

# SAVANNAH SPARROW BREEDING AND TERRITORIALITY ON A NOVA SCOTIA DUNE BEACH

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THE literature on bird territoriality has increased greatly since Eliot Howard (1920) introduced the subject. In spite of the many studies and the many attempts at synthesis since then, no single unifying theory has been found to explain the existence of bird territoriality to everyone's satisfaction and one frequently reads that the answer lies in more intensive study.

The Savannah Sparrow (*Passerculus sandwichensis*) breeds in a number of open habitats. On the east coast of Canada and northeastern United States it nests quite densely on beach dunes. On this habitat it is easy to follow the birds' movements and develop some understanding of what happens during the breeding season.

This paper presents the results of an intensive small scale study during one season, and indicates that polygyny may be a regular component of the life history of Savannah Sparrows. Information on territory, nesting cycles, and feeding of young is presented and the brief discussion concentrates only on those questions directly pertinent to this study.

## MATERIALS AND METHODS

The study was made on a short section of the Martinque Beach Game Sanctuary, a sandspit 3 km long and 0.5 km wide, on the Atlantic coast of south central Nova Scotia. The general structure of the spit is rather simple with an unconsolidated sand beach seaward of dunes stabilized by beach grass (*Ammophila breviligulata*). Vegetated sand flats behind the dunes slope down to an inner lagoon beach. The basic vegetational pattern is shown in Fig. 1. Beach grass is by far the most abundant plant and beach pea (*Lathyrus japonicus*) is thick along much of the consolidated dune. Myrtle clumps (*Myrica pennsylvanica*) are prominent on the flats and often served as nesting sites. Crowberry (*Empetrum nigrum*) and cranberry (*Vaccinium macrocarpon*) are common on the flats near the lagoon beach. Occasional small spruces (*Picea glauca*) are important as song perches. As seen in Fig. 1 some of the study spit adjoined woodland that the birds used little except to escape disturbance.

Birds on the spit were captured with mist nets, sexed by presence or absence of cloacal protuberance (Wolfson 1952), and marked with colored plumage marks and colored leg bands. On the basis of these markings and natural plumage differences it was possible to distinguish between individual birds and watch territorial and breeding habits of 13 males and their females. Observations were made almost daily from late April to late August 1969.

Territorial boundaries were determined by watching bird movements, and the ground a bird normally occupied was considered to be its territory. Territories were thus essentially home ranges, which the male advertised as his by singing and perch-

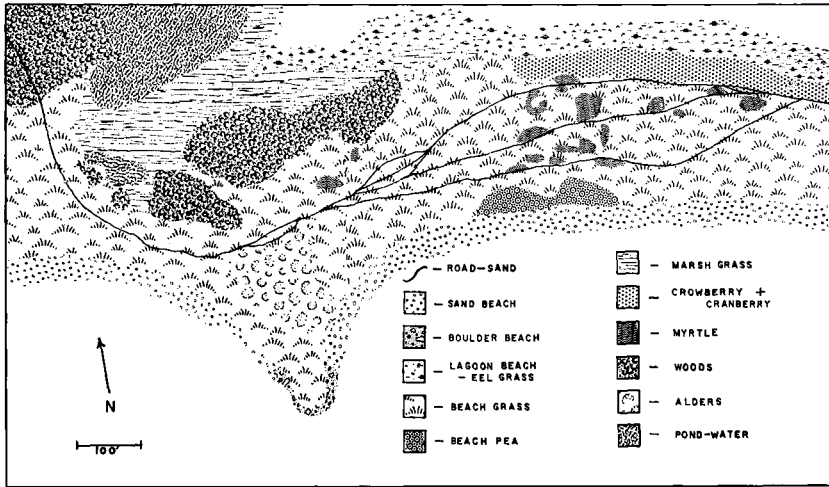


Fig. 1. Map of study area showing major types of vegetation.

ing conspicuously at some points on the boundaries, but individual males were not seen defending every segment of boundary delineated in the figures. Both mating and nesting took place within the territory.

Territories were numbered as they were discovered and the resident male was given this number. Females were identified by letters given in the sequence that they nested on each territory. Successive clutches of each female were also numbered. For example, 10-B-2 indicates male and territory number 10, the second nesting female B, and her second clutch 2.

Feeding of nestlings was watched with a 20 $\times$  telescope from far enough away to ensure that the birds were not disturbed. The 13 nests used in this part of the study were watched three times daily for 20 min at about 0800, 1200, and 1800, from the day the young hatched until they left the nest. A dead branch or stick placed near many of the nests to give the birds an open perch greatly facilitated identifying individual parents.

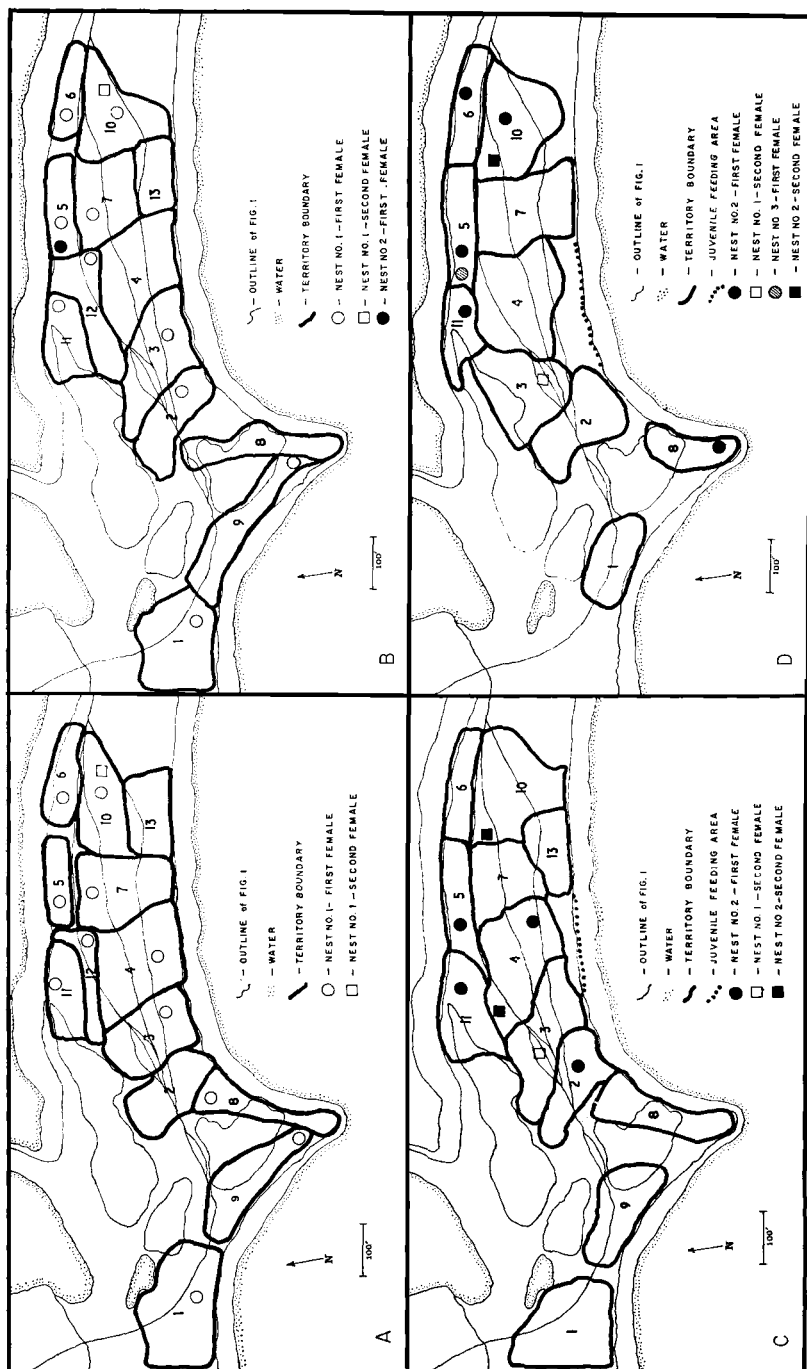
Martinique Beach is a recreational area and visitors disturbed the birds considerably, especially on weekends.

#### TERRITORIALITY

*Preterritorial behavior and establishment.*—The first birds arrived in the latter half of April and began singing in early May. The region around the woodlands (territories 2, 3, and 4, Fig. 2) was filled with many

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Fig. 2. Map of study area showing territorial boundaries and nest sites. A, 1 to 14 June; B, 15 to 30 June; C, 1 to 14 July; D, 15 to 31 July. Territories are numbered.



birds during this time, presumably awaiting suitable weather to begin nesting. Perhaps because spring was late, birds arrived throughout May.

During the second week of May the birds gradually began to disperse and by mid-May they started to establish territories. The establishment phase was prolonged and, as the weather improved, new territories were occupied adjacent to those already established, more or less successively along the beach. Territories 2, 3, and 4 in the shelter of the woods got an early start, and before the end of May females in each had complete clutches while other territories farther along the beach were still being disputed.

*Territory maintenance.*—Each territory abutted the territory of another male on at least one side and changed in size during the season (see section on territory size). Original boundaries were established over a period of several days and involved frequent fights early in the season. Males moved up and down the line chipping and watching constantly until each one was apparently satisfied about the line's position. Small spruce trees and other objects that projected above grassy (shrubby) ground cover were often focal points in the boundary lines. In a few cases a single tree apparently belonged to two males who used it as a singing perch, one using one side and the top and the other using the opposite side and the top, at different times of the day. It was around these trees that most fighting occurred.

Birds sang both from the ground and from song posts and each had a few favorite singing and perching spots. They followed no obvious pattern of song post use. They sang most often early in the season and in early morning and evening.

Watchfulness is the byword in Savannah Sparrow territoriality and the main defense tactic of males is to guard the territory constantly so that an intruder is anticipated before he arrives. In most cases intruders were repulsed without overt aggression, by posturing and puffing of feathers. When an intruder was not noticed before it had violated his territorial confines, the male immediately flew towards it uttering rapid chipping sounds and chased it away, frequently returning to sing on a perch near his territorial boundary.

Throughout the season, particularly at the beginning, unknown birds or "floaters" (Brown 1969) drifted through the area and, although not harried relentlessly, the territorial males kept them moving, normally only chasing them when they ventured to sing. These were presumably subordinate males looking for a territory.

Once the boundaries were established there was very little conflict between adjacent males. Territorial females chased all other females that

TABLE 1  
TERRITORY SIZE<sup>1</sup>

Territory No.	Average <sup>2</sup>	Maximum <sup>2</sup>	Feeding <sup>2</sup>
1	0.328 (0.810)	0.397 (0.982)	0.237 (0.583)
2	0.163 (0.404)	0.223 (0.551)	0.138 (0.342)
3	0.208 (0.514)	0.242 (0.597)	0.163 (0.402)
4	0.249 (0.615)	0.255 (0.631)	0.249 (0.615)
5	0.107 (0.264)	0.111 (0.275)	0.098 (0.241)
6	0.093 (0.229)	0.111 (0.275)	0.074 (0.184)
7	0.197 (0.488)	0.244 (0.604)	0.108 (0.266)
8	0.161 (0.387)	0.208 (0.514)	0.102 (0.252)
9	0.158 (0.390)	0.213 (0.526)	0.142 (0.351)
10	0.214 (0.530)	0.257 (0.634)	0.245 (0.606)
11	0.126 (0.312)	0.182 (0.450)	0.094 (0.232)
12	0.134 (0.332)	0.161 (0.399)	0.111 (0.275)
13	0.126 (0.312)	—	—
Average	0.174 (0.430)	0.212 (0.526)	0.151 (0.373)

<sup>1</sup> In hectares, acres in parentheses.

<sup>2</sup> See text.

ventured near them during nesting and mating. While incubating and feeding young the females paid little attention to other birds. Territorial males occasionally chased females of adjacent territories but the circumstances under which this occurred were not clear. Little interspecific aggression was noted except among the alders (*Alnus rugosa*) in territory 11 where nesting Song Sparrows (*Melospiza melodia*) occasionally chased Savannah Sparrows that ventured too close to their nests.

Territorial behavior was complicated by males allowing some types of intrusions. The lagoon shore (Fig. 1) with its heavy covering of drifted eel grass (*Zostera marina*) proved a popular feeding ground and most birds on the study spit went there for food for their nestlings. Males were allowed to cross over another's territory while feeding young, and feeding females apparently traveled as they wished, often landing in another's territory.

*Territory size.*—Table 1 shows the size of 12 successful and one unsuccessful male territories. The territory average is the result of five different size estimates made throughout the season. The areas the male defended and utilized persistently were mapped as accurately as possible several times each week. These results were averaged by eye to provide the maps for successive periods (Fig. 2). The "maximum" column of Table 1 is the size of the territory a week after completion of the first female's first clutch. The "feeding" column is the size of the territory a week after the first female's first clutch hatched.

During the season territorial boundaries shifted extensively as shown in Fig. 2. One male (12) disappeared and his territory was taken over by adjacent males (3, 4, and 11). Males 3 and 4 abandoned the rich beach pea growth in their territories (see section on juvenile feeding areas). All males enlarged their territories during the incubation period of their first female's first clutch (Table 1). Males 4 and 10, the only males to have two nesting females on territory at the same time, were the only ones that did not reduce the size of their territory during feeding. In all cases when a male reduced his territory size while feeding nestlings he quickly reclaimed any lost to his neighbors as soon as his young had fledged.

*Juvenile feeding grounds.*—Young birds concentrated in a few spots after leaving the nest, the main one being the juvenile feeding ground shown in Fig. 2. Feeding there seemed to develop spontaneously when young from nests 3-A-1 and 4-A-1 moved there after leaving the nest. Males 3 and 4 gradually reduced their territory boundaries so that they noticeably excluded this area, and during the summer as many as six females attended their young there. This spot was the most luxuriant on the study site, being covered with a heavy growth of beach pea and beach grass by midsummer. The concentrations of small midges and flies here was by far the highest, presumably offering the young birds readily attainable food.

#### BREEDING AND NESTING

Of 13 males holding territories within the study area, 12 bred successfully. Of these 12, three were bigamous and the rest monogamous. The nesting season began in late May and spanned 3 months. The first clutch was completed 23 May and the last young left the nest 17 August. Early May was cold with some freezing weather, a factor that most certainly delayed the start of nesting. All first nests were completed by 12 June except for that of one late-arriving second female (3-B) who may well have nested elsewhere earlier.

Females laying a second clutch usually did so within 2 weeks after the previous young left the nest, and several instances were noted of females feeding earlier young after completing a new clutch. Female 5, the only one to have a third clutch, completed laying her second clutch 8 days after the first young left the nest.

The few matings seen took place prior to and during nest building. On three separate occasions females were seen copulating with males other than their mates. This was early in the season before these females began laying.

Nest 10-B-1 was abandoned on hatching day after human disturbance

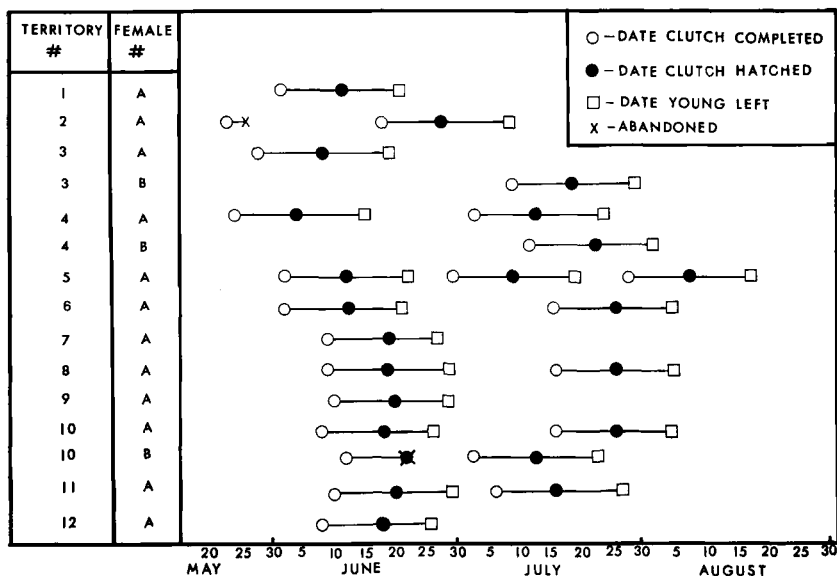


Fig. 3. Nesting phenology.

before the female was marked. As it was well within the territory of male 10, it seems safe to assume that it was his. A female remained in the vicinity of nest 10-B-1 for several days and subsequently renested and successfully raised young with the help of male 10. It is assumed that the female that built 10-B-1 and 10-B-2 were one and the same.

Male 3 gained a second female halfway through the season and although his first female was seen with nesting material in late June and remained on the territory until mid-July, she apparently did not have a second clutch. Male 4 gained a second female from male 12 after the latter disappeared midway through the season.

*Nest building.*—Females were seen carrying nesting materials from mid-May onward. Males were always present on their territories at this time, but nothing suggested that they helped in nest building though they often accompanied the females closely.

The spacing on nests is apparently not critical, as one female nested within 30 feet of another's active nest on an adjacent territory. Distances between successive nests of individual females varied from 20 to 125 feet. The data obtained are not extensive enough to analyze the implications of distance between successive nests of females of monogamous and polygynous matings.

From limited observations 4 to 5 days is the best estimate for time of

TABLE 2  
LENGTH OF INCUBATION AND NESTLING PERIODS<sup>1</sup>

	Average	June	July	August
Incubation time	10 (6)	10 (1)	10 (5)	—
Nestling time	9.4 (20)	9 (10)	10 (5)	10 (5)

<sup>1</sup> Time is in days; number of nests in parentheses.

nest building. Apparently one egg is normally laid per day until the clutch is complete, although in one case a female laid one in the morning and another in late afternoon.

*Nests.*—Nests were built of coarse grasses with a lining of fine grasses and all were well-concealed on the ground in clumps of myrtle, tufts of old beach grass, heavy crowberry growth, and even under large clumps of reindeer moss (*Cladonia* sp.). All nests were roofed or domed, at least in part, by the adjacent vegetation so that only one side was normally used as an entrance. Of 24 nests examined seven faced the north quadrant, four faced east, seven faced south, and six faced west.

*Nesting phenology.*—The data in Fig. 3 are based on 24 nests of 14 females, but not all nests were discovered at the same phase of the nesting cycle and in several cases dates are estimated from those of more accurately timed nests.

In all six clutches observed from a time before laying was completed the incubation time was 10 days, measured from the day the last egg was laid until the day the last young hatched. In three of the six clutches one egg did not hatch; by assuming that each of these eggs would have hatched last and adding a day for each, the incubation time was 10.6 days, but 10 days seems a more reliable figure. The average nestling time of 20 broods was 9.4 days, with a range of 8–11 days. On a monthly basis the average was 9 days for 10 nests in June, 10 days for five nests in July, and 10 days for five nests in August. Weak flight occurred about 3 days

TABLE 3  
GENERAL NESTING DATA<sup>1</sup>

	Season	May	June	July	August
Average clutch size	4.2 (24)	4.0 (3)	4.5 (12)	3.6 (9)	—
Average No. hatching/ nest	3.9 (23)	—	4.2 (12)	3.5 (10)	3 (1)
Average No. leaving/ nest	3.7 (23)	—	4.1 (11)	3.5 (6)	3.6 (5)

<sup>1</sup> Number of nests in parentheses. Abandonment of one nest on hatching day is the only source of difference between hatching and leaving success.



TABLE 4  
MALE AND FEMALE FEEDING DATA<sup>1</sup>

	Nestling day											
	1	2	3	4	5	6	7	8	9	10	11	12
Male	2	3	18	17	36	36	47	44	39	29	11	0
Female	3	26	35	37	51	71	73	72	78	58	34	4

<sup>1</sup> A summary of the average number of feedings by males and females during three 20-min observation periods on each nestling day for 13 nests. Day 1 is the day after the last egg hatched.

after the young left the nest. Table 2 summarizes incubation and nestling data.

*Clutch size and hatching rates.*—General nesting data are summarized in Table 3. The average clutch size was 4.2 (range 3–5) and the differences between months are not significant. An average of 3.9 (range 2.5) hatched and 3.7 (range 2–5) left the nest. Human disturbance on hatching day caused the abandonment of one nest, the only nestlings that did not survive. There was no significant difference in hatching success between first and second clutches.

*Incubation and feeding.*—Males were not seen incubating, although they flushed very close to the nest several times, usually when the female was incubating. Studies of female incubating habits were not extensive enough to allow any generalizations.

Feeding data are based on 13 nests watched for 20-min periods three times each day. Some patterns are evident in these limited data. All comparisons use contingency Chi-square tests of the variously grouped data, with identical rates as the null hypotheses. Active feeding began on the first or second day after hatching and rose to a peak on the seventh and eighth day (Table 4). There is no significant difference ( $P > 0.90$ ) in the number of visits to the nest made by adults with broods of 2, 3, 4, or 5, and no significant difference ( $P > 0.25$ ) in the feeding rate per young in clutches of different sizes (Table 5). The total feeding rate per brood averaged 6.2 feedings per hour, with an average of 1.8 feedings per nestling per hour.

Early in the season Lepidoptera larvae formed a substantial portion of the diet; later, adults of these larvae constituted the main diet. The size of food particles and amount apparently increased during the feeding period and only very small insects were fed on the first 2 days. There was no significant difference ( $P > 0.80$ ) in the total feeding rate of both sexes combined between morning and noon, and evening. In total, females fed the young more than the male ( $P < 0.01$ ), individual variation was considerable (Table 5).

TABLE 5  
A SUMMARY OF FEEDING DATA<sup>1</sup>

Nest	No. of nestlings	Monogamous or polygynous	Total male feedings	Total female feedings	Total adult feedings
1-A-1	5	M	20	33	53
3-A-1	2	P	22	36	58
3-B-1	2	P	15	23	38
4-A-2	3	P	28	80	108
4-B-1	4	P	32	37	69
5-A-1	4	M	17	34	51
5-A-2	4	M	24	30	54
5-A-3	3	M	4	71	75
7-A-1	5	M	35	42	77
8-A-1	5	M	28	40	68
8-A-2	4	M	17	31	48
10-A-2	4	P	12	36	48
10-B-2	3	P	24	39	63

<sup>1</sup> Number of feedings is the total number seen during 20-min observation periods three times per day for the whole nestling period.

There was no significant difference ( $P > 0.70$ ) between the number of female feedings of first and second broods or the number of male feedings of first and second broods ( $P > 0.20$ ), although male feeding rates seemed to taper off at the end of the season and the female 5-A-3 raised her young almost completely alone.

Although both parents usually participated in feeding, it was possible for one parent to feed young alone. Male 1 fed his offspring from the fifth day after hatching, when his female disappeared. These young were noticeably smaller and "buzzed" constantly when not being fed. Female 12 fed the young alone after they left the nest. They quickly moved to the juvenile feeding ground (Fig. 2) where they could feed more easily. After leaving the nest most young were fed for up to 2 weeks principally by the female, although the male assisted for the first few days.

*Reproductive success.*—Table 6 summarizes some measures of nesting success. The overall hatching success was 88.1% and 95.5% of the young left the nest. The exceptionally high success rate was presumably related to the rarity of predation, disturbance and destruction of nests by humans being responsible for the only deaths of young. Of the 16 losses between laying and leaving, eight may be attributed to human disturbances (including the observer) and eight to eggs not hatching, in which human disturbance that kept the female from incubating may well have been important.

TABLE 6  
NESTING SUCCESS RATES

	No. of eggs laid	No. of eggs hatching	No. of young leaving	% of eggs hatching	% of young leaving
Total	101	89	85	88.1	95.5
First clutches	65	56	52	86.2	92.8
Second clutches	33	30	30	90.9	100.0
Third clutches	3	3	3	100.0	100.0
Females with one clutches	22	18	18	81.8	100.0
Females with two clutches	68	60	56	88.2	93.3
Females with three clutches	11	11	11	100.0	100.0

*Polygyny and monogamy.*—Nesting data for monogamous and polygynous matings are compared in Table 7. The small sample size and the uncertain nature of the data distribution preclude statistical analysis. Females of polygynous males laid 66% more eggs (36 for three polygynous males and 65 for nine monogamous males) and 32% more young left the nest (26 for three males and 59 for nine males).

It is important to note that the first nest of the second female in territory 10 (i.e. 10-B-1) was destroyed by humans and the other two polygynous male territories (3 and 4) were among the most highly disturbed on the beach. Between females of monogamous and polygynous males there were no significant differences (*t*-test corrected for small sample size) in the number of eggs laid per clutch, the number of eggs hatching per clutch, or the number of young leaving per clutch. The inadequacy of this comparison is discussed later.

TABLE 7  
NESTING DATA OF MONOGAMOUS AND POLYGYNOUS MATINGS

	No. of in- dividuals	Eggs laid	Eggs hatching	Young leaving	Hatching success (%)	Leaving <sup>1</sup> success (%)
Monogamous males	9	7.2	6.5	6.5	90.0	100.0
Polygynous males	3	12.0	10.0	8.7	83.4	87.0
Monogamous females	8	8.1	7.4	7.4	91.3	100.0
Polygynous females	6	6.0	5.0	4.3	83.3	86.0

<sup>1</sup> Based on percent young leaving of those that hatched.

## DISCUSSION

Many types of territory have been described in birds, but my comments concern only that type where a male defends a site against other males of the same species and in which mating and nesting occur. This is Nice's (1941) type A if food for young is procured within the territory and type B if it is obtained outside the territory. Savannah Sparrows on Martinique Beach seem to be between the two types, as they obtained nestling food both from within and from outside of the territory.

The number of functions that have been ascribed to bird territoriality is large and the past has seen much confusion between consequence and function. Carpenter (1958) named 31 possible functions of bird territory and recent reviews have concentrated on at least seven or eight (Nice 1941, Hinde 1956, Brown 1964, Crook 1965, Klopfer 1969). Many authors have emphasized the importance of the food resource and have suggested that protection of food supply for the young is the main function of passerine territoriality. Recently McLaren (1972) suggested that polygyny is a "general and sufficient selective force for the evolution of territoriality." The limited results of the present study cannot be expected to settle the question, but I believe they do cast serious doubt on the defense of food supply as a basis for territoriality and are consistent with the theory that polygyny is the adaptive basis for territoriality.

It can be assumed that territorial behavior confers some adaptive advantage to those birds practicing it and that it must have a heritable component. If this were not true, the effort involved in maintaining a territory would be maladaptive. I argue, as did McLaren (1972), that those male passerines that establish territories first and in the best places are in some way superior, and that all males maintain a territory in an attempt to maximize their reproductive output.

At Martinique Beach Savannah Sparrows concentrated in the woodlands (Fig. 1) in May presumably because of high winds and bad weather. Those males that were superior because their age, state of sexual readiness, or strength were able to set up territories earlier than others did. Females that were ready to breed settled in these territories. Early in their breeding cycle territorial females chased other females. Males accompanied their females during nest building at the same time as they set up and defended their territory boundaries. I assume that the combination of these activities was sufficient to prevent other females from choosing these territories and to prevent the males from further courting at this time.

The pattern of occupation of territories outward from the woods along the beach seems to have obvious advantage if one assumes that females were attracted to the places where males were singing. Males not yet

mated would probably have more chance of obtaining a female by staying in close proximity to established ones than they would alone farther down the beach.

Nice (1943b) and others have suggested that song and display of plumage function as a warning to other males and an invitation to females, probably indicating sexual readiness as well as possession of a territory. Females presumably practice mate selection on the basis of characteristics of the territory (and its other occupants) and characteristics of the male. Orians (1969) discussed this likelihood in considerable detail. The small amount of singing was probably due to the nature of the habitat as was the small amount of overt aggression. The open nature of the beach, with exposed perches, allowed the male Savannah Sparrow to be seen by both males and females without constant singing, and thus he achieved his goals with less effort. Weins (1969) found that Savannah Sparrows near Fitchburg, Wisconsin advertised their territory by singing extensively on exposed perches. His study tract was covered with denser vegetation than on Martinique Beach and the differences in behavior are probably due to "site-dependent economics" (Brown 1964), with males in both regions singing as much as was necessary to defend a territory successfully and attract a female.

The average territory size of 0.174 ha agrees with other reports for this and similar species (Nice 1943a, Smith 1963, Weins 1969, Murray 1969, Robins 1971) although it is slightly smaller than most. Seasonal shifts in territory boundaries have been reported in Savannah Sparrows by Weins (1969), in the Grasshopper Sparrow (*Ammodramus savannarum*) by Smith (1963), and in several other species, and are presumably a normal occurrence.

McLaren (1972) reviewed evidence against the food value of territory among passerines in general. The present study also suggests that defense of food is not important for the Savannah Sparrow. The lagoon shore (Fig. 1) apparently provided an ample food supply and was not defended. Also, territorial males allowed adjacent males and females to trespass into their territories when feeding young. Potter (1972) also saw a female Savannah Sparrow feeding young in another's territory. Males 3 and 4 abandoned the juvenile feeding ground (Fig. 2) during the peak of the breeding season. At that time it was the most luxuriant part of the beach and had a high concentration of flies and midges; if they were holding a territory to protect food supply, one would expect them to have maintained this as part of their territories.

The changes in territory size with stage of breeding further support the previous argument and give a clue to the real function of territory.

Nests were built of grass and were well concealed on the ground. Building took 4 to 5 days and one egg per day was usually laid after nest completion.

The hatching time was 10 days in six observed cases and nestlings stayed in the nest an average of 9.4 days. An average of 4.2 eggs per nest was laid and 88.1% of them hatched. Lack of predation let 95.5% of the young leave the nest and the only observed deaths followed human disturbance.

Nests of the females of three bigamous males were made successively so that the male was able to feed young of both females without division of effort. Bigamous males had 66% more eggs and 32% more young leaving the nest, with no apparent disadvantage to their females.

The possible adaptive value of territoriality in protecting food resources is not supported by the behavior observed in this study. It is argued that the possibility of being polygynous is sufficient reason for the maintenance of territory.

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