attractive prey. It may be that some source of food becomes available to crows when most of the sparrows have young in the nests. Also, the steady growth of vegetation during the season means that the nests are better con-

TABLE 7. Reproductive success of the Savannah Sparrow reported as percentages of eggs and nests surviving

	1965	1966	1967	1968	1965–68
Number of nests	111	83	52	152	398
Number of eggs	413	308	202	591	1,514
Number hatched	183	154	96	205	638
Percent hatched	44.3	50.0	47.5	34.7	42.1
Number fledged	143	126	67	127	463
Percent of eggs hatched fledged	78.1	81.8	69.8	61.9	72.6
Percent of eggs fledged	34.6	40.9	33.2	21.5	30.6
Mean number fledged per nest	1.29	1.52	1.29	0.84	1.2

cealed the longer they remain in place, so crows may be cropping the early, less well-concealed nests.

Parasitism.—Parasitism by the Brown-headed Cowbird (*Molothrus ater*), which strongly affects survival in many small passerines, was an insignificant mortality factor in the Kent Island population between 1965 and 1968. Only 5 of 398 nests examined contained cowbird eggs. Four of these contained one cowbird egg and one nest contained two. In none of the parasitized nests did the clutch size exceed the normal limits for the Savannah Sparrow. Two of the five parasitized nests were destroyed by predators. Both Savannah Sparrow and a cowbird nestling fledged from each of the other three nests, although in one of these a sparrow nestling disappeared from the nest before its siblings fledged. It will be interesting to see if the cowbird population increases in the future on Kent Island.

Hatching failure.—The Kent Island Savannah Sparrows hatched a high percentage of eggs incubated full term. Only 4.6% of the eggs incubated full term failed to hatch. This is comparable to the 5.1% hatching failure that Ricklefs (1969) reported for six other passerine species.

Nestling death (exclusive of predation).—When nestling losses were not losses of entire broods, I did not attribute the loss to predation or desertion. During the 4 years of this study 61 such partial losses occurred; 42 nestlings were found dead in the nest and 19 disappeared before they could be presumed fledged. Since upon two occasions a nestling found dead in the nest one day was gone the next, I assume the 19 nestlings that disappeared from the nest died and were removed by the parents. The percentage of Savannah Sparrows dying in the nest was comparatively high; 9.6% as compared with 2.2% for six other passerines analyzed by Ricklefs (1969). Most of the nestling death occurred late in the breeding season. Only 9 of the 314 nestlings known to have hatched prior to the mean date of hatching died in the nest, as constrasted with 47 of the 242 nestlings known to have hatched after the mean date of hatching. The daily mortality rate due to nestling death was 0.0035 prior to the mean hatching date as compared with 0.0278 after the mean hatching date, a difference significant at the 0.01 level. The high nestling mortality may be due to a seasonal decrease in food for nestlings, but I have no evidence to document such a seasonal decrease. I have limited evidence of a slackening of parental attentiveness late in the season.

Desertion.—My records show 39 of 398 (9.8%) clutches of eggs deserted by the female. The deserted clutches contained 8.9% of the eggs produced. Desertion of nestlings is rare; a single deserted brood of four nestlings is the only record I have of parental desertion of nestlings and here the possibility of death of the adults exists. The percentage of desertion is three times that which Ricklefs (1969) reports for six passerine species. In a few cases the cause of desertion is clear. In two nests, desertion

TABLE 8. Reproductive success in terms of nest-days of exposure

	1965	1966	1967	1968	1965–68
Total number nests	111	83	52	152	398
Number of nest-days observed during incubation	607	367	222	543	1,793
Number of nests deserted before hatching	16	7	5	10	38
Number of nests destroyed before hatching	39	33	19	84	175
Total nests lost before hatching	55	40	24	94	213
Nests lost per nest day before hatching	0.091	0.109	0.108	0.173	0.119
Number of nests between hatching and fledging	56	41	28	58	183
Number of nest-days observed between hatching and fledging	494	374	189	352	1,409
Number of nests deserted between hatching and fledging	0	0	0	1	1
Number of nests destroyed between hatching and fledging	6	2	4	14	26
Total nests lost between hatching and fledging	6	2	4	15	27
Nests lost per nest-day between hatching and fledging	0.014	0.008	0.026	0.043	0.021

followed partial destruction of the nest by a predator, and in another case, desertion followed a heavy rain that flooded the nest. Human interference cannot be eliminated as a possible cause of desertion, although nearly all of the birds tolerate daily nest inspections.

REPRODUCTIVE SUCCESS

Most authors reporting nesting success give the number of eggs that hatch, the number of young that fledged, and the various percentages derived from these. In order to compare the reproductive success of the Savannah Sparrow with other species I have reported my findings in this way in Table 7.

Reproductive success calculated from nest-days of exposure.—Mayfield (1961) pointed out that, as a cohort of birds declines exponentially, data on mortality are most meaningful when reported as a mortality rate rather than as a percentage lost over a given period of time, and that mortality and survival are best reported as probabilities of dying or probabilities of surviving. In addition, he pointed out that the hazards of existence vary according to the length of time a nest is exposed, and nests are frequently not found until the nesting period is partly over. This introduces a possibility of error, since mortality/survival rates are calculated for the entire nest period. As a correction, he suggested data be reduced to units of exposure that reflect not only the number of nests but the length of time each nest was observed. A convenient unit of exposure is the nest-day, that is, one nest observed for one day. If the mortality per nest-day is r, the survival rate is clearly $(1 - r)$ and the proportion of nests remaining after d days of exposure is $(1 - r)^d$. Given an incubation period of 12 days and a nestling period of 9 days, probabilities of survival based on nest exposure can be calculated.

Data presented in Table 8 show a daily mortality rate during incubation of 11.9% (daily survival rate of 88.1%) during the years 1965–68, ranging from 9.1% in 1965 to

TABLE 9. Nests deserted or lost to predators, 1965–1968

	1965	1966	1967	1968	1965–68
Number of nests found	111	83	52	152	398
Number of nests lost before eggs hatched:					
Desertion	16	7	5	10	38
Predation	39	33	19	84	175
Totals	55	40	24	94	213
Number of nests lost after eggs hatched:					
Desertion	0	0	0	1	1
Predation	6	2	4	14	26
Totals	6	2	4	15	27
Total nests lost to predators	45	35	23	98	201
Percentage of nests lost to predators	40.5	42.2	44.2	65.5	50.5
Total nests deserted	16	7	5	11	39
Percentage of nests deserted	14.4	8.4	9.6	7.2	9.8
Total nests deserted or lost to predators	61	42	28	109	240
Percentage of nests deserted or lost to predators	55.0	56.6	53.8	71.7	60.3

17.3% in 1968. The incubation period of the Savannah Sparrow is 12 days; consequently, the probability of a nest remaining to hatching time is $(.881)^{12}$ or 22.0%.

Mayfield (1960) reported a daily mortality rate of 4% for the Kirtland's Warbler, and Ricklefs (1969), in his summary of 50 studies of small altricial birds of the North Temperate Zone, reported a range of 0.5–7.28%. Clearly, as compared with other songbirds, the mortality rate of the Savannah Sparrows on Kent Island is high during incubation.

The daily mortality rate among Savannah Sparrow nestlings during the years 1965–68 was 2.1% (daily survival rate 97.9%) (Table 8). This is comparable to the daily mortality rates ranging from 0.28–3.86% reported by Ricklefs (1969). The average nestling period is 9 days; consequently, the probability of a nestling remaining in the nest long enough to fledge is $(.979)^9$ or 82.5%.

Total nest success can be calculated by combining the survival rate of the egg period with the survival rate for the nestling period. As the probability of a nest surviving through incubation is 22.0% and the probability of its surviving through fledging is 82.5%, the probability of the nest surviving from laying to fledging is $.220 \times .825$ or 18.1%. This is comparable to the 19% probability of survival that Mayfield (1960) reports for the Kirtland's Warbler, but is less than half the 46% figure given by Nice (1957) for a large number of altricial birds.

The mean number of young fledged per nest can be readily calculated from nest exposure. Given a mean clutch size of 4.02 and a 22.0% probability of surviving through incubation we can expect $4.02 \times 0.22 = 0.88$ nestlings per nest at the end of incubation. Of these, 82.5% or 0.73 nestlings per nest can be expected to fledge.

Production per pair.—In order to calculate the number of fledgings produced per pair of birds, it is necessary to consider nest replacements. Nests deserted or destroyed are often replaced. Consequently, desertion and predation frequently result in delay rather than loss. The delay is particularly important in the population of Savannah Sparrows on Kent Island. Of all nests found, 60% were deserted or lost to predators (Table 9). Furthermore, 89% of these losses occurred before the eggs had

TABLE 10. Success of nests: first, second, third, and fourth attempts[a]

Attempt	Nests started	Nests lost	Nests succeeding
First	100	82	18
Second	82	67	15
Third	67	55	12
Fourth	48	39	9
Total	297	243	54

[a] Hypothetical sample

hatched. This high rate of nest loss prior to hatching (54%) means that a great many replacement nests were produced.

I have used the method proposed by Mayfield (1960) to calculate the hypothetical success in replacement nesting. If a number of nests, a, start incubation with a loss rate of r_1 and a loss rate per day during the nestling period of r_2, the number of nests existing on day d during incubation will be $a(1 - r_1)^d$; but at $d = 12$, the average day of hatching, the loss rate during the nestling period, r_2, applies and the first-attempt nests existing on any day after hatching $d = 13, 14, \ldots d = 21$ becomes $a(1 - r_1)^{12} (1 - r_2)^{d-12}$. If we assume a typical nestling period of 9 days, the day of fledging of the average nest in first nesting attempt is day 21. Thus, if we start with 100 nests on day 0, on day 21 there will be $100(0.88)^{12}(0.98)^9 = 18$ nests remaining. Ignoring for the moment nests lost during building and egg-laying phases, all 82 nests lost up to day 21 are replaced by second attempts. But the earliest second nesting attempt will begin incubation on d-9. The second attempts in daily installments continue from d-9 through d-29. Third attempts begin on d-17 and continue through d-37. As no nests can be replaced after 17 July, not all third-attempt nests that are lost will be replaced by a fourth nesting attempt, which begins on d-28 and terminates on d-44. It is assumed that second and third nesting attempts will ultimately succeed in the same ratio as the first attempt, that is, 18% of the attempts will succeed. To deal with the fourth attempts we must recognize that third attempts lost after d-44 will not be replaced. The number of third attempts lost up to and including d-44 is $ar_1^2[1 + 2(1 - r_1) + 3(1 - r_1)^2 + 4(1 - r_1)^3 \ldots 12(1 - r_1)^{11} + 13(1 - r_2) + 14(1 - r_2)^2 \ldots 20(1 - r_2)^8] = 48$ nests, where $a =$ the number of nests started in the third nesting attempt.

The hypothetical success of these nesting attempts is presented in Table 10. In this hypothetical sample 100 birds produce 297 nests (2.97 nests per pair) of which 54 succeed. Losses occurring before the onset of incubation make this figure conservative.

This model describes fairly well what has been observed in the field (Table 11). Records of color-banded birds attending a sequence of nests give direct evidence regarding the number of nests a pair produces in a single season. Records from 1968 are especially illuminating as predation was intense during that breeding season. Also, in 1968 nests were systematically destroyed in one section of the study area in an effort to understand the pattern of replacement nesting. Table 11 shows that 7 out of 17 nest replacement sequences in 1968 involved at least 3 nests. In three instances that appear to be two-nest sequences, the time interval between the destruction of the first nest and the appearance of the first egg in the next nest makes an intervening nest possible. All other two-nest sequences occurring in 1968 involve first-nest destructions occurring after 4 June, which makes possible the destruction of an earlier nest. It is very difficult to find the entire series of nests produced by a pair of

TABLE 11. Record of renesting and nest replacements 1965–1968

First nesting attempt	First egg nest 2	Days btwn. 1 & 2	Second nesting attempt	First egg nest 3	Days btwn. 2 & 3	Third nesting attempt	First egg nest 4	Days btwn. 3 & 4	Fourth nesting attempt
				1965					
Deserted 3 June	9 June	6	Fledged 2 July						
Fledged 26 June	6 July	10	Fledged 29 July						
Fledged 23 June	27 June	4	Fledged 19 July						
Fledged 24 June	29 June	5	Starved 22 July						
				1966					
Fledged 19 June	28 June	9	Starved 18 July						
Fledged 28 June	4 July	6	Fledged 29 July						
Fledged 29 June	13 July	14	Fledged 6 August						
Fledged 25 June	3 July	8	Fledged 27 July						
Deserted 18 June	8 July	20	Fledged 23 July						
				1967					
Destroyed 18 June	23 June	5	Fledged 13 July						
				1968					
Destroyed 22 June	28 June	6	Fledged 21 July						
Destroyed 23 June	3 July	10	Destroyed 10 July						
Destroyed 6 July	11 July	5	Nestlings 29 July outcome unknown						
Destroyed 6 July	14 July	8	Destroyed 17 July	24 July	7	Destroyed 28 July			
Destroyed 6 July	10 July	4	Destroyed 28 July						
Destroyed 12 June	2 July	20	Fledged 26 July						
Deserted 14 July	20 July	6	Deserted 21 July						
Deserted 7 June	19 June	12	Destroyed 27 June	1 July	4	Fledged 24 July			
Deserted 8 June	14 June	6	Destroyed 23 June	28 June	5	Destroyed 6 July			
Destroyed 11 June	15 June	4	Deserted 16 June	20 June	4	Destroyed 25 June	2 July	7	Fledged 26 July
Destroyed 12 June	17 June	5	Destroyed 24 June	2 July	7	Destroyed 5 July	10 July	5	Destroyed 11 July
Destroyed 13 June	22 June	9	Destroyed 28 June	5 July	7	Destroyed 11 July			
Destroyed 14 June	20 June	6	Destroyed 7 July						
Destroyed 16 June	30 June	14	Fledged 21 July						
Destroyed 15 June	29 June	14	Fledged 23 July						

birds, so there is no assurance that the last nest reported is the final one. Two nest replacement sequences involving four or more nests are of particular interest.

(1) What is presumed to be a first-attempt nest was destroyed 11 June. The first egg was in the second nest on 15 June. This nest was deserted 16 June, and the first egg was in a third nest 4 days later (20 June). The third nest was destroyed 25 June and the first egg was in nest 4 on 2 July. Four young fledged from this nest on 26 July.

(2) What is presumed to be a late first-attempt nest (onset of laying 7 June) was destroyed 12 June. The first egg was in the second nest on 17 June. This nest was destroyed 24 June, and 7 days later (2 July) the first egg was in nest 3. Nest 3 was destroyed on 5 July. The first egg was in nest 4 on 10 July, and the nest was destroyed 11 July. As a nest destroyed as late as 17 July can be replaced, it is possible that this pair of birds made a fifth attempt, but we did not find another nest for this pair. It is also possible that what was assumed to be a first-attempt nest was actually a second nesting attempt. Thus, the field data document the hypothetical pattern of nest replacement, and it is clear that most birds in this population produce at least three nests during the breeding season.

Returning to the hypothetical nest replacement success shown on Table 10, if 297 nests produce an average of 0.73 fledglings per nest (mean number of young fledged per nest calculated from nest exposure), the young fledged per 100 pairs of adults will be 216, an average for the season of 2.16 young per pair of Savannahs. Using the same method of calculation, Mayfield (1960) found 1.4 young per pair of Kirtland's Warblers. For several other passerine species Lack (1954) reported fledglings per year per pair of adults ranging from 1.7 to 8. Although the Savannah Sparrows on Kent Island have low nesting success, as compared with other passerine species, their nest replacement activity compensates for their high egg mortality, and each pair of birds is able to fledge approximately two young during the breeding season. It is obvious that this does not mean that each pair of birds produces two breeding adults each season, as losses occur in the fledgling state and beyond.

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