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TERRITORIALITY AND BREEDING BIOLOGY OF THE IPSWICH SPARROW (PASSERCULUS PRINCEPS)

by

WAYNE T. STOBO

Submitted in partial fulfilment of the
requirements for the Degree of Doctor
of Philosophy at Dalhousie University
(February, 1973).

Approved by: [redacted]

DALHOUSIE UNIVERSITY

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Author Wayne Thomas Stobo

Title Territoriality and Breeding Biology of the
Ipswich Sparrow (*Passerculus princeps*)

Department or School Biology

Degree Ph.D. Convocation - Spring Year 1973

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ACKNOWLEDGEMENTS

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The research project was financed by a National Research Council of Canada grant to Dr. McLaren.

ABSTRACT

The territoriality and breeding biology of the Ipswich Sparrow on Sable Island were studied in a rich habitat from 1968 to 1970, and also in a sparse habitat in 1970. Territorial birds were distinguished by plumage marks and colored leg bands. A total of 98 territories was examined; the size varied from 0.16 to 0.77 ha. and 0.77 to 1.81 ha. on the rich and sparse areas respectively.

A percentage of the males, (5% to 47% in the rich habitat and 23% in the sparse habitat) practiced successive bigamy. In 1969 polygynous males had significantly larger territories only when the population density was highest, but produced on average 60.3% more young than monogamous males.

The females were highly productive, producing as many as 4 successful clutches per season, with clutch sizes ranging from 2 to 6 eggs. Incubation time averaged 12.5 days and the nestling period averaged 10.9 days. Both parents fed the young, and success rates were high, with over 85% of the young leaving the nest in all years. The first females of polygynous males produced as many young as monogamous females. Second females appear to produce less young only because they initiate fewer nests than first or monogamous females.

It is suggested that polygyny is an important adaptive function of territory. No birds were consistently polygynous from year to year. Females appeared to select nesting sites at random, relative to each other, in low density years, but dispersed themselves non-randomly in high density years. Thus a large territory is important for polygyny to occur, especially at high population densities. The possibility of obtaining a second mate is sufficient reason to maintain a large territory. Polygyny is as likely to occur in sparse habitats since the larger territories probably equalize the resource requisites of rich habitats.

Population estimates from 1967 to 1972 indicate that the breeding population varied between 2000 and 4000 birds and the autumn population from 6000 to 14,000. There is no evidence for density dependent regulation of recruitment.

INTRODUCTION

The Ipswich Sparrow (Passerculus princeps) nests almost solely on Sable Island, a crescent-shaped sand island some 90 miles from the nearest mainland of Nova Scotia. A few have recently been found on the mainland (Finch, 1972) mated with the closely related Savannah Sparrow (Passerculus sandwichensis). However it is doubtful that the offspring of such interbreeding would ever reach Sable Island, and for all practical purposes the Sable Island population is a closed one. Long considered a rare and endangered species (Fisher et al., 1969), little has been added to our knowledge of the Ipswich Sparrow since Dwight's (1895) monograph. Elliott's (1968) summary aptly illustrates the limited information available on this interesting bird.

Thus a prime purpose of the study, monographic in intent, was to examine the life history of the Ipswich Sparrow. It was quickly realized, however, that this species would also be an ideal subject to illuminate some of the controversy concerning territoriality and breeding biology, and the present thesis is largely devoted to these topics. The habitat on Sable Island is essentially two-dimensional, thus facilitating observation throughout the breeding season. In addition the birds appeared impertubable, thus reducing the possibility that our activities would affect their behavior or reproductive success. Although the literature abounds with studies of territoriality and breeding biology, most workers have concentrated on only one of these two topics, usually territory size and male interactions, or less frequently the nesting behavior and reproductive output of females; few studies are sufficiently extensive to interrelate these two aspects of the life history of birds. Notable exceptions are the exhaustive work on the genus Parus by Kluijver (1951), Lack (1958,1966), and others, and on the Song Sparrow (Melospiza melodia) by Nice (1937, 1943). It was my primary aim to study as many territories as possible, consistent with finding and following all nests on these territories.

Howard (1920) in his classic book on bird territoriality claimed that population density was regulated by territoriality, and this has since been accepted by many authors. But, although territoriality may limit the number of birds breeding in a particular area, Lack (1954,

1966) claims it to be of little importance in population regulation. Brown (1969a,b) has gone farther and shown that territoriality may maximize the productivity of a population in some cases.

In addition, Verner and Willson (1966, 1969) have cast doubt on the long standing assumption that cases of polygyny among territorial passerines were accidental. Their compilation of available data indicates that some birds are normally polygynous, most notably those of two-dimensional habitat. The Ipswich Sparrow appears to be such a bird. The males tend to be polygynous and study of this species may offer some insight into the significance of this behavior.

Since their breeding grounds are restricted to a fragile and threatened island, the future of the Ipswich Sparrow, and indeed the island itself, could be affected by climatic changes or by ecological negligence of man. If the island is to be managed with a view of ensuring the bird's future survival, information on the numbers of breeding birds and their yearly production is essential. Thus a second purpose of this study was to acquire such data. The relatively small area of Sable Island (3134 hectares) allows for reasonably accurate censusing, and reliable estimates of population fluctuations to be made. By simultaneously examining territoriality and breeding biology, and population estimates, it may be possible to gain a better perspective of the interrelationships involved.

MATERIALS AND METHODS

The study of the Ipswich Sparrow began in 1967 with a preliminary census of selected areas on Sable Island by I.A. McLaren in the period June 1-12. McLaren also spent most of the summer of 1968 (May 25 to June 9; June 19 to August 4; August 20-24) on the island, commencing an intensive examination of the territoriality and breeding biology of the bird, and censused the population on November 3-5. He also conducted an autumn census in 1972 during September 19-20. I spent the following periods of time collecting similar information on Sable Island: May 23 to September 3, 1969; April 18-22, May 10 to September 15, and November 17 to December 1, 1970; April 12 to May 24, June 10 to August 7, and September 18-23, 1971. A brief trip from May 24-29 was made in 1972 to conduct a spring census and examine the study areas for returning birds. In 1971 the field work involved refining population estimates and acquiring taxonomic data for the monograph, thus only territorial data were collected on the study areas.

The data on territoriality and breeding were collected in 1968-70 from a richly vegetated area where the birds were expected to be most productive, and additionally from a sparse, dry area in 1970 for comparative purposes. In all years our arrival on the island was determined by the occurrence of weather condusive to breeding and the migration of Ipswich Sparrows through Halifax County on their way to Sable Island.

In the spring, adult birds were captured with black mist nets (12 x 2.6 m; 30 mm mesh) as they appeared on the study area. Due to the difficulties in catching some birds, netting continued after breeding had begun. All captured adults (174) were sexed by the presence or absence of a cloacal protuberance (Wolfson, 1952) which is present in mature males during the breeding season. The birds were banded with U.S. Fish and Wildlife Service aluminum leg bands (size 1B) and individually marked with colored plastic leg bands (size XCS)[1] and dye, in 1969 and 1970. The various colors were applied to different parts of the plumage with ordinary felt marking pens. Some of the banded birds did not remain on the study area. All female birds which nested on the study areas were marked; the few males that were too elusive to catch became recognizable by idiosyncracies of song and

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[1] A.C. Hughes, 1 High Street, Hampton Hill, Middlesex.

character.

In the summer and autumn of 1968 and 1969, a total of 395 juveniles were similarly captured and banded with the aluminum leg bands. In 1970, 243 juveniles were banded in the 9th or 10th day of the nestling period with both aluminum and plastic bands, in an attempt to obtain information on juvenile returns in 1971.

In subsequent years, previously marked birds were identified by recapture or by reading the aluminum band numbers using a 25X telescope. The presence of plastic bands was not sufficient as a means of sole re-identification since at least one bird lost its plastic bands.

Throughout the season, in 1968 and 1969, daily observations were usually made on the activity of the breeding birds on the study area. In 1970, observations were taken on each study area on alternate days. The territory was considered to be the area in which the resident birds mated and nested, and normally fed themselves and their young. These areas were really the home range of the resident males, but the males frequently sang within and along the borders and defended the area from adjacent or wandering males. It is in this context that the term territory is used. No attempt was made to determine fluctuations in the size of these areas during each clutch cycle or to distinguish between maximum and utilized territory as suggested by Odum and Kuenzler (1955). Territory size was determined from the final territory maps using a polar planimeter. Females were observed mainly for nesting data. Approximately 5 days after the completion of one clutch, each female was closely watched for her next nest. The nests were checked daily in 1968 and 1969, and every second day in 1970.

In all five years censuses for population estimates were conducted. Census areas were selected in 1967 as representative of different types of habitat (McLaren, 1968). The number of census areas was increased in 1968 and again in 1971, based on increasing knowledge of the vegetational structure of the island. Each year two censuses were conducted, one in late May or early June, and another in late August or early September. These data permitted estimates for annual production to be made. A full island census conducted in June, 1971, gave a definite number of adult birds on the island. This census also permitted a more accurate estimate of production to be made, based on a greater knowledge of the distribution of birds relative to the variety and density of vegetation on the island.

The census technique consisted of 3 or more people, evenly spaced, weaving through the specified area, making noise, either mechanically or vocally. The flight of the flushed birds was easily followed in the low vegetation, and the birds were included in the count only when they left the census area or flew behind the observers (see McLaren, 1968). If a bird was on the boundary when first seen, or thought to have entered the census area during the censusing, it was only counted as 0.5. The method appeared reliable since repeated counts corresponded closely.

In the analysis of breeding and territoriality, all males were numbered sequentially so that their presence or absence in subsequent years could be easily followed. The method of numbering was arbitrary; the data, however, are cross-referenced with the U.S. Wildlife band numbers and all data are filed with the Maritimes Nest Records Scheme[2].

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[2] New Brunswick Museum, 277 Douglas Avenue, Saint John, N.B.

DESCRIPTION OF HABITAT

In the study of avian ecology, physiognomic description of habitat may be adequate, indeed the only valid method of discerning habitat preference. As Odum suggested (1945), the density or appearance of the vegetation may be more important than the species composition.

Sable Island is situated approximately 180 miles (290 Km) east of Halifax, N.S., at 43°57'N and 59°55'W (Fig. 1). The total area of the island is about 3134 ha. but only 1473 ha. (47%) consists of consolidated terrain; the rest is shifting sand. Since Sable Island comprises virtually the entire breeding range of the Ipswich Sparrow, the ideal study would examine the activities and success of the bird on the different habitat types. However, simultaneous study of several plots is impossible if any thoroughness is desired. Consequently, only two radically differing habitat types were chosen for comparison.

The Main Study Area (Fig. 2), adjacent to the West Light, consists of approximately 8.5 ha. of densely vegetated terrain bordering the northern edge of an extensive series of ponds. The northern edge of the study area is demarcated by a dune ridge; these dunes immediately drop off into a series of blowouts, which are slowly being colonized by marram grass (*Ammophila breviligulata*). The extreme in relief is about 10 m and the terrain is uneven. The micro-relief generally increases the prominance of the low shrubs used for territorial surveillance, or provides other prominant lookout areas.

The entire area is a composite of shrubs, forbs, grasses and sedges such that breakdown into possible community types is likely unimportant for the birds. The main shrubs are winterberry (*Ilex verticillata*), dewberry (*Rubus arcuans*), bayberry (*Myrica pensylvanica*), blueberry (*Vaccinium angustifolium*), northern wild raisin (*Viburnum cassanoi[illegible]*), and rose (*Rosa virginiana*). Some clumps of winterberry and dewberry attain heights of more than half a meter and are so indicated on the vegetation map. Marram grass dominates the northern ridge of the study area around Lilly Pond. Sedges are localized around the edges of the ponds. Iris (*Iris versicolor*) is abundant on the two peninsulas and in the southwestern part of the study area; the common strawberry (*Fragaria virginiana*) is abundant in the western part. In addition to the shrubs, the birds often used dead yarrow (*Achillea lanulosa*) stalks, and various

Figure 1. Map of Sable Island showing the position of the study areas and the census plots.

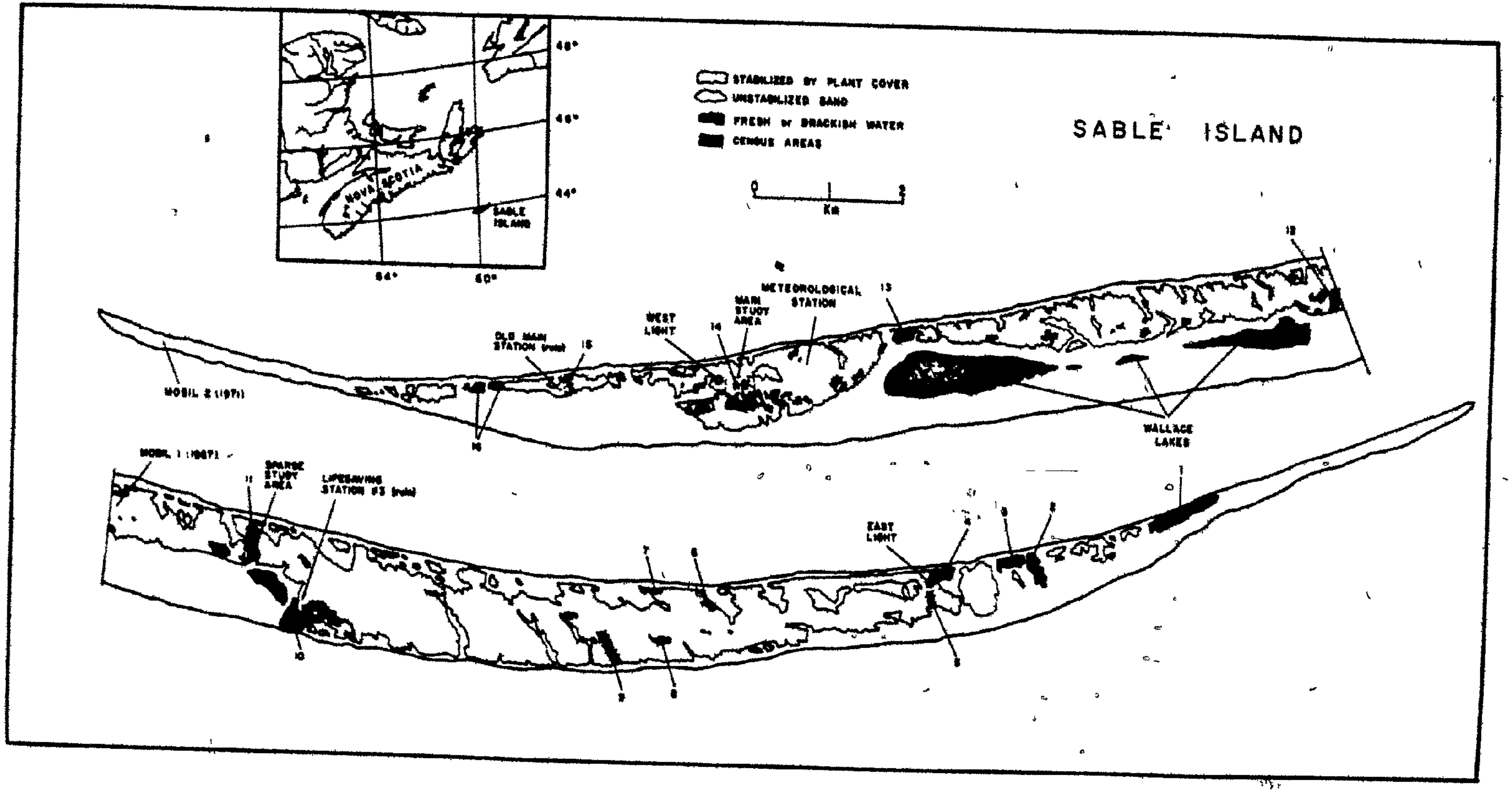

SABLE ISLAND
STABILIZED BY PLANT COVER
UNSTABILIZED SAND
FRESH or BRACKISH WATER
CENSUS AREAS
0
1
2
Km
46°
44°
64°
60°
NOVA SCOTIA
SABLE ISLAND
MOBIL 2 (1971)
OLD MAIN STATION (ruin)
15
16
WEST LIGHT
14
MAIN STUDY AREA
METEOROLOGICAL STATION
13
12
WALLACE LAKES
MOBIL 1 (1967)
11
SPARSE STUDY AREA
LIFESAVING STATION #3 (ruin)
10
9
8
7
6
EAST LIGHT
5
4
3
2
1

Figure 2. General vegatation and geographic structure of the Main Study Area. The unshaded areas adjacent to the dune edges represent the steep sides of unconsolidated blowouts. Only tall artificial perches such as old telegraph poles are indicated on the map.

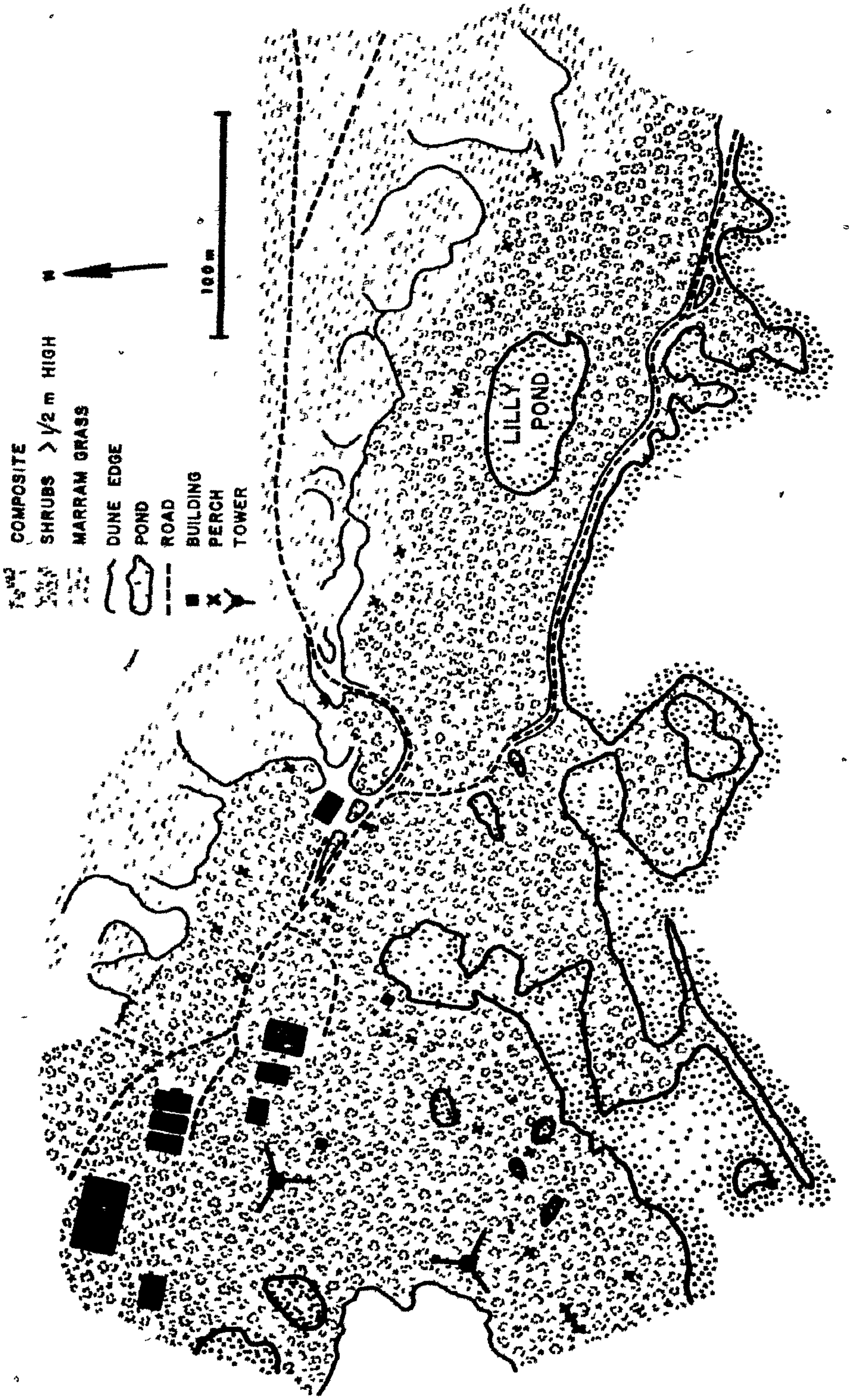
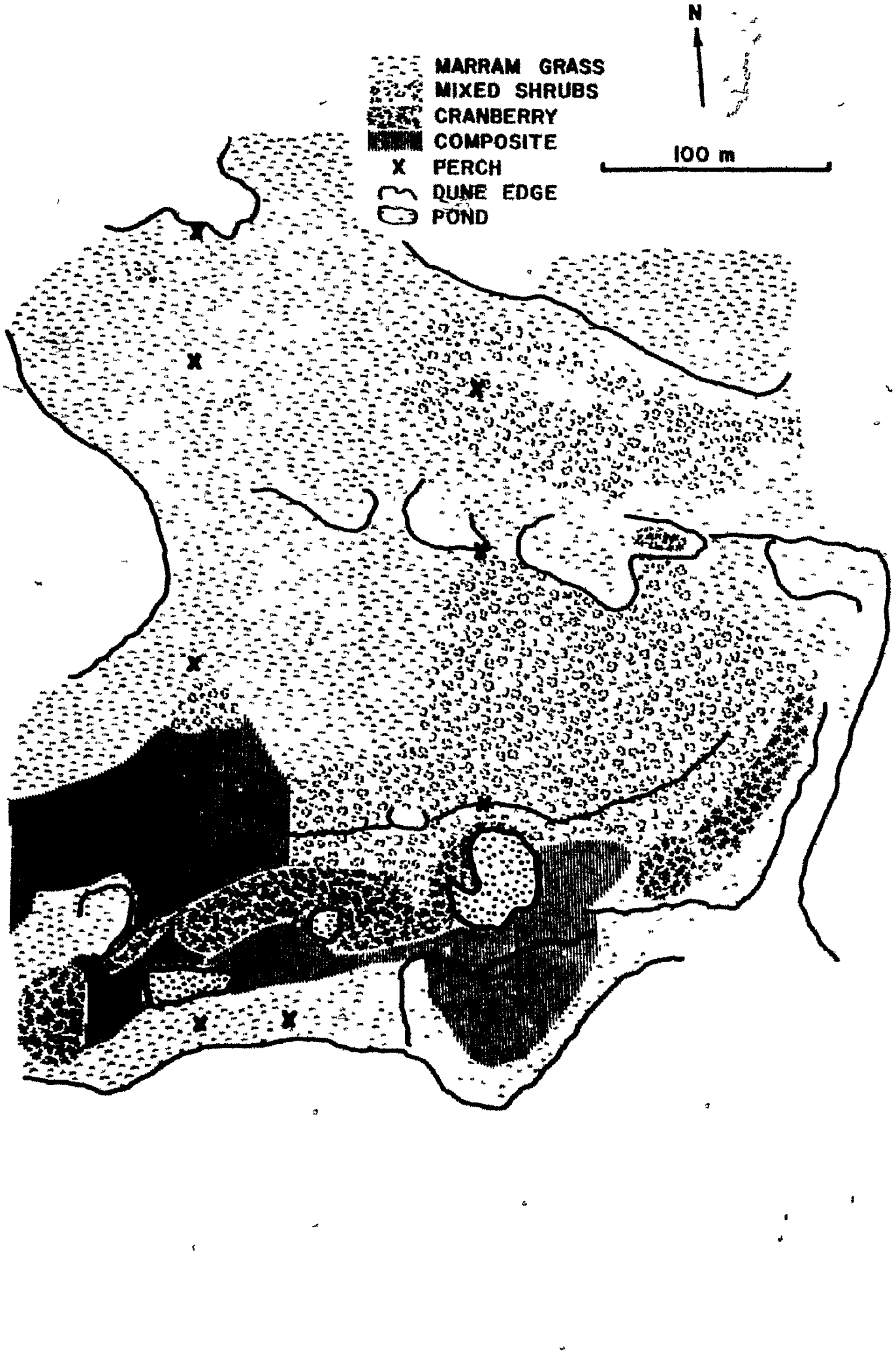

COMPOSITE
SHRUBS > 1/2 m HIGH
MARRAM GRASS
DUNE EDGE
POND
ROAD
BUILDING
PERCH
TOWER
N
100 m
LILLY POND

Figure 3. General vegetation and geographic structure of the Sparse Study Area. The unshaded areas adjacent to the dune edges in the study area represent the steep sides of unconsolidated blowouts. The pond in the south-western portion was dry by mid-June. Only tall artificial perches are indicated on the map.


MARRAM GRASS
MIXED SHRUBS
CRANBERRY
COMPOSITE
X PERCH
DUNE EDGE
POND
N
100 m

poles (marked as perches on Fig. 2) for perches.

The Sparse Study Area (Fig. 3) is located about 11.3 Km east of the Main Area. At this point, the island is approximately one mile wide; the northern half is largely consolidated dunes while the southern portion is low, flat beach. The size of the study area is approximately 15 hectares and extends from the southern limit of the dunes to two large blowouts near the northern extremity. A large blowout to the west and a high dune cliff to the southeast aids in naturally delineating the area. The vegetation is generally much more sparse and not nearly as uniform as on the Main Study Area. Although the boundaries of vegetational types in Figure 3 appear distinct, it should be noted that often they demarcate the dominance of certain vegetation types. The gradual transition, in most cases, is overlooked by this representation. The present breakdown, however, does seem consistent with bird activity and habitat utilization.

Along the dune edges and in the western part of the study area, marram grass (A. breviligulata) is the dominant plant, although the vegetation cover is very sparse with bare sand prominant throughout. But it is important to note that small, dense clumps of shrubs and forbs are scattered within this sparse cover, and females in this area generally used these clumps for nesting. Marram grass gradually decreases in importance toward the more densely vegetated portion. The vegetation of the eastern and southern areas is dominated by shrubs, but also contains an abundance of mixed forbs and grasses. Blueberry (V. augustifolium) is the tallest shrub and is mainly found in the northern portion; elsewhere territorial males used substrate micro-relief for surveillance points. Bayberry (M. pensylvanica) is the most abundant shrub of the area, providing a low but dense cover for nesting birds. Clumps of the junipers (Juniperus communis megistocarpa and J. horizontalis) and rose (R. virginiana) were similarly utilized. The cranberry (Vaccinium macrocarpon) patches are extensive around the ponds but are restricted to low lying areas and utilized by the birds only for feeding, presumably being too damp for nesting. The remaining area consists of a mixture of shrubs, forbs, and grasses with no species being dominant. Strawberry (F. virginiana) is an important forb since the birds eat the berries and feed them to their young; blueberries are also a food source.

CLIMATE

The climatic factors deemed to influence the length of the breeding season and reproductive output of Ipswich Sparrows on Sable Island are temperature, precipitation, and fog. Wind speed averages 29 Kmph and comes predominantly from the southwest, but does not seem to affect the birds.

On Sable Island temperature variations appear to be moderated by the surrounding sea during the breeding season and between years. In all four years, the mean daily temperature (Fig. 4) generally peaked by the end of July, and subsequently declined in September. It should be noted however, that the mean temperatures in 1969 were generally lower than in the other years. Mean temperatures oscillated around 15°C in early July, 1969, and never reached 20°C during the breeding season. In other years the mean temperatures exceeded 15°C for most of July and attained or exceeded 20°C at times in August.

Precipitation could be important since the birds nest on the ground, but only one nest desertion in the 3 years could be attributed to rainfall. Heavy rains occurred in all years at various times (Appendix 1), but did not appear to affect the birds. Generally the 1969 season was the wettest (Table 1) with a monthly average of 106.3 mm for the breeding season. In both 1968 and 1969, the birds commenced breeding 2 weeks later than in 1970 which is coincident with the greater amounts of rainfall in May. Also, the heavy monthly rainfall in July, 1969, was mainly due to a downpour of 76.5 mm on July 27. This coincides with the time that many birds should have begun their third clutches; few third clutches were in fact initiated.

Sable Island is often shrouded in fog, and such conditions, if they persisted, could affect success rates or alter the physiological state of breeding birds. Although no records exist for the amount or duration of fog, Fig. 5 presents 5-day averages of the hours of sunshine throughout the season. Although this presentation will include other interference such as rain or overcast, experience shows that fog often accompanies any inclement weather. Again, at the time when females should have been starting their third clutches in 1969, the first 5-day period in August had no sunshine and the next 5 days averaged only 0.7 hr. In no other year was the absence of sunshine as persistent or extreme, nor did it occur at such a crucial time.

Figure 4. Daily mean temperatures (°C) recorded on Sable Island between April and September from 1968 to 1971.

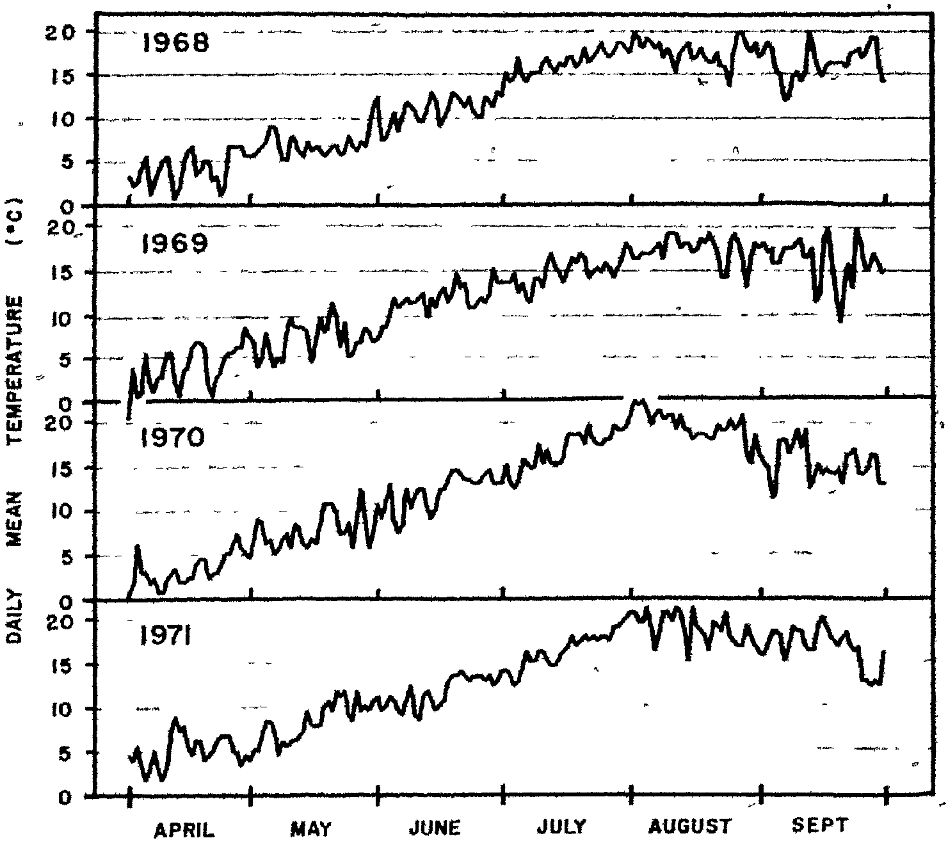
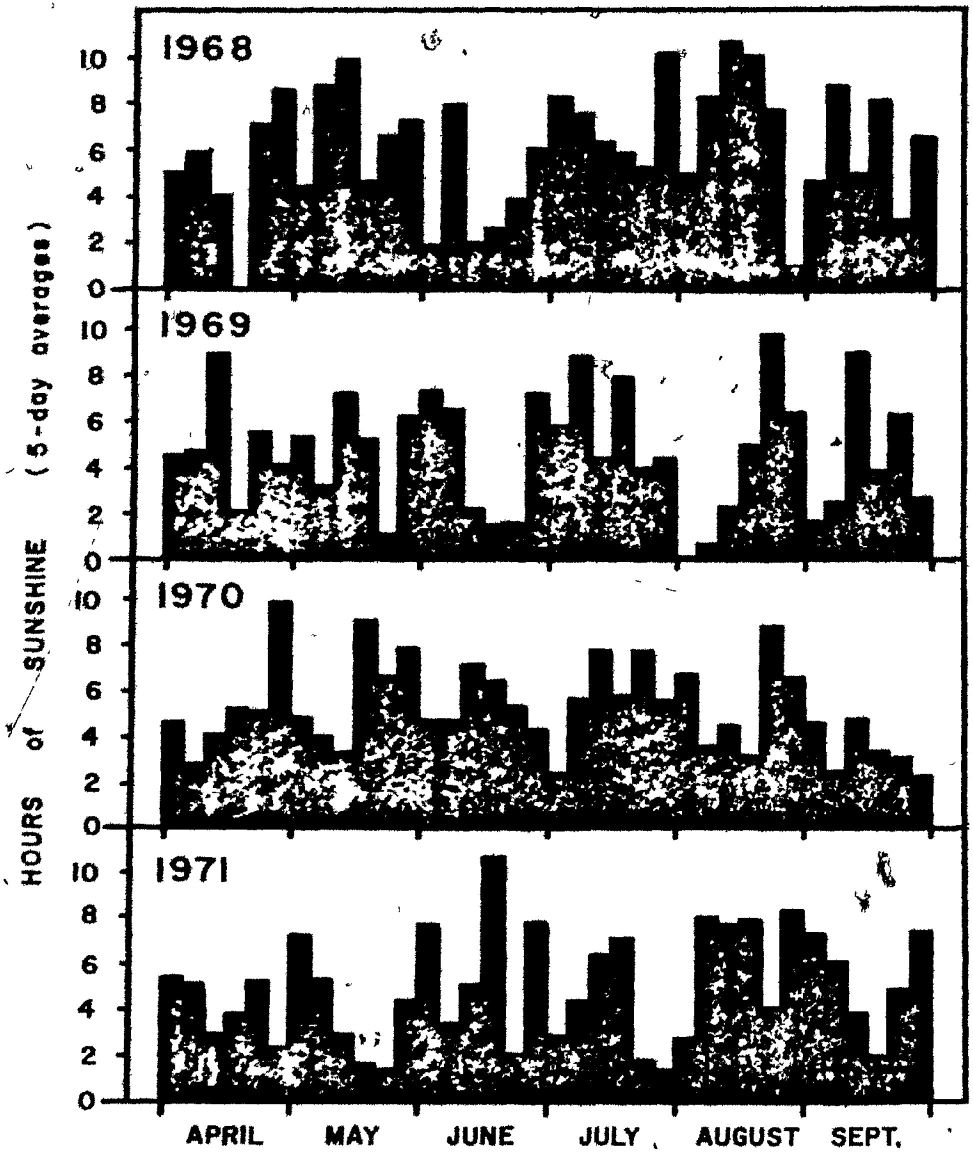

DAILY MEAN TEMPERATURE (°C)
1968
1969
1970
1971
0
5
10
15
20
APRIL
MAY
JUNE
JULY
AUGUST
SEPT

Table 1. Precipitation on Sable Island as monthly totals (mm).

	1968	1969	1970	1971
April	55.9	124.2	42.1	110.2
May	161.5	186.4	74.7	99.8
June	73.7	58.4	93.0	71.1
July	65.8	131.3	67.6	61.0
August	118.9	65.3	126.0	39.6
September	43.4	72.1	158.2	90.9
Total	519.2	637.7	561.6	472.6
Monthly average	86.5	106.3	93.6	78.8

Figure 5. Hours of sunshine on Sable Island grouped into 5-day averages between April and September from 1968 to 1971. Indirectly this figure indicates the amount of rain and fog occurring each year during the breeding season. During the first 10 days of August, 1969, fog shrouded the island almost continually.


1968
1969
1970
1971
HOURS of SUNSHINE (5-day averages)
0
2
4
6
8
10
APRIL
MAY
JUNE
JULY
AUGUST
SEPT.

TERRITORIALITY

Establishment

The commencement of studies in late May of 1968 and 1969 followed the arrival of most of the birds and no data on territorial establishment were available. In 1970 and 1971 however, I arrived in mid-April. Birds were still arriving on the island in the latter part of April and early May. The arrival time of males and females coincided, but they were not observed to arrive in established pairs. Occasionally a female arrived at a site before any males and frequented a circumscribed area until both she and the area were claimed. More often however, males secured a territory and subsequently acquired a mate. The establishment of territories did not appear to follow a pattern in space as noted by Welsh (1970) for the Savannah Sparrow. Rather, experienced males reclaimed their old territories and new birds acquired the unoccupied spaces.

The earliest males occupied an initial area often 2 to 3 times larger than their final territory. This excess area was relinquished little by little under pressure from newly arrived males.

The establishment phase was prolonged, with some females incubating clutches while other males had not yet secured a female. This was especially evident in 1970 when the two study areas were compared. On the Main Study Area many females were incubating clutches by the end of May and one brood had left the nest. On the Sparse Study Area, however, some females did not complete their first clutches until late June. This delay may have been due to a late arrival on the island which forced these females to nest in poor habitat. Alternatively, some females residing on the Sparse Area may have delayed nesting until the habitat quality improved. Although these females may have deserted unsuccessful nests elsewhere, the frequency of re-nesting after nest failure, on the Main Area, does not support this possibility.

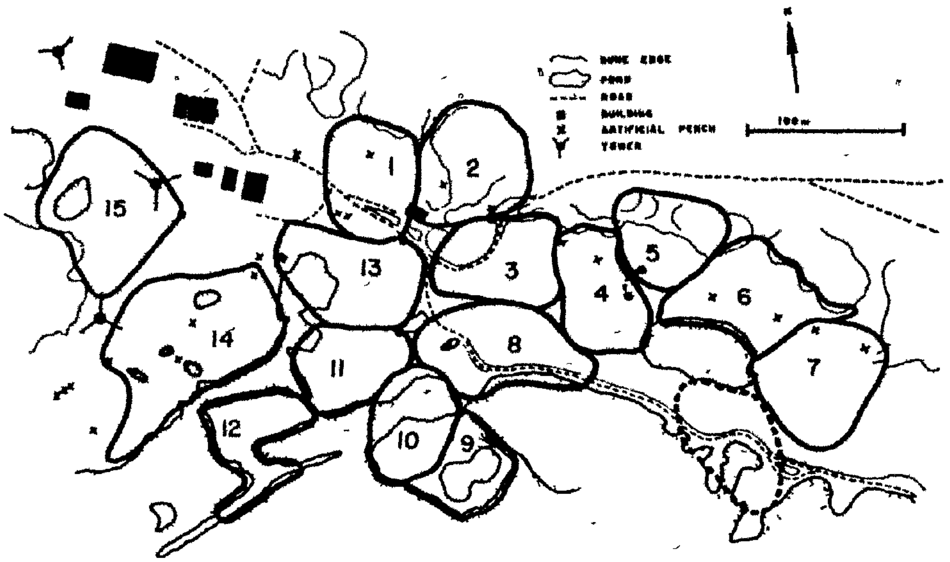
To proclaim ownership, the males perched conspicuously and sang frequently. Generally, after driving off an intruder the males returned to the territorial border and sang. Birds sang more actively at the beginning of the season and singing was largely confined to early morning and evening. As Verner (1965) suggests, the prevalence of song at these times may be adaptive. Birds are most active in the morning and unestablished birds will be looking for a territory; in the evening these same birds will be looking for a place to roost. Proclaiming ownership at these times could serve to deter males from settling on the territory and attracting females. Early in the season, males often abandoned their territories during the day to feed communally in unclaimed areas. This agrees with Howard's (1920) suggestion for resident birds that the gregariousness prevalent in birds in winter "was gradually yielding its position of importance to the new factor - the territory". Until this physiological or psychological change was complete, the birds would continue to desert their territories for varying periods of time. Although Howard did not find this gradual transition in birds which migrate, it seems applicable to the Ipswich Sparrow.

Defense

The micro-relief of the area appears to be important in determining territorial boundaries. These boundaries often followed noticeable micro-relief patterns and offered elevated perches for the males along the borders of their territories. Also the males often had at least one elevated perch within their holdings that allowed almost complete territorial surveillance. These factors facilitated territorial defense. The value of such choice of boundaries can be appreciated if the territorial boundaries are compared between years (Fig. 6-9). For example, on the Main Area the crest of a small ridge extending northwest from Lilly Pond was used in all years to separate territories. In 1969 and 1970 when the density was greatest, the territorial configurations were amazingly similar. Granted, this similarity was partly governed by returning males but this cannot explain resemblances between territories in 1968 and 1971, with no males in common. The larger territories in 1968 and 1971 often encompassed that area occupied by two birds in 1969 and 1970. The micro-relief on the Sparse Area (Fig. 10-11) was not as pronounced and the birds had larger areas to defend. Few birds returned in 1971, but the territory configurations were again quite similar.

Generally intruders were repulsed in an aerial chase immediately upon entering the territory. The resident male usually successfully

Figure 6. Map of the Main Study Area showing fluctuations in territorial boundaries during the first (upper) and second (lower) clutches in 1968. The territory in the south- eastern portion was not studied intensively, thus the boundaries are indicated by dotted lines only. Closed circles on the lower map indicate nest locations and the open one in territory 14, a suspected nest site. Successive nests of each female are indicated by arrows; a dotted arrow means that the female changed mates between nests. For clarity, the nests of female 5, who moved from territory 5 to territory 4 are shown on the upper map.


N
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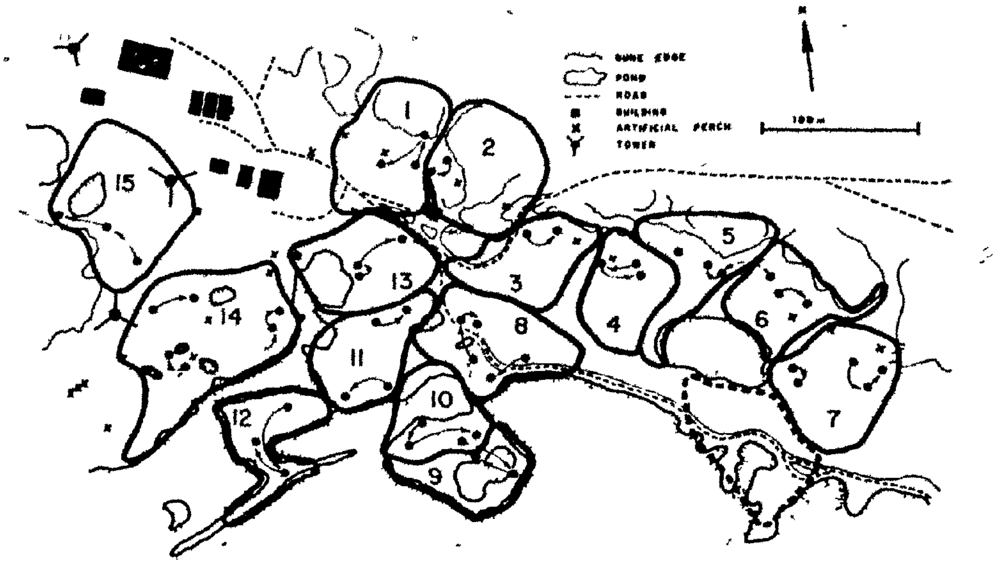
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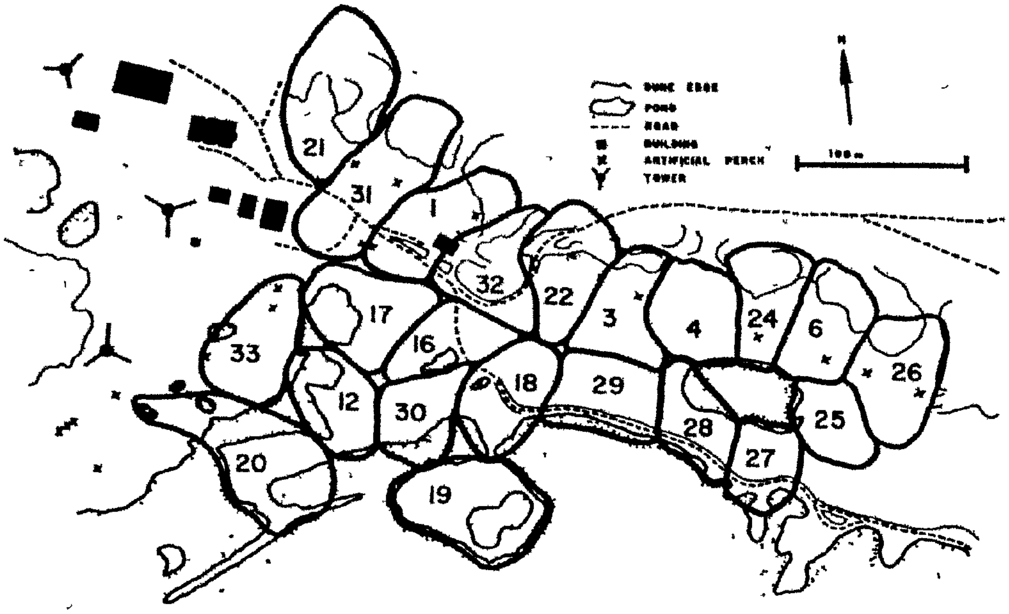
Figure 7. Map of the Main Study Area showing fluctuations in territorial boundaries during the first (upper) and second (lower) clutches in 1969. Closed circles on the lower map indicate nest locations, and successive nests of each female are indicated by arrows. Dotted arrows mean that a female changed mates between successive nests.


21
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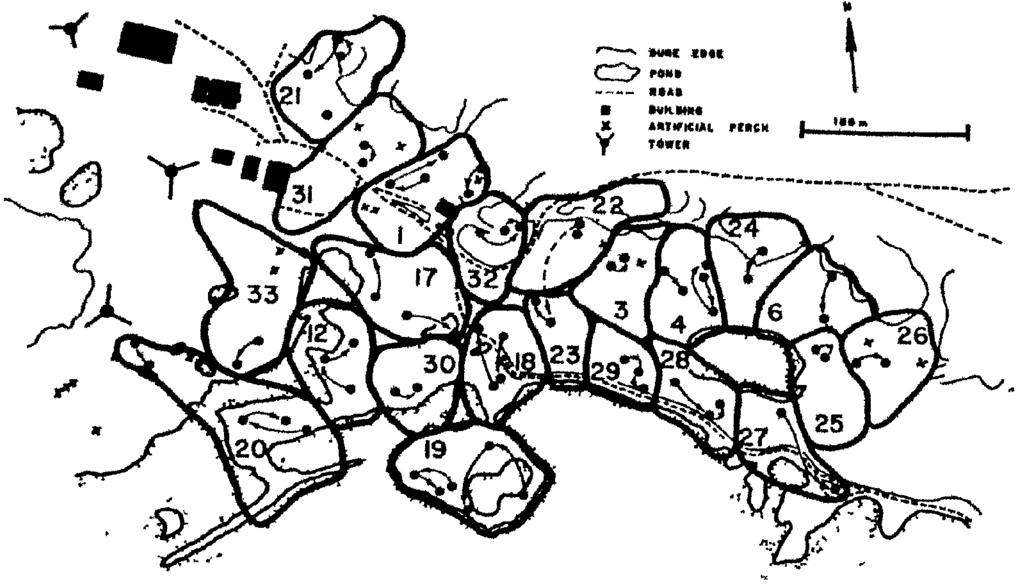
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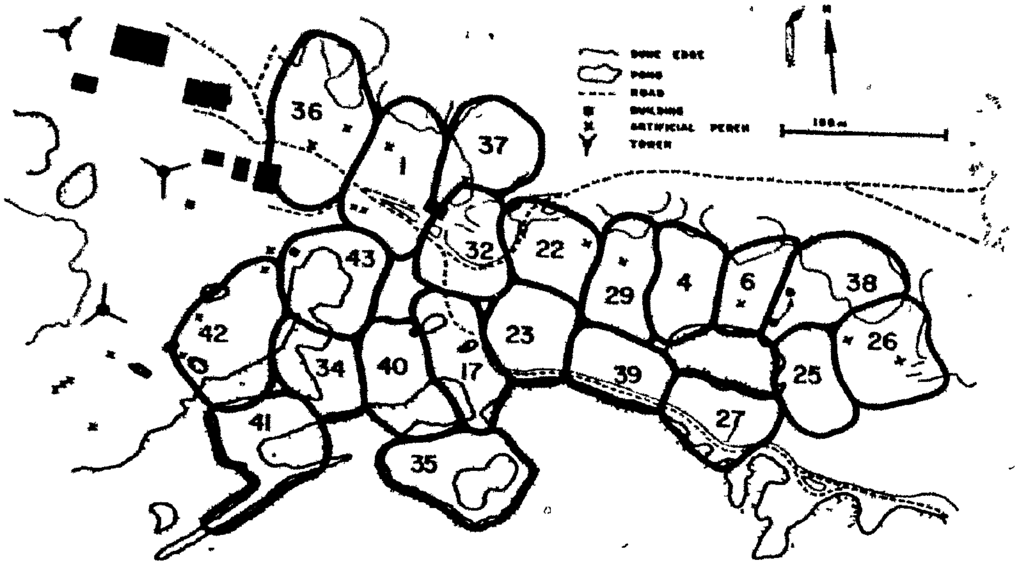
20
19
DUNE EDGE
POND
ROAD
BUILDING
ARTIFICIAL PERCH
TOWER
N
100 m

Figure 8. Map of the Main Study Area showing fluctuations in territorial boundaries during the first (upper) and second (lower) clutches in 1970. Closed circles on the lower map indicate nest locations, and successive nests of each female are indicated by arrows. For clarity, the nests of female 8 in territory 38 are indicated on the upper map.


N
DUNE EDGE
POND
ROAD
BUILDING
ARTIFICIAL PERCH
TOWER
100 m
36
1
37
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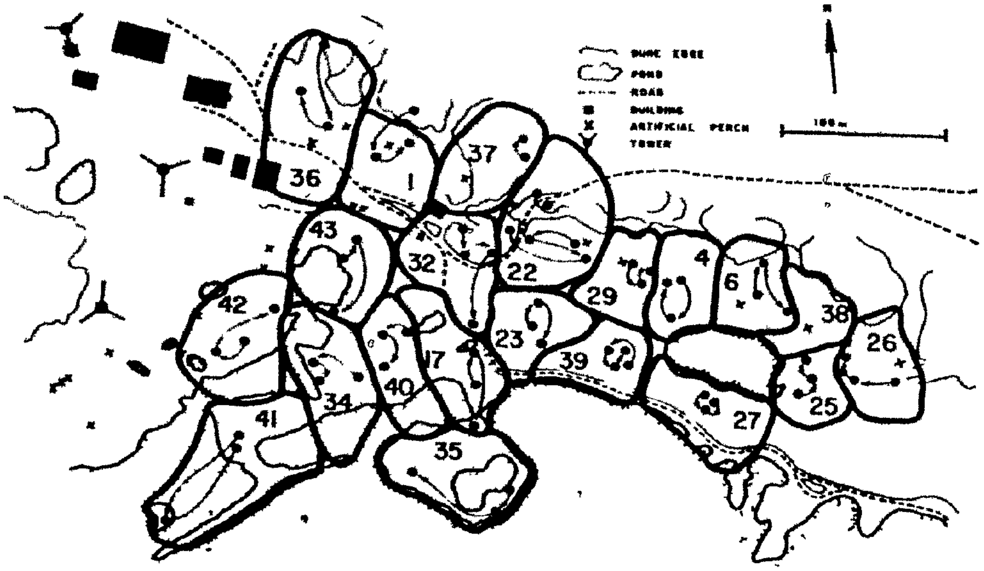
41
35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41
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Figure 9. Map of the Main Study Area showing territorial boundaries in 1971. Only 5 known males returned that year and no additional banding was conducted.

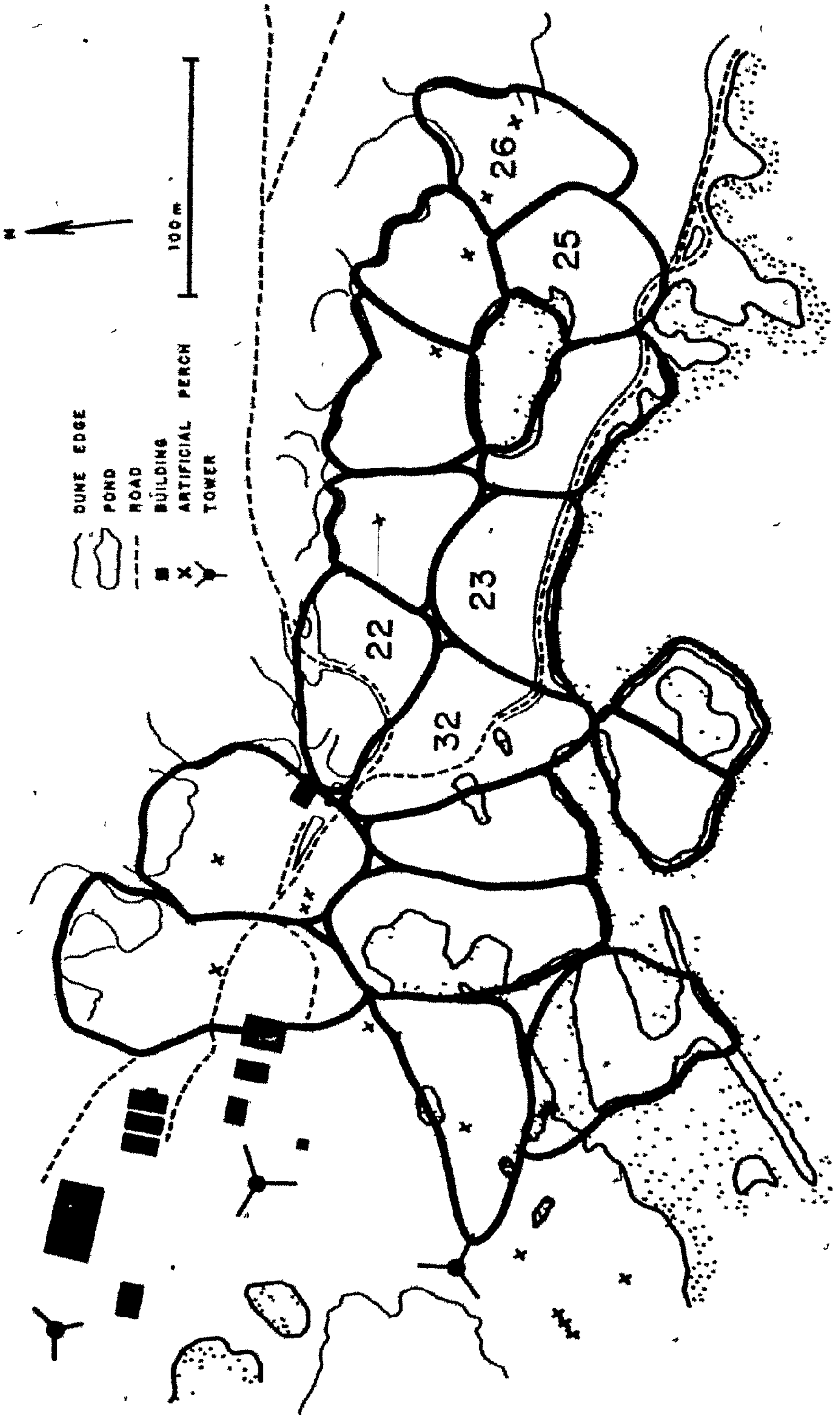
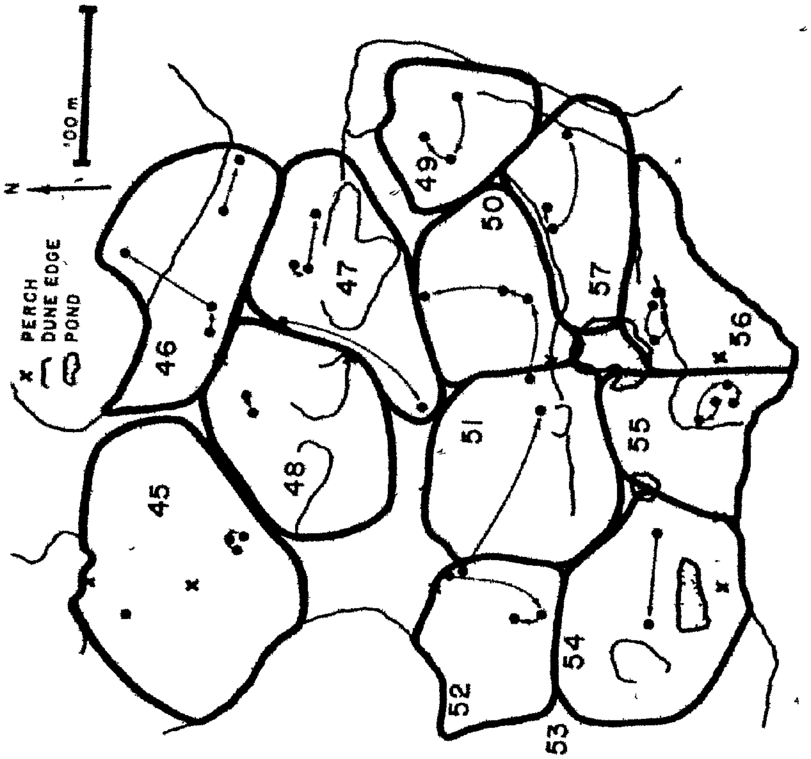

N
100 m
DUNE EDGE
POND
ROAD
BUILDING
ARTIFICIAL PERCH
TOWER
26
25
23
22
32

Figure 10. Map of the Sparse Study Area showing fluctuations in territorial boundaries during the first (left side) and second (right side) clutches in 1970. Closed circles indicate nest locations and successive nests of each female are indicated by arrows. Note the large territorial adjustments in territories 46 and 47 to accomodate female movement between nests. Male 53 resided east of the study area and his activities were followed for nesting success data only.


x PERCH
DUNE EDGE
POND
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100 m
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56
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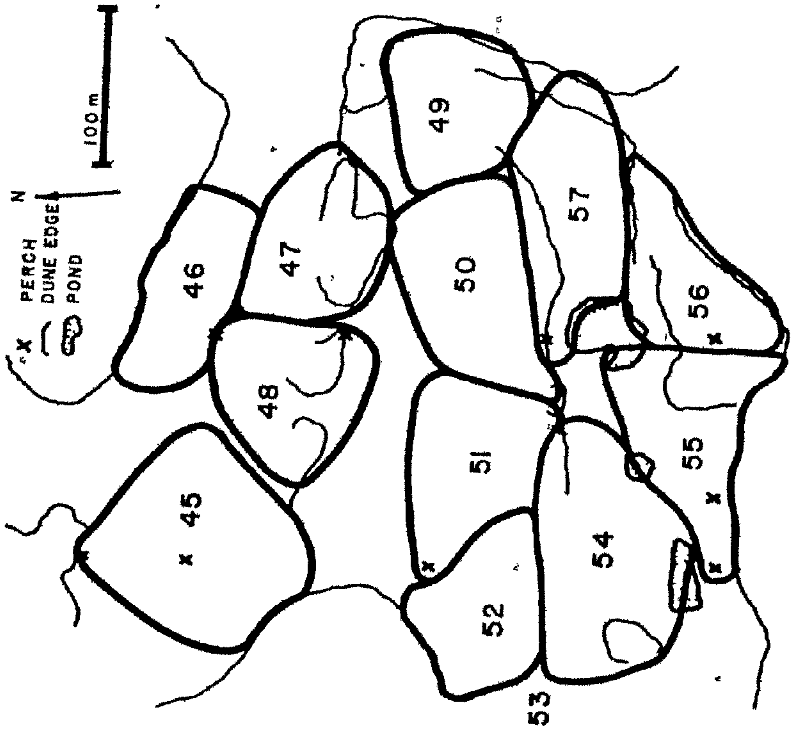
x PERCH
DUNE EDGE
POND
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100 m
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56
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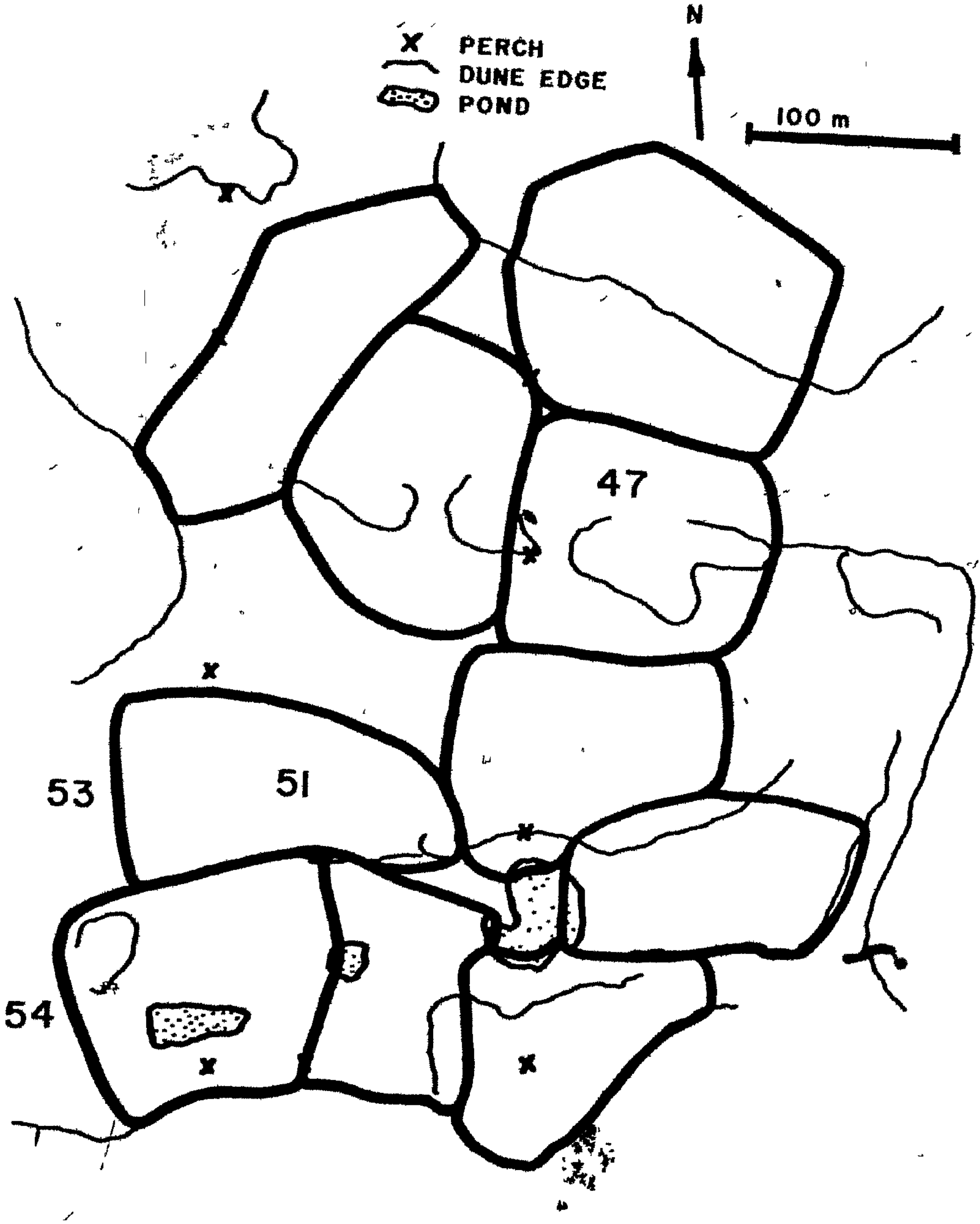
Figure 11. Map of the Sparse Study Area showing territorial boundaries in 1971. Only 4 known males returned that year and males 53 and 54 resided east of the study area.


X PERCH
DUNE EDGE
POND
N
100 m
47
53
51
54

defended his territory from potential competitors by posturing and puffing of feathers, but occasionally would attack a persistent intruder. Similar tactics were used with neighboring males, although such aggression was quickly reduced to threat gestures along mutually agreeable boundary lines. Resident females sometimes challenged intruding females from adjacent territories, and on 2 occasions females of a polygynous male quarreled between themselves.

The territorial males reacted quickly to any territorial intrusions early in the season, even resulting in interspecific aggression on several occasions. The territorial birds harassed transient species such as warblers, kinglets, and other sparrows. Such harassment was ignored by the resident House Sparrows in 1968 and 1969. This sensitivity decreased as the season progressed. Females also reacted to chase out male intruders, but invariably they were the third bird in the chase. It appeared as though the females were excited by the male's activities and assisted him in chasing intruders away after the initial encounter.

The territorial males did allow certain intrusions however, and may, as Welsh (1970) suggests, be capable of judging the intent of an intrusion. Territorial males around Lilly Pond allowed birds from north of the study area unmolested access to the water's edge, although flights to and from the pond were generally made along territorial boundaries.

Juveniles were ignored by the resident males unless they attempted to sing. If such an attempt were made, the resident male would immediately drive them out, immaterial of how fragmentary the song. Nice (1937) also observed juvenile Song Sparrows warbling in the autumn. Females were not attacked by territorial males and freely entered adjacent territories in search of food. Fledged young would inadvertently cross territorial boundaries and males, who feed the fledglings for several days after they leave the nest, were usually tolerated in adjacent territories under these circumstances.

TERRITORY SIZE

The intent of this study was to examine as many territories as possible, while assuring that every nest was found. As such, no time was available for detailed examination of changes in the areas used during the different phases of the breeding cycle.

The sizes of 98 territories examined in the 4 years of study are shown in Table 2. The averages are a compilation of observations made throughout the breeding season. Originally, estimates were made during the incubation stage of the first (early June) and second (early July) clutches of the first females in 1968-70. The averages (ha.) and standard errors of these estimates are shown below.

	Main Area			Sparse Area
	1968	1969	1970	1970
First Clutch	0.43 ± 0.04	0.31 ± 0.02	0.31 ± 0.02	0.97 ± 0.07
Second Clutch	0.42 ± 0.03	0.30 ± 0.02	0.32 ± 0.02	1.20 ± 0.11

But t-test (P = 0.05) comparisons indicated no significant differences between means of the two estimates and they were combined. No additional estimates were made because the sanctity of territories diminished rapidly after the second clutch, in most cases. Only one estimate was made in 1971.

The territories in the Sparse Area in both 1970 and 1971 averaged over three times as large as on the Main Area (Fig. 8-11). There were only 15 territories on the Main Area in 1968 as opposed to 23, 21, and 17 in 1969, 1970, and 1971 respectively. The territories in 1968 averaged significantly larger (t-test, P < 0.01) than those of 1969 and 1970, but not 1971. No significant difference existed between the other 3 years, nor between the territories in the Sparse Area in 1970 and 1971.

Major changes in territorial boundaries occurred only when a member of a pair disappeared. In 1969 (Fig. 7), male 16 disappeared during the nestling stage of the first clutch. Male 17 claimed most of this territory and the female, with minor adjustments in adjacent territories. Also in 1969, male 23 secured a territory after first clutches had already been laid in the territories of adjacent males, largely from

Table 2. Average territory size (hectares) on the two study areas on Sable Island. The values given are the average of two separate estimates made during the first and second clutch of the first females. Territorial males are numbered sequentially from 1969 to 1971. New males on territory in 1971 are not numbered. Male 53 in 1970 and 53 and 54 in 1971 were outside the Sparse Study Area and their territories were not delineated. Polygynous males are indicated by an asterisk.

Main Study Area								Sparse Study Area			
1968		1969		1970		1971		1970		1971	
No.	Size	No.	Size	No.	Size	No.	Size	No.	Size	No.	Size
1	0.46	* 1	0.35	1	0.38	22	0.39	*45	1.81	47	1.30
2	0.50	3	0.26	4	0.22	23	0.36	*46	1.06	51	1.19
3	0.31	* 4	0.23	6	0.21	25	0.32	*47	1.09		1.20
* 4	0.35	6	0.29	17	0.29	26	0.36	48	1.17		1.36
* 5	0.37	12	0.28	*22	0.39	32	0.44	49	0.76		1.78
* 6	0.40	16	0.24	23	0.26		0.65	50	1.02		1.13
* 7	0.49	*17	0.37	25	0.22		0.57	51	1.18		0.91
* 8	0.47	*18	0.25	26	0.33		0.26	52	0.85		0.80
9	0.28	*19	0.39	27	0.28		0.32	53	--		0.77
10	0.32	*20	0.44	29	0.23		0.24	54	1.45		1.34
*11	0.31	*21	0.43	32	0.32		0.28	55	0.87	53	--
12	0.24	*22	0.35	34	0.31		0.33	56	0.80	54	--
13	0.46	23	0.16	35	0.36		0.50	57	1.00		
*14	0.77	24	0.28	36	0.54		0.41				
15	0.61	25	0.22	37	0.32		0.38				
		26	0.32	38	0.26		0.21				
		27	0.23	39	0.22		0.19				
		28	0.19	40	0.29						
		29	0.22	41	0.37						
		30	0.25	42	0.43						
		31	0.44	43	0.35						
		32	0.28								
		33	0.39								
Ave.	0.42		0.30		0.31		0.37		1.09		1.18

males 18 and 29; he also acquired a female from male 22. The second female of 22 was hurt while being banded and deserted a newly hatched clutch; she remained in the area but did not nest again. Male 22 gradually shifted his activities to the northeast to accommodate this second female; by mid-July, he seldom appeared in the southern portion of his territory. In 1970 (Fig. 8) the female of male 38 was found dead on July 12 beside her second nest; the newly hatched young also died. Within a week, the male had lost a sizable portion of his territory to male 6, and by the end of July was ignoring territorial intrusions.

Males also had to adjust territorial boundaries to accomodate new nesting sites chosen by their females. For male 27 in 1969 (Fig. 7), and 41 (Fig. 8), 46 and 47 (Fig. 10) in 1970, these territorial extensions were large. Generally, the males in the Sparse Area had to make the greatest adjustments to retain their mates. Although not significant due to the large variance, distances between nests in this area averaged 35 m as opposed to 25 m on the Main Area in 1970. However, the territorial boundaries in the Sparse Area were sufficiently flexible to allow males to make such adjustments. This flexibility seemed related to the difficulty in surveillance of the prevailling grassland habitats, containing few elevated perches. On the Main Area however, the density of birds was greater and the size of territories much smaller. The boundaries were rigidly defined and intrusions quickly repulsed. Consequently, males 5 and 6 in 1968 (Fig. 6) and 22 in 1969 (Fig. 7) could not adjust their boundaries to include new nests and lost their females to adjacent males.

Polygynous males averaged significantly larger territories (polygyny: $n = 8$, mean size = 0.35 ha.; monogamy: $n = 15$, mean size = 0.27 ha.; $t = 2.574$, d.f. = 21, $P < 0.02$) than monogamous males in 1969, but not so in 1968 (polygyny: $n = 7$, mean size = 0.45 ha.; monogamy: $n = 8$, mean size = 0.41 ha.; $t = 0.600$, d.f. = 13, $P > 0.5$) on the Main Area or in 1970 on the Sparse Area (polygyny: $n = 3$, mean size = 1.32 ha.; monogamy: $n = 9$, mean size = 1.01 ha.; $t = 1.672$, d.f. = 10, $P > 0.1$). No calculation were made for the Main Area in 1970 since only one case of polygyny occurred (male 22).

It is interesting to note that polygynous males generally occupied areas that had 2 nesting females every year. Thus in 1968 the territory of male 7 occupied essentially the same area as males 25 and 26 in 1969, and male 8 occupied the area of the polygynous male 18 in 1969; male 11 in 1968 occupied much of the areas of 12, 17, and 30 in 1969, and male 14 held the areas of 20 and 33. The territories of males 4, 5, and 6 in 1968 occupied the area of four males (3, 4, 24, and 6) in 1969 and may account for the movement of females between these territories in 1968. In 1969, male 19 controlled the peninsula that males 9 and 10 occupied in 1968.

An apparent exception is the territory occupied by monogamous male 3 in 1968 and polygynous male 22 in 1969 and 1970. However, 22 claimed only the eastern portion of the 1968 territory (male 3 had lost large portions of his 1968 territory to males 2 and 8 by the end of July and subsequently deserted the area) and extended north to where his injured second female resided in 1969 and his second female nested in 1970.

The data suggest that the effect of territory size on the probability of being polygynous may be important only at a critical density of birds. In 1969, 23 territories occupied the area of 15 in 1968, and under these crowded conditions only males with larger or superior territories could accomodate more than one female. Most territories were significantly larger in 1968 than in 1969 and this could have eliminated the effects of size differences among the 1968 territories. In 1970 the average territory size was not significantly larger than in 1969, but the population density on the study area was lower. The virtual lack of polygyny in 1970 may have been the result of a greater dispersion of females than in 1969 (to be discussed later under female dispersion). The average territory size in 1971 was not significantly different from that in 1968; observations of territorial birds in 1971 suggest that at least 6 males were polygynous.

TERRITORY AND SITE FAITHFULNESS

Main Study Area

A total of 14 (38%), 22 (42%), and 12 (28%) adults returned to the Main Area in 1969, 1970, and 1971 respectively. These percentage returns, or survival, are comparable to the values obtained from the population estimates (Table 16) of 41%, 42%, and 27% respectively, for those years.

Males

Virtually the entire population of Ipswich Sparrows migrate off Sable Island in the fall. Information gathered on the birds returning in subsequent years may provide a better understanding of local homing.

Some male Ipswich Sparrows return to the same territory year after year (Appendix 2). On a yearly basis 33% (5 of 15), 48% (11 of 23), and 21% (5 of 21) returned in 1969, 1970, and 1971 respectively. Of a total of 43 banded territorial males (42 adults and 1 nestling of 1970 which returned in 1971 and 1972) on the Main Area, 7, 7, and 1 bird respectively, returned for 2, 3, and 4 successive years. Some males not only returned to the study area, but successfully reclaimed their old territories for 3 or more years, notably males 1, 22, 23, 26, and 25 (4 years). Due to the increased population density, even these males lost some peripheral area to adjacent birds in 1969 and 1970. Other returning birds were forced to claim a slightly different territory due to density pressure, or earlier establishment by adjacent males; this was true of males 3, 4, 6, 27, and 32, and of male 37 who occupied a similar area in 1969 and 1970, but who was not studied for breeding success in 1969. Males 12, 17, and 29 however, adopted entirely new territories adjacent to their former ones. Male 17 made the shift "voluntarily", as his former territory was vacant on his arrival in 1970. The reasons for the other changes were not determined. Nice (1937) noted similar territorial adjustments by returning males.

Females

A number of females also return to the same nesting area (Appendix 2). On a yearly basis, 41% (9 of 22), 38% (11 of 29), and 32% (7 of 22) returned in 1969, 1970, and 1971, respectively. Twenty-two females successfully returned, 14 birds for 2, and 8 birds for 3 successive seasons. Female 14 nested on the study area in 1968 and 1970, but occupied a nearby island in the ponds in 1969. Her return is included in the 41% return for 1969. Eighteen females returned to their nesting area of the previous year and 6 were re-united with former mates; the remaining 12 females acquired new mates because their former mates either did not return, or established their territories elsewhere. Female 8 returned to her former nesting area in

1970 but mated with male 39; male 6, her mate in both 1968 and 1969 possessed the adjacent territory. He had shifted his territory west of the 1968-69 location and another female had commenced nesting there. It is difficult to determine which factor prevented this pair from reuniting. But in eight other cases in which females shifted their nesting location, new females had begun nesting earlier in their former domains. Four of these females nested in adjacent areas, while four moved greater distances.

Sparse Study Area

Less information on returns is available from the Sparse Area since data are available only from 1970 and 1971. Four males (31%) returned in 1971 (Fig. 11), and three reclaimed most of their previous territories; the fourth claimed an area adjacent to his former territory. This rate of return is substantially higher than the 21% return to the Main Area for 1971. However, the return rate for females is substantially lower for the Sparse Area than the Main Area. Female 63 was the only returning female (6%) on the study area; she returned to her former nesting site and acquired a new mate. Two other color-coded adults were also seen in 1971, but disappeared before they could be identified. They did not remain on the study area. Including the 2 unidentified birds, a total of 7 (24%) adults returned in 1971, and this is comparable to the value of 27% obtained from the population estimates.

Juveniles

Between 1967 and 1970, 687 nestling and flying juveniles were banded. Eighteen were subsequently re-captured on the study areas, but only 11 of these remained as territorial birds. Of 328 banded juveniles of known parentage, only 3 returned as territorial birds on the study areas and all nested away from their parents' former territories. Other sparrows banded in 1968 and 1969 were observed, generally in the western part of the island, but the banding techniques did not distinguish juveniles from adults, thus the observations are of limited value.

In 1970, 243 nestlings were banded with distinguishing color bands. I had hoped to obtain information on juvenile dispersal during the season and returns as territorial birds in 1971. Unfortunately, few of these banded birds were found in 1971. Observations during the 1970 season suggest that the juveniles dispersed widely once they were able to fly. Juveniles were observed 3-4 miles west and east of the study areas by July and August. In 1971 one male fledged from the Sparse Area, claimed a territory two miles west of his birth-place. In addition, one fledged from each study area in 1970 returned in 1971 and claimed a territory.

Although few returns were obtained, it is interesting to note that 6 juvenal males banded in 1968 returned to claim territories in 1969. They represented 33% of the new territorial males on the Main Area in 1969. Since the number of banded birds was only a small proportion of the juveniles fledged in 1968, the data suggest that many vacated territories are occupied by first year birds.

BREEDING AND NESTING

General

Table 3 provides general information on the nesting biology of the Ipswich Sparrow. The length of the breeding season varied from 91 days in 1968 to 127 in 1970 on the Main Area. The total reproductive output represented as young leaving the nest fluctuated with the length and the quality of the nesting season. As mentioned earlier, the low production in 1969 is probably related to the climatic differences between the years. The absence of sunshine and the average monthly precipitation was greatest in 1969, with heavy rainfall during the critical period before commencement of the third clutch. The nesting season on the Sparse Area in 1970 commenced almost 2 weeks later than on the Main Area and the shorter season is reflected in the lower production.

Seventy-two males and 89 females were studied during the three years. The males tend to be polygynous. The degree of polygyny varied from 47% in 1968 to 5% in 1970, yet the number of females on the Main Area was the same in both years. It is also interesting that the decrease in females from 29 to 22 on the Main Area from 1969 to 1970 was accompanied by a large decrease in the percentage of polygyny, but only by a small decrease in the numbers of males. Further, the Sparse

Table 3. General information on the nesting biology of the Ipswich Sparrow from 1968 to 1970. The total numbers of males, females, attempted nests, and young to leave the nest are given. The numbers of polygynous males are given in parentheses. The length of the breeding seasons are given as the date of completion of the first clutch to the date when the young of the last clutch leave the nest on the study areas.

	Males	Females	Nests	Young Fledged	Length of Breeding Season
Main Study Area					
1968	15 (7)	22	54	203	May 27 - Aug. 26
1969	23 (8)	29	67	221	May 24 - Aug. 28
1970	21 (1)	22	67	228	May 10 - Sept. 13
Sparse Study Area					
1970	13 (3)	16	44	144	May 22 - Sept. 12
Total	72 (19)	89	232	796	

Area in 1970 had three polygynous males as opposed to only 1 on the more densely populated Main Area.

It has been generally accepted that a female selects a mate on the basis of his attributes, or because of the territory he possesses. The above data suggest, however, that such a method of selection by itself, is insufficient to explain the changes in the degree of polygyny relative to the number of birds from 1968 to 1970. Nor can the above method explain the greater degree of polygyny in the poorer habitat in 1970. Other factors must also be involved.

Female Dispersion

A possible explanation of the changes in the amount of polygyny lies in the distribution of females over an area. Above a certain population density, females may initially disperse themselves evenly over a given area by some subtle means of mutual repulsion, regardless of male distribution. Below this minimum density, more nearly random dispersion may occur. At low population densities any male could be polygynous since all will have large territories. But at higher population levels, the average size of territories will decrease. Then a polygynous male's territory may have to be large enough to contain two mutually repulsed females; males with smaller territories are more likely to be monogamous.

To determine if females were dispersed in an even pattern, I used the procedure outlined by Barton and David (1959) for determining contagious occupancy, applying the method to the first nests of females on the Main Area. This method involves arbitrarily superimposing a grid over the area concerned. Then the deviation of the number of empty cells from the expected is calculated as follows:

$$E(x) = \frac{N(N-1)^n}{N^n}$$

where $E(x)$ = expected number of empty cells
N = number of grid cells
n = sample size (number of nests)

$$\mathrm{var}(x) = \frac{N(N-1)(N-2)^n}{N^n} + E(x) - [E(x)]^2$$

Then if the pattern of distribution is random

$$Z = \frac{k - E(x)}{\sigma_x} \quad \text{is normal } (0,1)$$

where k = observed number of empty cells

Thus if Z falls within the interval ($\pm$ 1.96, for a two-tailed test) the null hypothesis (H_0) of a random pattern is accepted. When $Z > 1.96$ then the organisms are significantly clumped, and when $Z < -1.96$ then an even pattern of dispersion occurs.

Since our alternative hypothesis (H_1) is that the pattern is even or regular, we can use a one-tailed test and reject H_0 if $Z < -1.64$ (5% one-tailed test).

Table 4 presents the results of the analysis for the Main Study Area. Several grid sizes were superimposed on the study area to ascertain which grid best conformed to the irregularities of the study area boundaries. Calculations were made for two grids, with cells smaller than the ones finally used giving similar significance. The number of cells varies somewhat due to slight changes in the area studied from year to year.

The Z values indicate that H_0 is accepted in 1968, but rejected in favor of H_1 in 1969 and 1970. That is, females dispersed themselves in a relatively even pattern for their first nest in 1969 and 1970. Positions of subsequent nests were not examined since association with a particular male could conceivably affect subsequent nest site selections. McLaren (1972) used a t-test comparison of means to examine the spacing of females. He found that the mean distance between successive nests of the same female was significantly smaller than the mean distance between nests initiated by adjacent females in the same nesting period. This analysis indicates that females do restrict their movements in re-nesting. However, the fact that males often had to adjust their territorial boundaries to accomodate subsequent nesting, suggests that the restriction of movements may have been caused by the presence of the other females rather than by association with the male.

The analysis coincides with my earlier suggestion that such dispersion is significant only at certain population densities. This critical density was not attained in 1968. In addition to the more

Table 4. The dispersion of females on the Main Area as indicated by the position of first nests. Total number of cells (N), empty cells (k), and first nests (n) given for each year. The 'Z' value indicates whether the pattern of dispersal is random or regular (regular if Z < − 1.64).

Year	Cells	First Nests	Empty Cells	Z
1968	33	22	15	− 1.13
1969	31	29	8	− 2.32
1970	32	22	12	− 2.50

nearly random dispersion by females in 1968, the territories in that year were significantly larger than in 1969 and 1970 and no significant difference existed between mean territory size of monogamous and polygynous males. Although the number of first nests was the same in 1968 and 1970, Fig. 6 and 8 indicate that the birds were more concentrated in 1970. The population density was greater in 1969, the females were dispersed in an even pattern and the mean territory size of polygynous males was significantly larger than that of monogamous males.

In 1970 the density of both males and females decreased but was still sufficiently high for the females to disperse in a regular pattern; the territories of the males remained almost the same, but the decrease in the absolute number of females resulted in only one case of polygyny.

Nest Construction and Placement

Measurements and nest descriptions were taken from 129 nests in 1969 and 1970 after the young had left the nest. Female Ipswich Sparrows scratched a depression in the ground averaging 3.3 cm deep (range 1.0 to 4.6 cm). In this cavity she constructed the nest essentially as Dwight (1895) described: "It has two distinct parts, an outer shell of coarse material disposed as a rim and an inner cup finely woven. The excavation is filled in at the sides and around the margin with dead weed stalks, various coarse grasses and sedges, bits of moss or similar materials. These form a shell rising about an inch above the surface of the sand and straggling out over it for an inch or two. The shell is lined almost wholly with the finer bleached blades of an unidentified species of Carex, a few wiry horse hairs, or tufts from the shaggy ponies or cattle[3] being sometimes added. The lining is circularly disposed, and smoothed down as only a bird can do it, leaving between the eggs and the sand beneath an inch, more or less, of closely woven grass, while higher up the walls are considerably thicker on account of the added outer shell."

The depth of the nest ranged from 3.4 to 6.6 cm (average 5.0 cm), and the inside diameter from 6.2 to 8.3 (average 7.0 cm). Often one side of the rim of the nest was enlarged to form a platform on which

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[3] Cattle are no longer present on the island.

the birds perched while feeding the young.

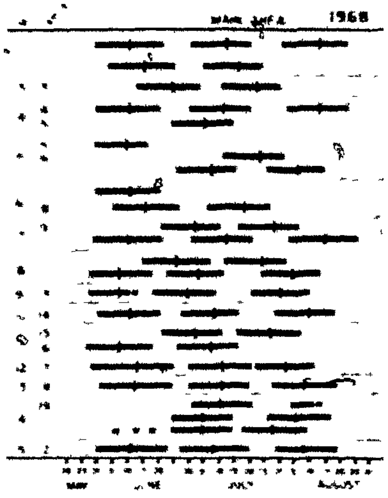
Most nests were sturdy and well concealed. On the Main Area the usual nesting sites were beneath dense clumps of rose, bayberry, dewberry, or the larger forbs. At the Sparse Area they also nested in crowberry and juniper. In the spring, females nested under tufts of dead marram, due to the lack of other emergent vegetation, but they avoided such sites later in the summer. On the Sparse Area, females occupying mainly grassy habitats nested in small, dense clumps of shrubs and forbs.

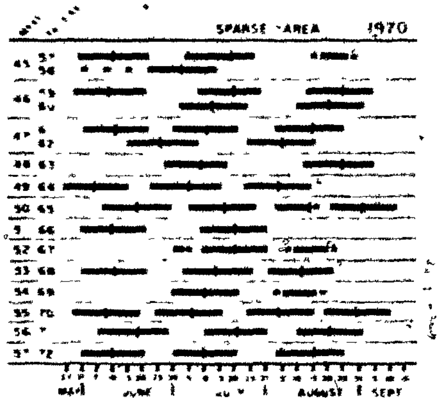
The nesting sites were rated as "preferred" (well concealed) or "poorly concealed" based on the height of the vegetation around the nest and the ease with which the author was able to initially locate the nest. In the preferred nesting sites, most nests were roofed and difficult to find. Females not proficient in concealing the nest were reproductively less successful. Only 26 of the 129 nests described were arbitrarily rated as being poorly concealed. However, 10 of the 23 nesting failures on the study areas occurred in nests classified as poorly concealed (the nests of the two failures in 1968, and one in 1969 were not classified). Concealed nests are partially insulated against changes in the weather. Those poorly concealed are exposed to temperature extremes and inclement weather, and are more visible to aerial predators. In 1970, 5 nests were predated, and all were rated as poorly concealed. The fact that 43.5% of the nesting failures occurred in poorly concealed nests suggests that concealment is important to breeding success and females building exposed nests may be inferior birds.

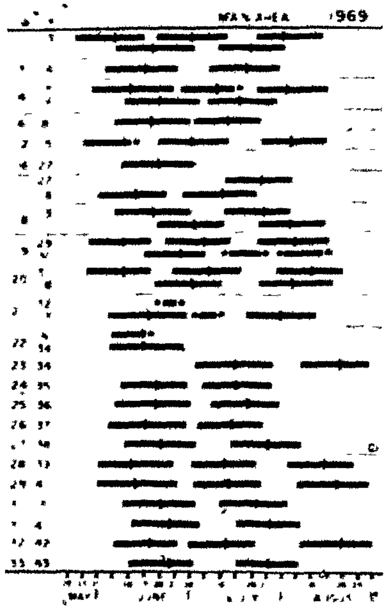
Nesting Phenology

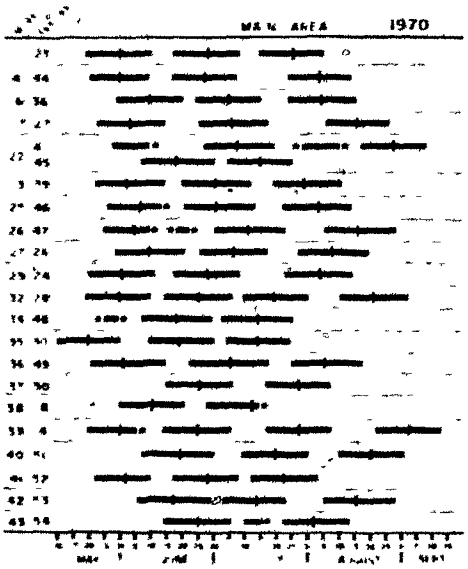
Observations were based on 232 nests of 89 females over three years, from two study areas (Fig. 12). Not all nests were discovered at the same phase of the nesting cycle and in several cases, estimates of clutch completion dates and occasionally hatching dates, have been made from observations of better known nests. Chi-square tests (Appendix 3) indicate that there were no significant differences in the number of nests initiated per female between years on the Main Area and between the Main and Sparse Areas in 1970. Nor were there any significant differences between females of monogamous and polygynous

Figure 12. Nesting phenology of the birds on the Main Study Area from 1968 to 1970, and on the Sparse Study Area in 1970. Both males and females are numbered sequentially so that returning birds are distinguishable. The solid lines indicate the length of each nesting cycle from the clutch completion date to the date of departure of the young from the nest. The vertical lines indicate the hatching date. Stars following a bar indicate that the nest was abandoned or destroyed, and one preceding means that no definite clutch completion date could be estimated. Three stars in a row indicate a suspected nest. Dotted lines joining bars indicate when a female changed mates. Female 14 nested on an island adjacent to, but outside of, the study area in 1969 thus appears only in the 1968 and 1970 data.


MAIN AREA 1968
MAY
JUNE
JULY
AUGUST


SPARSE AREA 1970
MAY
JUNE
JULY
AUGUST
SEPT


MAIN AREA 1969
MAY
JUNE
JULY
AUGUST


MAIN AREA 1970
MAY
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SEPT

males, or first and second females of polygynous males in average number of nests initiated.

Females of monogamous males and first females of polygynous males began nesting at approximately the same time, with first clutches being completed in late May or early June. Generally, second females began considerably later, and terminated nesting earlier in the season than did first females. As a result, second females brought off a maximum of two broods, while first females attempted at least three nestings. On the Main Area, few females initiated a third clutch if the second brood had not left the nest by late July. In 1970, the nesting season was the longest of all three years. Three females (14, 28, and 47) whose third broods left the nest in late July and early August successfully fledged a fourth, although nest failures were involved in the output of females 14 and 47. On the Sparse Area in 1970, nesting began about two weeks later, yet one female (70) successfully fledged four broods, and another (65) fledged a fourth after losing her third at hatching. Eighteen (90%) and seven (70%) females of monogamous males on the Main and Sparse Areas respectively, attempted at least three clutches. In 1968, six (73%) females of monogamous males attempted three, while only four (31%) did so in 1969.

Only 25 nests were discovered before laying was complete; the incubation time for these nests ranged from 9-15 days and averaged 12.5 days. This period was measured from the day the last egg was laid until the day the last young hatched. Although not all the eggs hatched in ten of the nests, the incubation time did not appear to be shortened in these, and no time corrections have been made. The mean incubation time differed slightly between years and areas (Table 5), but not significantly (t-test, P = 0.05).

Incubation time (from the last egg laid to the last to hatch) did not appear to be related to clutch size. The hatching times were spread over two days for 94 clutches and three days for an additional 11 clutches. The size of these clutches varied from 3 to 6 eggs. These data suggest that many females began incubation prior to completion of clutches.

Table 6 presents data on nestling times for different size broods in 1968 and 1969. Data from 1970 were not included since nestlings were

Table 5. Average length and standard errors in days of incubation periods. The number of observations are given in parentheses.

Main Area			Sparse Area
1968	1969	1970	1970
11.8 ± 0.6 (4)	13.0 ± 0.3 (11)	12.8 ± 0.9 (4)	11.8 ± 0.6 (6)

Table 6. Combined data from 1968 and 1969 on nestling time based on the number of young leaving the nest. Values in the table refer to the number of nests in each category.

Days in Nest	Number of Young Leaving Nest				
	1	2	3	4	5
8			1	1	1
9			1	2	1
10	1	3	9	12	13
11		2	11	13	9
12	1	1	7	10	2
13		1	3	4	2
Average nestling time	11.0	11.0	11.0	11.0	10.6

Overall average: 10.9 days

banded on the 9th or 10th day and this may have shortened the nestling time. The majority of broods stayed in the nest from 10-12 days although extremes of 8 and 13 days occurred. The average nestling time was 10.9 days, with no significant differences among the different brood sizes.

The time between successive nests of a female was highly variable, ranging from 2-17 days on the Main Area and 6-26 days on the Sparse Area. Averages and standard errors for all years and both study areas are given in Table 7. Although not significant, the time between first and second nests averaged less than that between the second and third on the Main Area. The reverse occurred on the Sparse Area, although generally females took longer to renest there. Still, the time interval appears to be at the whim of the female. Females which abandoned a nest appeared to initiate another quickly. However, the degree of success with one nest did not seem to influence the speed of re-nesting.

Mating

On six occasions birds were observed copulating between fledging one brood and completion of the next clutch. During this time, the females were also observed carrying nesting materials. Observations on nests found before the clutch was complete indicate that females usually lay one egg a day. On only two occasions did a female lay two eggs in one day. Nice (1937) found one egg per day to be the rule for Song Sparrows, as did Welsh (1970) for Savannah Sparrows.

It is also generally accepted in accounts of passerine breeding that nest building and egg laying occur after the previous brood has left the nest. However, some of the data suggest that copulation and nest building, and possibly laying, may be initiated before the current brood leaves the nest. Female 17 in 1968, and female 8 in 1969, had completed clutches of 4 and 5 eggs respectively, two days after their previous broods had left the nest. Table 8 summarizes these and other data on clutches completed in the 6-day period following the departure of earlier broods. Twelve clutches were completed in less time than necessary for a female commencing to lay one egg per day after her previous brood left the nest. In an additional ten cases females would have had to commence laying the day after their young left the nest to

Table 7. Average time and standard errors in days between the departure of one brood and the completion of the next clutch. The number of observations are given in parentheses. The time between the first and second clutch is above the time between the second and third clutch.

Main Area			Sparse Area
1968	1969	1970	1970
7.2 ± 0.4 (18)	8.0 ± 0.7 (26)	7.3 ± 0.6 (18)	12.4 ± 1.8 (13)
9.5 ± 1.1 (11)	12.7 ± 1.1 (6)	9.6 ± 0.9 (17)	10.0 ± 1.2 (9)

Table 8. The distribution of clutches completed in the 6-day period following the departure of a previous brood from the nest. Data from all years and areas are combined. The values in the table refer to the number of clutches in each category.

Interval (days)	Clutch Size					
	1	2	3	4	5	6
1						
2				1	1	
3				3	2	
4					2	2
5			1	1	8	1
6			1		13	2

complete their clutches if one egg is laid per day. Such a situation would allow no time for courting, or nest building after fledging. Clearly these females were courted and built their nests during the latter stages if the previous nesting cycle. Indeed, in several cases, the females must have begun laying before completion of the earlier nesting cycle. Such simultaneous activity would certainly impose a heavy energy strain on the female and it is interesting to note that such reproductive effort occurred only twice on the Sparse Area.

Clutch Size

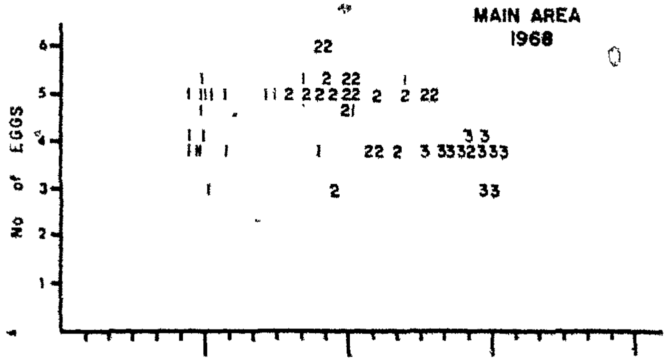
Figure 13 presents the data on clutch size related to time. A definite peak is evident in mid-summer in all years and on both study areas. Seel (1968) found similar variations for House Sparrows, and Lack (1947) suggested that such seasonal adjustment was related to future food availability.

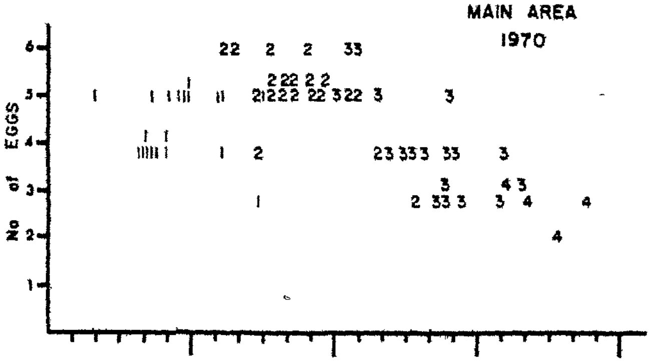
The clutch size ranged from 2 or 3 to 6 eggs in all years. First and second clutches of 5 were common. Third clutches contained a maximum of 4 eggs, except in 1970 when some of 5 and 6 eggs were laid. Fourth clutches occurred only in 1970 and attained a maximum size of 4 eggs. Six clutches of 6 eggs were found in 1970, two in 1968, and one in 1969 on the Main Area; one clutch of 6 eggs was also found on the Sparse Area.

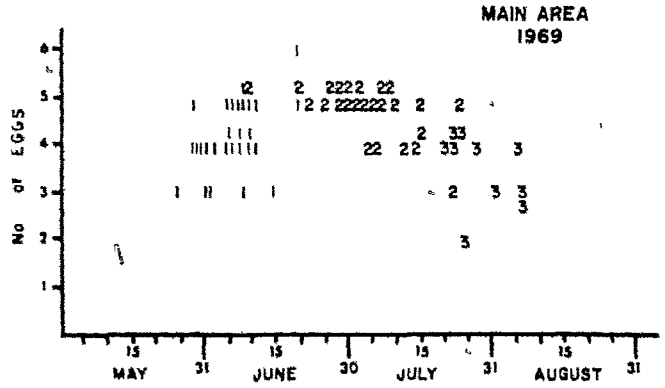
A few females laid clutches consistently smaller than the majority of birds. Normally second clutches were the largest, and occurred in late June or early July. However it is evident from Fig. 13 that variations in clutch size were related to time rather than merely the numerical sequence. Late first clutches tended to be as large as the early second clutches. Similarly, the size of the later second clutches approached that of most third clutches.

Table 9 summarizes the average clutch size of the total nests each year divided into three equal, successive groups. Table 10 gives the t-test comparison of the mean clutch sizes during the season. The smallest clutches were usually laid late in the season and, in all years, averaged significantly smaller than those in mid-summer. No significant differences occurred on the Main Area in 1968 and 1970 between the means of early and middle clutches. This suggests that

Figure 13. Seasonal variations in clutch size on both study areas. The numbers in the figure indicate whether the clutch was the first, second, third, or fourth. Note that late first clutches tended to be larger, and late second clutches smaller, than average.


MAIN AREA
1968
No of EGGS
1
2
3
4
5
6


MAIN AREA
1970
No of EGGS
1
2
3
4
5
6


MAIN AREA
1969
No of EGGS
1
2
3
4
5
6
15
MAY
31
15
JUNE
30
15
JULY
31
15
AUGUST
31

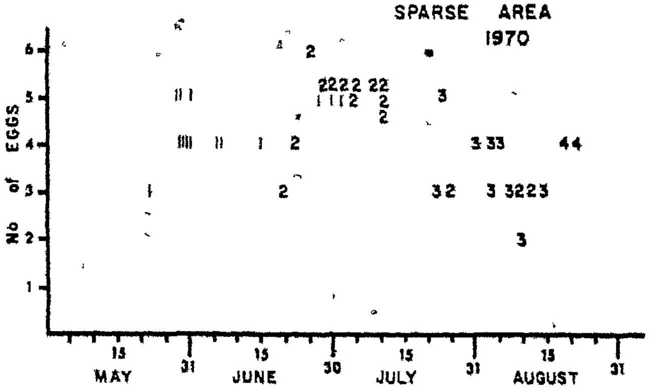

SPARSE AREA
1970
No of EGGS
1
2
3
4
5
6
15
MAY
31
15
JUNE
30
15
JULY
31
15
AUGUST
31

Table 9. Seasonal variations in clutch size are given for all years and study areas. The total number of nests in each season is divided into 3 equal groups according to the date of clutch completion.

	Main Area			Sparse Area
	1968	1969	1970	1970
Early	4.5 (18)	4.2 (23)	4.6 (22)	4.0 (14)
Middle	4.9 (18)	4.7 (22)	5.0 (22)	4.9 (14)
Late	4.0 (18)	3.9 (22)	3.5 (23)	3.4 (15)
Total	4.5 (54)	4.3 (67)	4.4 (67)	4.1 (43)

Table 10. Comparison by t-tests of seasonal variations in mean clutch size within each year. Significance at t 0.05 is indicated by an asterisk.

	Early	Middle
Main Area		
1968		
Middle	1.80	
Late	2.47*	4.19*
1969		
Middle	2.61*	
Late	1.29	3.57*
1970		
Middle	1.79	
Late	5.37*	6.97*
Sparse Area		
1970		
Middle	3.79*	
Late	2.28*	2.09*

conditions were more nearly optimal when the birds began nesting, or that the environmental conditions or the physiological state of the females deteriorated after mid-summer in 1968 and 1970, relative to 1969. Early clutches averaged significantly larger than late clutches, except in 1969; in that year, the early clutches also averaged significantly smaller than the middle group. On the Sparse Area, the time between re-nesting was longer and resulted in more discrete groupings. Significant differences occurred between all groups, the largest on average being the middle clutches and the smallest, the late clutches.

Seasonal variations in clutch size may not fully represent the reproductive efforts involved, since the size of the individual eggs may be affected by the size of the clutch. A total of 32 egg sets (3 nests of 6 eggs, 9 nests of 4, and 10 nests of 3 to which was added 1 nest of 2 eggs) were measured to examine this possibility. Since eggs tend to vary in shape, instead of comparing lengths and widths, relative volume was estimated as L x W^2. Subsequent t-tests ($P = 0.05$) indicated no significant difference in mean relative egg size between the different clutch sizes, nor was any trend evident.

Nice (1937), however, warned that there was a difference in egg size between successive clutches of the same female, thus only "first sets should be compared with first sets". Unfortunately, there are insufficient data to make such an analysis. But there are egg measurements from two successive nests of six females and from three successive nests of one female. For five of the six females, the eggs of the first set were larger than those of the second, and the difference was significant in three (t-test comparison of means). In the case of the three successive nests, there was no significant differences in the egg size of the first and second sets, but both had significantly larger eggs than those of the third set. In most of the significant cases, the earlier sets had a larger clutch size, as well as larger eggs. This may suggest that these females may not be able to put as much reproductive energy into later sets, a state which could ultimately affect the survival of these offspring. These findings are the reverse of Nice's (1937) results, in which the average egg size of later sets was decidedly larger than the first sets.

Incubation and Feeding

Males were not seen incubating the eggs although they were attentive to the female during this time. The males usually gave warning calls as I approached and generally the females were gone when I reached the nest. Only a few nests were observed to document female incubating habits. Considerable variation occurred between females, and periods on and off the nest were affected by weather or other activity nearby. One incubating female was observed for hourly periods on eight successive days. As incubation progressed, she appeared to make no adjustments in her habits. She averaged 3.6 trips from the nest per hour. The time interval off the nest ranged from 24 seconds to 11.4 minutes; the incubating periods ranged from 8.9 to 14.0 minutes. Generally a long period off the nest was followed by a long period of incubation.

Information on the feeding of nestlings is insufficient for detailed analysis, but some patterns are evident. Both males and females fed the young on the nest, but individual variation was high. The frequency of feeding was greatest on quiet sunny days. Rain, fog, or wind seemed to increase the search time, thereby decreasing the frequency of feeding. Females are capable of raising a brood alone, but may experience difficulty. Female 27, in 1969, lost her mate just after a clutch of 5 eggs had hatched and only 3 young succeeded in leaving the nest. She refused to allow male 17, her subsequent mate, near the nest during this time, although on at least one occasion he carried food. Welsh (1970) noted that a male Savannah Sparrow also raised a brood alone.

Table 11 summarizes feeding observations made on 5 nests in 1969 and 1970. Observations were taken for one hour periods in 1969 and half-hour periods in 1970; the table frequencies are adjusted to hourly averages. The time of day did not seem to influence the rate of feeding and these data were combined.

Active feeding began on the first day and rose to a peak on the seventh and eighth day. For the first three days the females averaged 2.5 to 5.9 minutes at the nest after bringing food. They may have been brooding young, or the time spent may have been a function of the ability of the young to handle food. Her time at the nest during the remaining seven or eight days was reduced to less than a minute. The

Table 11. Summary of hourly feeding data collected from 5 nests in 1969 and 1970. The time that the female spent at the nest during the first three days (A) is presented separately from the remaining days (B). The averages with standard errors are given in all cases.

Female	Average adult feedings	Time spent at nest			Time between successive feedings	
		Female		Male	Female	Male
		A	B			
1969						
1 (2nd nest)	15.2 ± 1.8	4.9 ± 0.6	0.5 ± 0.1	0.3 ± 0.1	5.3 ± 0.6	7.1 ± 0.8
1970						
54 (1st nest)	10.0 ± 0.5	5.9 ± 1.8	0.3 ± 0.1	0.3 ± 0.1	6.1 ± 0.9	10.8 ± 1.4
46 (2nd nest)	10.4 ± 0.5	5.0 ± 1.8	0.6 ± 0.2	0.3 ± 0.1	5.9 ± 0.7	10.5 ± 1.9
39 (2nd nest)	10.6 ± 0.5	3.1 ± 0.7	0.3 ± 0.0	0.5 ± 0.1	6.3 ± 0.7	5.5 ± 1.6
27 (2nd nest)	13.8 ± 0.7	2.5 ± 0.7	0.2 ± 0.0	0.3 ± 0.1	5.3 ± 0.5	7.3 ± 1.1

male began feeding the young on the second or third day and did not appear to increase or decrease his devotion. On two occasions males were apparently brooding young. The time males spent at the nest never exceeded one minute. Females fed the young more frequently than the males, averaging between 5.3 and 6.3 minutes between feedings; males averaged from 5.5 to 10.8 minutes. The one bigamous male in 1969 was no less attentive than the four monogamous ones in 1970 (Table 11).

Adult midges (Chironomidae) were the predominant food for very young birds, but later adult and larvae lepidopterans along with other insects were included. Pieces of strawberries and blueberries were also fed to the young, but were utilized more commonly on the Sparse Area. The adults seldom returned with small insects in the latter part of the nestling phase. While searching, they ate the smaller insects and seeds which they encountered, returning to the nest only with larger prey. However, if a swarm of small insects were encountered, the parents would often return with a mouthful of these. Such a technique would most efficiently utilize the time and energy spent in searching for food.

As a result of this feeding method, a considerable proportion of the adult birds' diet consisted of insects. I took no specimens for food analysis, but Dwight (1895) presented the results from 56 adults. The contents of the 19 summer birds from Sable Island contained 75.5% animal matter and 15.2% vegetable matter, the remainder being mainly sand. Analyses of the contents revealed "Beetles and their larvae, represented by scarabaeids (Aphodius fimentarius identified), carabids, elaterids, cicindelids, and weevils; caterpillars, as well as pupae and pupa-cases; grasshoppers, ants (including one pupa), and other hymenoptera; hemiptera; diptera; spiders (also eggs and cocoons); snails; seeds, herbage, and rubbish,...". Obviously the adult Ipswich Sparrow is substantially carnivorous in summer, and presumably its young are even more so.

After leaving the nest, the young are fed by both parents for approximately two weeks. The young emit a "buzzing" begging sound when not being fed. Finally, the adults ignore the begging juveniles. The young are flightless for several days after leaving the nest, and are not capable of flying more than a few hundred yards for at least two weeks.

REPRODUCTIVE SUCCESS

General nest success is summarized in Table 12. In all years and in both areas, over 85% of eggs hatched. The poorest hatching success of 79.4% occurred during the third clutch on the Sparse Area. The opposite extreme was the 100% hatching success of fourth clutches in 1970 on both areas, although sample size is small.

The percentage of young birds which left the nest is equally high. Yearly success levels ranged from 87.7% in 1969 to 95.8% in 1968. The relatively low success of 70.4% during the third clutch on the Sparse Area was due to the predation of 2 nests after I had taken egg measurements. Presumably my extended presence at the nest was the cause of this predation (probably by crows).

The high success rates are probably due to the almost complete lack of predation. The only possible resident predators were 3 or 4 crows in 1970 and 2 or 3 cats. Crows were suspected of predating 4 nests in 1970. Transient Grackles (Quiscalus quiscula) were suspected in one nest predation in 1968, and the introduced Pheasants (Phasianus colchicus) of killing the brood of one nest in 1969. There is no evidence of cat predation. Occasionally, cats and gulls were seen taking weakly flying young, but this is unusual. The horses could step on nests, but no evidence of this was found, and the birds are not disturbed by them.

Chi-square tests were performed to determine if differences in hatching and fledging success were related to specific factors. No significant differences were found when comparisons were made between years or study areas, clutches, monogamy and polygyny, or first and second females.

The birds on the study areas obviously have very high nest success, with from 77.5% in 1969 to 84.2% in 1968 of the eggs which leave the nest as juveniles. In 1968, there were 3 nests parasitized by Cowbirds (Molothrus ater) in which one egg was added to each nest. These Cowbird additions were included in the calculations on reproductive success. Increased mortality probably occurred in the incubation

Table 12. Seasonal and yearly differences in nest success. The percentage of birds leaving the nest is based on the number of young. The number of nests are given in parentheses.

	Main Area									Sparse Area		
	1968			1969			1970			1970		
	Eggs Laid	% Hatch	% Fledge	Eggs Laid	% Hatch	% Fledge	Eggs Laid	% Hatch	% Fledge	Eggs Laid	% Hatch	% Fledge
First clutch	100 (22)	91.0	93.4	121 (29)	93.4	88.5	98 (22)	89.8	84.1	65 (16)	90.8	100
Second clutch	99 (21)	82.8	96.3	127 (27)	84.3	84.1	108 (22)	85.6	92.1	70 (16)	84.3	98.3
Third clutch	42 (11)	92.9	100	37 (11)	86.5	96 9	76 (19)	82.9	96.8	34 (10)	79.4	70.4
Fourth clutch	-------			-------			11 (4)	100	100	8 (2)	100	100
Total Eggs or Young	241	212	203	285	252	221	293	251	228	177	153	144
Total Success (%)		88.0	95.8		88.4	87.7		85.7	90.8		86.4	94.1

phase since the complement of Ipswich Sparrow eggs was less expected. No additional mortality occurred after hatching. Unfortunately, we have no direct information on mortality after the young leave the nest.

Monogamy and Polygyny

Success is the most important basis for comparison of monogamous and polygynous matings, as it would be most likely to indicate the adaptive value of such behaviors. Polygyny in the Ipswich Sparrow generally means bigamy by the male. One male, in 1968, had three females, but this would appear to be a very rare occurrence.

Table 13 compares the reproductive success, measured as young leaving the nest, for monogamous and polygynous matings. As mentioned in the previous section, there was no significant difference in the percentage of young leaving the nest between monogamous and polygynous matings. The production per male on the Main Area differed significantly in the three years ($\chi^2 = 12.755$, d.f. = 2, $P < 0.005$) with males in 1968 producing considerably more, and 1969 males fewer young than expected. There was no significant difference in production per male in 1970 between the Main and Sparse Areas. In all years, polygynous males produced significantly more fledglings per male than monogamous males (1968: $\chi^2 = 14.752$; 1969: $\chi^2 = 11.831$; Sparse Area 1970: $\chi^2 = 12.403$; d.f. = 1, $P < 0.005$). No calculations were made for the Main Area in 1970 since only one male was polygynous. Overall, polygynous males produced 15.5 young per male, 60.3% more than the 9.7 average for monogamous males. If, in 1969, I had not injured a female of male 22, so that she did not re-nest, the difference would have been even greater.

Females generally produced fewer young on average than the males except on the Main Area in 1970 where only one case of polygyny occurred. Females of monogamous males produced more young per female than did those of polygynous males every year. Although the differences were not significant, females of monogamous males produced almost 20% more young per female than did those of polygynous males in the three years.

Verner and Willson (1966) maintained that for polygyny to occur it must have adaptive value for females as well as males. By separating the production of first females of polygynous males from that of the

Table 13. Average reproductive success measured as the number of young to leave the nest. The number of adult birds is given in parentheses. Although 23 males were on the Main Area in 1969, males 16 and 23 were there for only part of the season, so averages are based on 22 males. The switching of mates in 1968 and 1969 changed the status of females 4 and 8, and 27, 28, 6, and 34 respectively, and their production is not included in the calculations for females of monogamous or polygynous males (referred to in table as monogamous and polygynous females); similarly the production of females 5 and 7 in 1968 are excluded in calculations for 1st and 2nd females.

	Main Area			Sparse Area
	1968	1969	1970	1970
Males				
All males	13.5 (15)	10.0 (22)	10.9 (21)	11.1 (13)
Monogamous males	10.1 (8)	8.3 (14)	10.6 (20)	9.3 (10)
Polygynous males	17.4 (7)	13.1 (8)	16.0 (1)	17.0 (3)
Females				
All females	9.2 (22)	7.6 (29)	10.4 (22)	9.0 (16)
Monogamous females	10.1 (8)	8.2 (13)	10.6 (20)	9.3 (10)
Polygamous females	8.5 (12)	7.6 (12)	8.0 (2)	8.5 (6)
1st females	10.5 (4)	9.8 (6)	7.0 (1)	10.0 (3)
2nd females	6.5 (6)	5.3 (6)	9.0 (1)	7.0 (3)

later, second females, we may resolve this problem. The production of these first females averaged slightly higher though not significantly than that of females of monogamous males. Overall, first females left 35.7% more young per female than the second females; the difference was significant in 1968 ($\chi^2 = 5.541$; d.f. = 1, $P < 0.025$) and 1969 ($\chi^2 = 8.011$, d.f. = 1, $P < 0.005$), but not on the sparse Area in 1970. Similarly, the production of females of monogamous males was significantly greater than that of second females (1968: $\chi^2 = 4.636$; 1969: $\chi^2 = 4.715$; d.f. = 1, $P < 0.05$).

Thus it would seem that second females suffer reduced output in polygynous matings. But if we compare the average reproductive success of female per nest (Table 14), we find this not to be the case. On a per nest basis, second females, generally do as well as first and monogamous females. All categories averaged between 2.7 and 3.8 young fledged per nest (excluding polygynous data from the Main Area in 1970). Chi-square tests indicated no significant differences between years or areas, monogamy and polygyny, or first and second females. The lower production of second females obviously was not due to reduced nest success, but simply to the result of fewer nests.

BREEDING POPULATION AND RECRUITMENT

It is not intended here to discuss the whole question of the population dynamics of the Ipswich Sparrow, but rather to relate fluctuations in population size to breeding and territoriality.

The density of the vegetation determines the distribution of Ipswich Sparrows on the island. To estimate total island populations, therefore, it was necessary to classify the island into vegetational types. McLaren (1968) estimated the total adult population in 1967 simply by counting birds on selected areas deemed representative of the island's vegetation. A more elaborate classification will be used here (Appendix 4), but McLaren's 1967 estimate of 4000 breeding birds, assuming an even distribution of birds over the different habitat types, did not differ much from the revised estimate (see below) of 4294. The stratified sampling procedure and the necessarily varied size of census plots, obviously allow no possibility of making fiducial limits of

Table 14. Average reproductive success per nest measured as the number of young to leave the nest. The number of nests is given in parentheses. Due to the switching of mates, the production of some females is omitted from the 1968 and 1969 calculations. The females of monogamous and polygynous males are referred to in the table as monogamous and polygynous females.

	Main Area			Sparse Area
	1968	1969	1970	1970
Monogamous males	3.7 (22)	3.5 (33)	3.5 (61)	3.2 (29)
Polygynous males	3.8 (32)	3.1 (34)	2.7 (6)	3.4 (15)
Monogamous females	3.7 (22)	3.6 (30)	3.5 (61)	3.2 (29)
Polygamous females	3.8 (22)	3.1 (29)	2.7 (6)	3.4 (15)
1st females	3.8 (11)	3.5 (17)	1.8 (4)	3.3 (9)
2nd females	3.5 (11)	2.7 (12)	4.5 (2)	3.5 (6)

estimates.

Vegetation Categories

During the full island census in 1971, the consolidated portions were subjectively subdivided into vegetation categories. Subsequently a survey of the island's vegetation in 1971 by D. Welsh was combined with information on vegetation density taken from aerial color photographs to divide the island into 7 vegetation categories (Fig. 14). Generally the subdivisions made during the full island census corresponded with the final vegetation map.

Although such a classification is a gross simplification, the density of the vegetation seemed to be the most important factor in determining bird distribution. Substrate relief, although not considered here, is probably also important since it affects surveillance distance, territorial encounters, and territory size (see p.21). The categories are described in Appendix 4, and the total area and number of birds in each vegetation category are given in Table 15.

Census Areas

From 1968 to 1972, spring and autumn censuses were taken on selected plots (Fig. 1) for estimates of the number of breeding birds and of production. Early winter censuses were also taken in 1968 and in 1970. Details on the census plots, and census results, are given in Appendix 4. An early spring census in 1972 (March 28 to April 1) gave a total count of 6 Ipswich Sparrows on all the census plots, indicating that very few birds over-wintered successfully that year. A detailed examination in 1971 suggested that most of the birds on the census plots at the time of the spring census were established territorial birds.

Population Estimates

Table 15 summarizes the vegetation analysis and the results of the full island census of breeding birds. The "juniper" and "heavy composite" areas were the most heavily populated with 8.11 and 4.32 birds per hectare respectively. "Heavy marram grass" is the most extensive vegetation type (633 ha.) but was not extensively used by breeding birds (1.07 per ha.).

Figure 14. General vegetation breakdown of Sable Island used for the population estimates. The "sandwort" category is restricted to the east tip of the island.

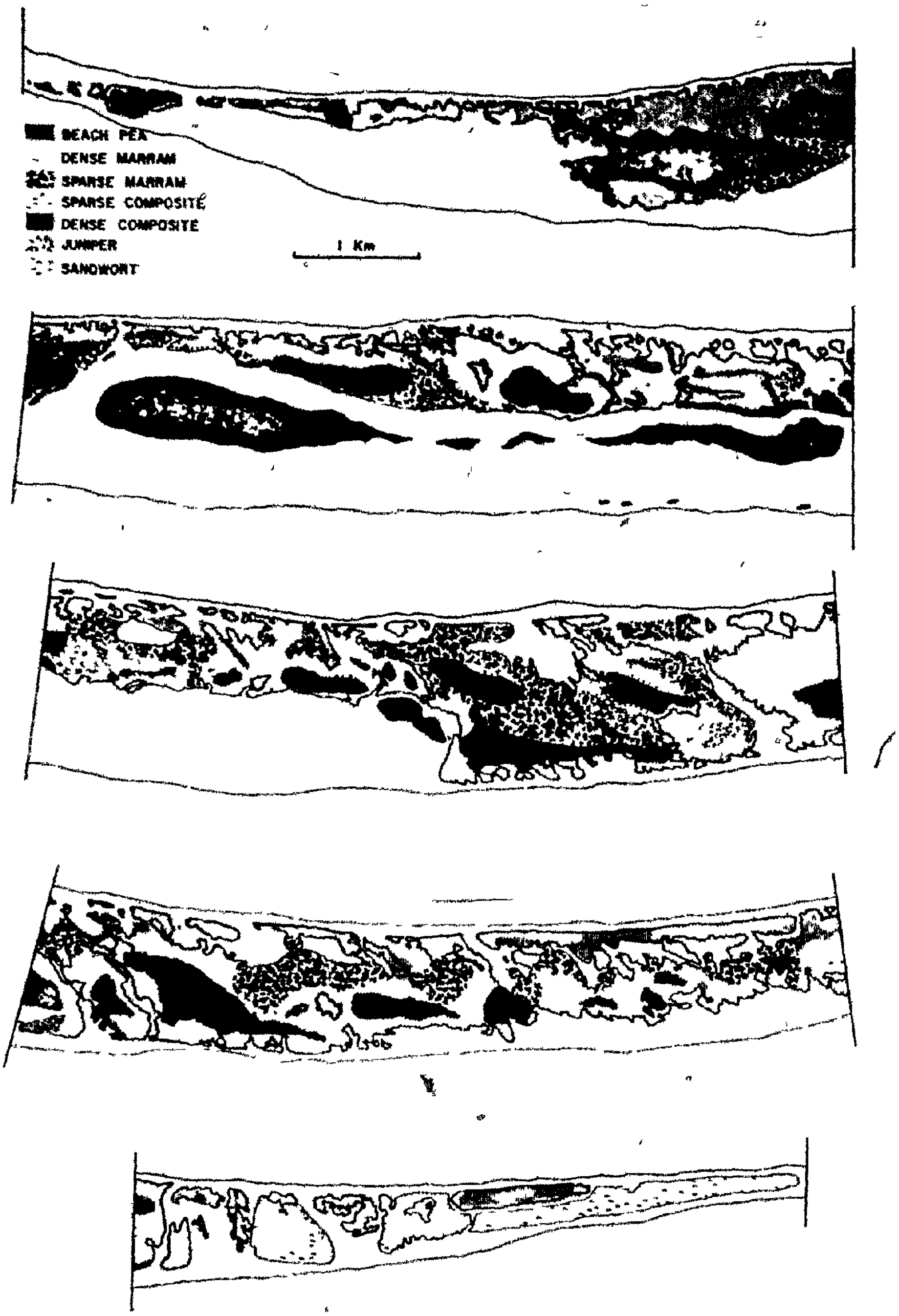

BEACH PEA
DENSE MARRAM
SPARSE MARRAM
SPARSE COMPOSITE
DENSE COMPOSITE
JUNIPER
SANDWORT
1 Km

Table 15. Summary of the bird counts made during the full island census in 1971. The island was subsequently divided into 7 vegetation categories. The total number of birds and the number per hectare are given for each vegetation type.

Vegetation	Area (ha)	Number of Birds	Birds per Hectare
Beach pea	104	143	1.38
Heavy Marram grass	633	676	1.07
Sparse Marram grass	326	98	0.30
Heavy Composite	272	1174	4.32
Sparse Composite	26	39	1.50
Juniper	36	292	8.11
Sandwort	76	2	0.03
Total	1473	2424	1.65

Table 16 summarizes the census results. The 1971 spring estimate from the census plots of 2961 breeding birds is 22% higher than the full island count (the difference between the full island counts in Tables 15 and 16 is due to the omission in Table 16 of the 2 birds in the sandwort category). The full island count represents the minimum number of breeding birds since some females may have been loathe to leave their eggs. However, there is still a possible 22% error in my estimates based on plot censuses. The greatest portion of this possible error is in the estimates of the number of birds in the "heavy marram grass". Several factors could contribute to such an error, but an over-simplified classification of the vegetation and its effects on the bird distribution, and possible bias in our choice of census plots were probably the main factors. The census plots were often located, for convenience, on the periphery of the consolidated areas (Fig. 1). The peripheral areas of "heavy marram grass" often contains more dense vegetation with a greater proportion of beach pea and forbs than did the interior areas, and thus may have been somewhat better for nesting. The vegetation difference need not be great to cause such an error. When the bird density estimates are derived from the 31 hectares of "heavy marram grass" in the census plots, a slight difference in the number of birds on the census plots would be magnified 20 times. Thus the difference of 337 birds between the estimated and observed values for "heavy marram grass" in 1971 would be more than accounted for if the census plots of "heavy marram grass" had 0.6 more birds per hectare than did interior parts.

However, accepting this level of error, it is still possible to observe relative fluctuations in population numbers. The spring census estimates are highest in 1967 and lowest in 1972. But care should be taken in comparing these with the estimates in the other four years, since only 9 plots were counted in 1967 and the addition of 4 plots in 1972 may have removed some of the estimation error.

The greatest relative increases in the number of birds in the autumn occurred in areas exhibiting the greatest seasonal increases in the density of the vegetation ("beach pea", "heavy marram", and "sparse marram"). The greatest autumn concentration of birds occurred in the "beach pea" areas, the numbers of birds being 5 to 11 times

Table 16. Estimates of the size of the Ipswich Sparrow population on Sable Island calculated from values obtained on the census plots. No autumn estimate was made in 1967. Winter estimates were made in 1968 and 1970. The actual counts obtained during the full Island census in 1971 are also given.

Year	Pea	Heavy Marram	Sparse Marram	Heavy Composite	Sparse Composite	Juniper	Total
1967							
Spring	291	1519	163	2094	—	227	4294
1968							
Spring	239	1266	130	1006	16	151	2808
Autumn	1926	3102	880	2040	42	432	8422
Winter	114	380	98	163	0	0	755
1969							
Spring	229	1013	130	1768	16	252	3408
Autumn	1279	2342	391	1931	55	259	6257
1970							
Spring	187	886	98	1251	13	169	2604
Autumn	2059	4431	1141	2747	26	407	10811
Winter	104	316	98	109	0	0	627
1971							
Spring	187	1013	130	1360	23	248	2961
Autumn	1414	8166	2543	1659	78	450	14310
1972							
Spring	250	886	228	503	13	162	2042
Autumn	510	8799	1076	870	52	169	11475
Full Island Census 1971							
	143	676	98	1174	39	292	2422

greater than in the spring. In 1970, 1971, and 1972, the estimates of overall production were relatively high, and in these years the numbers of birds in "heavy marram" and "sparse marram" areas also increased dramatically. The estimates for the more stable "heavy composite" and "juniper areas indicate a less than three-fold increase in all years.

The estimates of overall island production are considerably lower than the actual production per adult observed on the Main Area, as shown below.

Production per Individual

Year	Main Area	Sparse Area	Island Estimate
1968	5.5		3.0
1969	4.3		1.8
1970	5.3	5.0	4.2
1971			4.8
1972			5.6

Conceivably the differences could have been due to the fact that the Main Area was an optimal breeding area, but production on the Sparse Area in 1970 was also greater than the full island production estimates. Alternatively, a large non-breeding population may have been present. However such information is difficult to obtain for monomorphic species without detailed studies and I have no data to consider this possibility. The differences between the observed production on the study areas and the estimates from the censuses may therefore give us an idea of the relative mortality after the young left the nest in the three years. Both the 1968 and 1969 observed and estimated production levels differ by 2.5 young per adult respectively, yet in 1970 the difference is 1.1 young. As stated earlier, 1969 had relatively poor weather during the breeding season, the majority of birds initiated only 2 clutches, and the estimated population size increased by a factor of only 1.8. The breeding season commenced at about the same time in 1968 as in 1969, but in 1968 the weather was relatively good, many birds initiated 3 clutches, and the estimated population size increased by a factor of 3. In 1970 the weather was good, the breeding season longer, and the estimated population increased in size by a factor of 4.2.

It is possible then that production during the summer is related to the weather conditions, although lower production in 1969 may also be related to the denser breeding population in that year. The population estimates for 1972 agree with the density dependent production hypothesis. However, the greater estimated production in both 1971 and 1972 may be related to the increase in the number of census areas in 1971. In addition, the estimated initial breeding population was greater in 1971 than 1968 or 1970, yet the estimated production was also greater. Thus production cannot be highly related to the size of the breeding population.

It is clear from Table 16 that heavy mortality occurs during the winter. Although population regulation may be greatly influenced by conditions on the wintering grounds and during migration, the subject is not further considered in this thesis.

Discussion

The literature on bird territoriality and breeding biology is vast, however it is often anecdotal, and full of conflicting observations and arguments Observations to the effect that some species are single brooded, or monogamous, are of course based on negative evidence and often on inadequate inquiry. Verner and Willson (1969) in their excellent compilation of data on North American passerines lament the inadequacy of our knowledge of mating systems and the "sloppy reporting" of much of it. They were forced to assume that 273 of 314 species were normally monogamous, although only 22 of these were said to be monogamous on the basis of published references to their mating systems.

The requisites for a comprehensive investigation of territoriality and breeding biology include some "means of identifying all of a reasonably large number of birds on a continuous study area, careful mapping of territories, persistent observation through the breeding season, discovery of all nests, and no preconceptions about mating systems" (McLaren, 1972). In sexually monomorphic species, such as grassland sparrows, a means of identifying individuals is imperative if the degree of polygyny or the role of the male in the nesting cycle are to be ascertained Very few published studies meet these requirements. Also, many mainland species have been studied in or near populated or cultivated areas and have shown signs of human disturbance during the nesting cycle (see Nice, 1937, Welsh, 1970).

The Ipswich Sparrow is an ideal subject for an intensive study of territoriality and breeding biology. This species suffers from almost no terrestrial or avian predators on Sable Island. The birds have not been harassed by man on the breeding grounds, and multiple broods, high nesting success and polygyny may all partly reflect a degree of their indifference to our scrutiny.

As stated in the introduction, a prime purpose of this study was to examine the life history of the Ipswich Sparrow. A consequence of this type of study is that the implications of many of the observations presented in the results section are self-evident and require little or no further discussion. Therefore, reference to these observations will be limited to areas to which I feel the data can contribute to a better understanding of the nesting biology of passerine birds.

Since this thesis is particularly concerned with the interrelationships involved in territoriality and breeding biology, the discussion will be largely devoted to examining the adaptive values of such behavior, with special reference being given to the controversy on the function of territory and its role in the regulation of bird populations.

Nests and the Breeding Cycle

Ipswich Sparrows nest on the ground, as do the other grassland sparrows, and 80% of the nests described in this study were well concealed in dense vegetation. Females in the Sparse Area often nested in small dense clumps of vegetation and, even on the Main Area, the more dense patches of vegetation were generally preferred as nesting sites. These observations agree with Wiens' (1969) observations on grassland Savannah Sparrows. Placing the nest in dense vegetation would certainly be advantageous in concealing the nest from predators, but Kendeigh (1934) has also suggested that nest construction and placement is adapted to reducing temperature fluctuations around the nest

Females with well concealed nests were reproductively more successful than those with poorly concealed nests. Only 20% of the nests which I described were rated as poorly concealed, yet the exposed nests incurred 44% of the nesting failures. Nice (1941) found a similar correlation between success and nest concealment, but since successive nests of some females differed radically in the degree of nest concealment, she considered concealment to be a matter of chance. I think that this is an unsatisfactory explanation My observations agree that no female consistently built exposed nests, and natural selection should eliminate such behavior. But a poorly concealed nest, I suggest, indicates that the female is not at the optimal physiological state for nesting, and lowered reproductive success generally accompanies such attempts. This suboptimal state could occur at any time during the breeding season since the rigors of having multiple broods may be as strenuous as that of migration.

Nesting Phenology and the Number of Nests

Darwin in 1871 discussed the value of sexual selection in monogamous species and suggested that the "more vigorous and better nourished" females would be the first to breed, and the "earliest breeders would on average succeed in rearing the largest number of fine offspring". Basically, our results support his thesis, although male Ipswich Sparrows tend to be polygynous. Many monogamous females and the first females of polygynous males arrive on the study area as early as the males, and commence nesting while territorial borders are still being disputed. These females initiate more nests and, on average, produce more offspring (Table 13) than do the later starting second females of polygynous males. These second females along with some monogamous females, are probably either inexperienced birds nesting for the first time, or physiologically "late" birds. In either case, they commence nesting later and terminate activities earlier, thus their reproductive output and possibly their Darwinian fitness are lower than those of the other females. Obviously, birds which consistently produce few offspring will have a lower Darwinian fitness than other birds, but if the lower production is only temporary due to inexperience or physiological "lateness", then their fitness may be also lower only temporarily. Also, there may be some adaptive value in delaying the commencement of nesting by "late" females. By nesting later, such females in effect, wait for more extensive habitat cover which facilitates nest concealment, and an early termination of nesting activities may provide more time for these females to prepare for the autumn migration.

In 1970 on the Sparse Area, the territory establishment phase was prolonged, and nesting began about 2 weeks later (Fig. 12) than on the Main Area. Generally the time interval between successive nests was longer (Table 7) on the Sparse Area, and only two females initiated a second nest while still feeding young at the previous nest. Ten females had overlapping nesting cycles on the Main Area in 1970. This reduction in the reproductive effort on the Sparse Area could be caused by differences in habitat quality or the relative or Darwinian fitness of the breeding birds, relative to the Main Area. Obviously the two possibilities are related since the less fit birds could be excluded from nesting in the preferred habitat. However, the data suggest that relative fitness is not the most important factor. On the Sparse Area, two females attempted four clutches, and although 20% fewer females, of monogamous males, initiated third clutches than on the Main Area, the difference was not significant. Clutch sizes on the Sparse Area were slightly smaller than on the Main Area (Table 9), but no significant differences occurred in hatching success, or the number of young to leave the nest. The average number of young produced per nest in monogamous matings (Table 14) is slightly, but not significantly, lower than on the Main Area.

Since the various breeding parameters indicate little difference between the two areas, it is doubtful that there is much difference in the Darwinian fitness, and the later dates for commencement of nesting are thus probably largely related to habitat quality. In a sparse habitat, there would be fewer nesting sites and food would be more dispersed. Consequently, the searching time for food would be increased. This could increase the physiological strain on the female and may explain the additional time period between successive nests. I doubt that food limits the reproductive output; however, increasing the time required to find food for the young could cause females to be opportunistic (see MacArthur and Pianka, 1966), and may explain the presence of berries in the diet of the Sparse Area nestlings.

The average number of nests per female varied more between years than between study areas (1968: 2.5; 1969: 2.3; 1970: 3.0, and 2.8 on the Sparse Area), indicating the importance of the weather conditions. Second females brought off a maximum of 2 clutches. However, 3 clutches were normal for first females and females of monogamous matings. This is higher than the 2 clutches normally produced by the closely related Savannah Sparrow (Wiens, 1969; Welsh, 1970). Immelmann (1971) states that 4 clutches are rather exceptional even amongst the continuously breeding birds of the tropics, yet in 1970, three females successfully produced 4 clutches. This evidence may indicate that the Ipswich Sparrows are unusually productive. Alternatively, the reproductive efforts of other species may be seriously affected by the presence of observers, or not fully appreciated due to lack of observations late in the season or from successive seasons. In 1969, only 10 of 29 (34.5%) females on the Main Area attempted 3 clutches, yet in 1968 and 1970, 11 of 22 (50.0%) and 19 of 22 (86.4%), respectively, initiated 3 clutches. Even on the Sparse Area in 1970, 10 of 16 (62.5%) females attempted 3 clutches. Analysis of data from a single year could give a biased perspective of a species' potential reproductive output.

Females usually lay 1 egg per day (see Lack, 1968), although occasionally 2 may be laid together (Nice, 1953). It has been assumed that in multiply-brooded species successive clutches were laid after the young leave the previous nest. My data however, agree with Lack's comment that females of some passerine species often commence laying a new clutch while simultaneously caring for young in the current nest. While such overlapping of nests should greatly increase the physiological strain on the female, at this time the young are sufficiently developed to regulate body heat loss, a major caloric expenditure for young birds (Royama, 1966), and the male participates in feeding the young in the latter part of the nesting cycle. Also, overlapping nesting cycles is an effective way of maximizing the reproductive output of birds which appear to have an adult life expectancy of only 2 or 3 years.

Clutch Size

The seasonal peak in clutch size in mid-summer for all years (Fig. 13) is common in birds with multiple broods (Lack, 1954) and may be in accord with Lack's (1966) view that clutch size is adapted in many species to the ability of the parents to feed the young. This ability need not be dependent in any obvious way on food availability; unfortunately, I have no real data on food abundance or availability to discuss the subject further. The difference in mean clutch size (Table 9) and the levels of significance (Table 10) suggest that at the start of the breeding season, in 1968 and 1970 on the Main Area, conditions were near-optimal, then improved, before deteriorating late in the season. In 1969, and on the Sparse Area in 1970, the mean clutch size early in the season was significantly smaller than in mid-summer, thus also indicating sub-optimal conditions in the spring. Bad weather prevailed in 1969, and the Sparse Area is a sub-optimal habitat; thus in both cases habitat quality or the physiological state of the females could account for the differences in mean clutch size. Unfortunately, my data cannot resolve the problem further. However, Klomp (1970) suggests that the decline in clutch size late in the breeding season is due to physiological fatigue on the part of the female, and von Haartman (1971) while stating that no satisfactory explanation has been made, acknowledges that "there are indications that the condition of the female influences her clutch size...".

Incubation and Feeding

Only the female incubated the eggs, and the length of the incubation period was not correlated with clutch size. The incubation period ranged from 9 to 15 days, although Nice (1953) claims reports of less than 10 days to be generally erroneous. The average incubation period of 12.5 days corresponds closely with the 12 to 13 day period reported for the Savannah Sparrow (Knight, 1908; Wiens, 1969).

The hatching period often extended over 2 or 3 days, indicating that incubation often commenced prior to clutch completion. This agrees with Nice's (1941) findings, but disagrees with the commonly held belief that the eggs normally hatch on the same day because incubation starts after clutch completion. Lack (1968) argues that an extended hatching period occurs in a few small passerines as an adaptation which allows the adults to raise the greatest number of young in areas with a variable food supply. His explanation may be correct, but I cannot discuss it further since nestling mortality was not correlated with clutch size in this study. However, I think that an extended hatching period is more widespread than currently thought, and the lack of confirming data is a result of extrapolating hatching dates from the stage of development of the nestlings or the dates when the young leave the nest.

Both sexes participate in feeding the young, but females are capable of raising a brood alone, and feed the nestlings more frequently than the male in both monogamous and polygynous situations. The foraging technique employed by the adults agrees with Royama's (1970) observations that Great Tits also fed larger prey to their nestlings than they themselves were eating. The more efficient forager will generally be able to rear more offspring; thus by consuming smaller prey, or seeds while searching for larger prey for the nestlings, the adults optimize the energy gain per unit effort.

Role of the Male in Nesting

Verner and Willson's (1969) collation of the available literature indicates that the males of most monomorphic passerine species incubate the eggs to some extent, and often assist in building the nest. Such behavior was not observed in male Ipswich Sparrows. Using Knight's (1908) report, they list male Savannah Sparrows as actively participating in these phases of the nesting cycle. However the literature is full of conflicting reports and the results of many studies should be viewed critically. The studies of Wien's (1969) and Welsh (1970) report that male Savannah Sparrows are not active in nest building or incubation. My observations on the closely related Ipswich Sparrow agree with those of Wiens and Welsh. In view of the obvious conflicts in the literature, the whole subject of male involvement in the nesting cycle as summarized by Verner and Willson may be suspect. Any straight tabulation of all available studies, lacking a critical appraisal of the data involved, will be prone to erroneous generalizations. Again, only by persistent observation of well marked birds can one hope to discern the relationships involved.

The males began feeding the young 2 to 3 days after hatching, but they averaged fewer trips per unit of time than did the females. On two occasions in 1968, McLaren observed males possibly brooding newly hatched young, but he could not be certain. In 1969 and 1970, I found no evidence of such behavior. The fact that males never remained at the nest for more than one minute during the nestling period suggests that they normally do not brood the young.

The one polygynous male closely observed during the nestling phase, tended the nestlings as devoutly as did monogamous males. Verner and Willson (1969) concluded however that, on average, polygynous males gave less attention to the young than did monogamous males. But, they combined all cases of polygyny, and although this may be true for males involved in simultaneous polygyny such as Blackbirds (Orians, 1961), it should not be assumed for species employing successive polygyny. Asynchronous nesting by the females of polygynous males has been observed in several species (Smith, 1967; Verner, 1964; Zimmerman, 1966) and such nesting behavior should be adaptive since it allows the male to participate in feeding the young of each nest. Verner (1964) observed that male Long-billed Marsh Wrens did not commence feeding the young until they were at least 2 days old. A similar delay by male Ipswich Sparrows was also observed, and this behavior may be adaptive by increasing the degree of asynchrony between females. Verner also suggests that for multiple brooded species, this system limits males which feed the young to two females, and trigamy can only occur in cases where the males are not so parental. In the one case of trigamy observed in the Ipswich Sparrow in 1968, reduced parental behavior did occur. The male assisted in raising the broods of only two females, the third was essentially ignored. The suspected loss of a mate by this female may account for the trigamous situation and is considered to be irregular.

Polygyny

As mentioned above, bigamy is the rule for polygynous male Ipswich Sparrows. Nice (1941), Zimmerman (1966), and others who have observed polygyny, have generally assumed it to be accidental, and Lack (1968) writes "In many other passerine species, polygyny is very rare, showing that it is selected against". However, polygyny is prevalent in many species (von Haartman, 1969; Verner and Willson, 1969), and the various explanations for its occurrence have been discussed by McLaren (1972).

No male was consistently polygynous from year to year. Several status changes occurred between 1968 and 1970, and the status of any particular male appeared to be dependent on the location and size of his territory. Thus a polygynous male occupied essentially the same area as did two monogamous males in other years. With the status of the males being dependent on such circumstances, it is not surprising that the status of the females was similarly inconsistent from year to year. Second females of polygynous males of one year may have been first or monogamous females in another year, and thus cannot be assumed to be inherently inferior birds.

Obviously polygyny is advantageous for the males involved, since their production was significantly higher than that of monogamous males. As pointed out in the results, the level of success per nest was not significantly different for females of monogamous or polygynous matings, and thus it is doubtful that the success at individual nests suffered due to a polygynous situation. The difference in the total number of young produced by monogamous females, or first females of polygynous males, and second females is due only to the different numbers of nests initiated.

Hamer (1922) suggested that when a female is ready to mate, she will do so with the first available male. Although this may be too broad a generalization, it is doubtful that a female would delay mating for any prolonged period of time while the territorial male courts another female, especially if there are other available males in adjacent territories. Yet Verner (1964) and others have observed polygynous situations while males remain unmated on adjacent, but not necessarily inferior, territories. It appears evident that these second females arrive on the breeding grounds later than most monogamous or first females, and the fewer nests initiated by them are a consequence of this late arrival, not of being the second female of a polygynous male.

Like most polygynous species (see Lack, 1968; von Haartman, 1969), the Ipswich Sparrow practices successive bigamy, in which each female and her brood can receive some attention from the male. Our limited observations on feeding suggest that polygynous males are as attentive to the nestlings as are monogamous males. Thus the commonly held assumption that male participation at the nest is reduced in a polygynous regime, and Lack's (1968) argument that polygyny can only exist when there is an adequate food supply for the female to feed the young alone may be invalid.

The increased recruitment for polygynous males should result in strong sexual selection for polygyny among males, and my data suggest that Verner and Willson's (1966) requirement that the females cannot suffer disadvantage by polygyny, is also fulfilled. The first females of polygynous males commenced nesting on the average 4.1 days and 5.3 days earlier than monogamous females in 1968 and 1969 respectively, and generally produced more young (Table 13). If there is any expression of "superiority" or "dominance" among bigamous males, it may lie in their tendency to secure females earlier than monogamous males. The later second females may gain advantage by nesting in the territory of a polygynous male, if that territory is superior in some requisite to adjacent territories, even in inferior habitats.

Site Faithfulness

Both males and females attempt to return to their previous territory or nesting area. During the study, between 29% and 52% ofthe males, and 32% to

41% of the females returned to the Main Area in the following year, and several for 2 or more consecutive years. Such observations are common in passerine species, and Nice (1937) recorded a male Song Sparrow returning for 7 consecutive years.

If prior knowledge of an area conveys an advantage in reproduction or survival, then homing to a former nesting area should be adaptive in function. Homing must be equally important for birds nesting in inferior habitats, since several birds returned to the Sparse Area in 1971. A tendency to return to a previous nesting area could allow otherwise less fit birds to direct their efforts into reproduction rather than expending energy trying to secure a new place by competing with superior birds.

This does not necessarily mean that all birds nesting in inferior areas are genetically less fit. It is well known that inexperienced birds breeding for the first time have difficulty in competing with experienced birds (Lack, 1968; Immelman, 1971) for territories or nesting sites. My data suggest that the territories of birds which do not return are claimed by inexperienced birds. At low population densities the most fit first-year birds would breed in the preferred areas. But in years of high population density even relatively fit, but inexperienced, males and females would be forced to breed in inferior habitats. In subsequent years, these birds could return to the inferior habitats, thus reducing the genetic fitness differential between the different areas.

Concept and Function of Territory

In this study the territory was generally observed as "home range", but approximated Noble's (1939) definition that "territory is any defended area". For our purposes, the fluctuations which occurred in territory size during the breeding season, or the selective utilization of specific sectors of the territory, were unimportant, although such fluctuations have been documented by others (Odum and Kuenzler, 1955; Stenger and Falls, 1959; Weeden, 1965). Although "chance" habituations to different parts of a territory may be involved, its size during the various phases of the nesting cycle may be determined by the "defensibility" of the area, conceived in terms of the time and energy budgets of the male. Brown (1964) has eloquently summarized this idea of the economics of site-dependent aggression as a behavioral response to competition for requisites in short supply. He believes that each male would find a balance between the advantages and disadvantages of such defense which would maximize his reproductive success. This seems like a sound principle, yet in order to demonstrate the function of a territory we must discover what is really being defended.

Nice (1941) and others have proposed several types of territories on the basis of the activities occurring within the territorial boundary, and many authors have then assumed that these activities must be adaptive in function (see Hinde, 1956). Although some of these activities may be important functions of territoriality to some species in some circumstances, they are unlikely to be generally of selective advantage, and many are likely to be a consequence of rather than an adaptive function of territory.

The resources most often claimed to be defended are food supply and nesting sites. But many species co-inhabit areas and have superimposed territories (Wiens, 1969), and to some extent may utilize the same or similar resources. If food supply is dependent on bird density, it may in principle be worth defending. But Ipswich Sparrows often gather food outside their territories, and allow females and the young of adjacent territories, and other wandering juveniles to feed freely within their territorial boundaries. They do not seem to be defending a food supply. Defense of potential nesting sites is another, perhaps more probable function of their territoriality, but such a system requires that only the nest sites be defended, as observed in many colonial species.

McLaren (1972) has strongly criticized arguments that limiting, spatially dispersed resources are the ultimate objects of defense on the basis that the male bird defends a larger area than would seem necessary for the defense of resources. He argues "that polygyny is more prevalent among birds than generally accepted, and that it is a general and sufficient selective force for the evolution of territoriality...". The present thesis agrees with McLaren's views and thus I will attempt to develop the hypothesis wirh the data collected on the Ipswich Sparrow.

Many male and female Ipswich Sparrows arrive on the breeding grounds at the same time in the spring. The females select a suitable nesting site, many returning to their nesting area of previous years, and mate with the first available male. The early males initially claim a much larger area than they subsequently retain. Slowly parts of this area are relinquished to newly arrived males until it reaches a "defensible" size. Such strategy could be reproductively advantageous for the early males. Since females choose a nesting site, not a male, a male's chances of acquiring a female early would be increased if he held a large area. He could then adjust his territorial priorities to retain her nesting area within his territory. This suggestion coincides with Weeden's (1965) observations on the Tree Sparrow. He suggested that the males have an area of high activity which is inviolate and always contains the female's nest, and an outer area which is less extensively utilized and may represent the expendable portion of his territory. Tinbergen (1957) described this "defensible" size as a rubber disc which became more difficult to compress as it became smaller. The degree of compression obviously would vary from year to year according to the population density. According to Brown's (1964) site-dependent economics, the final size each year would be determined by the additional expenditure of energy required by newly arriving males to gain and defend a territory in that area weighed against the possible disadvantage of nesting elsewhere.

The possibility of obtaining a second female once the first female is nesting is sufficient reason to maintain the full territory size. Nice (1943) and others have observed a resurgence of territorial defense and song, and Morse (1967, 1970) observed that warblers have two types of song patterns, one associated with the presence of a female, the other with males. Both types were vocalized more frequently in densely populated areas, but during pairing the female-associated song decreased in the frequency of occurrence, then subsequently increased once incubation began. Such observations suggest that the male is still soliciting mates.

The acquisition of a second Ipswich Sparrow female however, appears to depend more on the territory size and disposition of the female than on the male song and display. There is evidence in some species (see Armstrong, 1955) that polygynous males may have larger territories than monogamous ones, but there is also considerable negative evidence (Orians, 1961; Verner, 1964; Welsh, 1970). Our data suggest that polygyny is a function of territory size only at relatively high population densities. At lower densities, such as on the Main Area in 1968, the mean territory

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size of polygynous and monogamous males were not significantly different, the first nests of the females were more nearly randomly placed, and polygynous situations occurred by chance. In the inferior nesting habitat of the Sparse Area, the population density would always be relatively low, territories large, nests placed randomly, and polygyny would always be due to the nesting site preferences of the females. At the higher densities in 1969 and 1970 on the Main Area however, the first nests of the females were more regularly dispersed, and the territories of polygynous males were significantly larger than those of monogamous males. This indicates that territory size can influence the degree of polygyny.

In such a system the females disperse themselves, perhaps for reasons similar to those of Brown's (1964) site-dependent economics. Orians (1971) has also suggested that a spacing pattern of nests of species with altricial young should occur, but believes it to be correlated with the spatial and temporal distribution of food resources. However, nesting sites, or a combination of several resource factors could cause such spacing.

Although few authors have considered this aspect of bird behavior in detail, several (reviewed in von Haartman, 1969; Smith, 1967; Welsh, 1970) have observed aggression, and the subdivision of the territory by the females of polygynous males. Presumably some form of competition, manifested as either overt aggression, or subtle mutual repulsion, must exist between females of most species for the preferred nesting sites. Aggression was seldom observed between female Ipswich Sparrows, thus I suggest that a subtle mechanism of repulsion could take the form of active avoidance of already occupied nesting areas by newly arriving females. Such avoidance was observed in the case of 8 returning females whose former nesting areas were already occupied. These later females subsequently nested elsewhere.

The implication of this hypothesis, of course, is that the males exert little control over the female's nesting activities. That this is true for the Ipswich Sparrow is suggested by the frequency with which females crossed territorial boundaries when re-nesting. On the Main Area in 1968 and 1969 such movements usually resulted in the female changing mates and suggests little or no attachment to the male or his territory. Similar female movement between nests occurred on the Sparse Area, but in all cases the males adjusted their territorial boundaries to retain their mates. The fact that such female movements occur should be sufficient cause for the males to maintain maximum territory size. Females of polygynous males appeared to cross territorial boundaries more frequently than monogamous females and may indicate a greater degree of repulsion in polygynous situations. McLaren (1972) found that the mean distances between successive nests of second and third female Ipswich Sparrows were significantly less than for first or monogamous females and suggested that the second females could have had their choice of nest sites circumscribed by the presence of the first female. I agree with McLaren, but suspect that the choice of nest sites are circumscribed by the presence of previously settled females in adjacent territories as well as by the first female on the territory, since any repulsion mechanism would function between all females in an area, not just between females in polygynous situations.

Thus I conclude that one of the prime adaptive functions of breeding territory is polygyny. Males try to defend as large an area as economically feasible to enhance the chances of getting a female early in the season, and retain this size for most of the season to increase the chances of obtaining a second mate and to retain females with their territories during subsequent nesting.

Recruitment and Population Regulation

Since Howard's (1920) claim that population density was regulated by territoriality, many authors have assumed that territoriality limits population growth, since the males defend more area than required for their resource needs. Lack (1954, 1966) has de-emphasized the role of territorial behavior as a limiting factor for breeding densities, although Tompa (1962) has shown that territoriality can be a limiting factor at high densities in localized populations of Song Sparrows.

For such a concept to be generally applicable, a portion of the population must be "non-breeders", but Brown (1969a) reviewed this subject and noted that " the prevention of females from breeding by territorial behavior has only very rarely been demonstrated in significant numbers". Brown also contested much of the evidence concerning non-breeding populations as being based on unsubstantial inquiry. Our observations on the

Ipswich Sparrow indicate little or no evidence of a non-breeding portion of the population. The highest breeding density on the Main Area occurred in 1969. Yet in both 1968 and 1969, the territory and female of males which disappeared during the breeding season, were claimed by adjacent males. Granted in 1969 a new territory was created amongst established ones, but this does not necessarily indicate a non-breeding population. First, the fact that the territories on the Main Area were "compressible" in this high density year indicates that the minimum territory size for successful reproduction had not been reached, a factor considered necessary if some birds are to be excluded from breeding. Second, observations in 1971 on the Sparse Area indicate that the arrival of birds on the nesting grounds occurs over a prolonged period. Thus birds claiming vacated territories are as likely to be late arrivals as "non-breeders" or "floaters".

Furthermore, Brown (1969b) has shown that when all possible areas are not saturated, the effect of territoriality may actually maximize the total production of the population. The production per breeding pair would obviously be lower in the marginal habitats than the rich ones but territoriality may prevent overcrowding and reduced output from the favorable habitats, and successful reproduction in both habitats should enhance competition for territories in both favorable and unfavorable habitats.

Orians (1971) has taken a similar line, suggesting "that birds should settle at those densities that will equalize their fitness in all of the habitats occupied". Orians relates this dispersion to food supply although in the final analysis, dispersion is probably related to a combination of resource requisites. But the fitness may not be equalized if net reproduction is considered, since in unfavorable habitats the resource requisites may be more limiting early in the season. However, our observations generally support Orians' hypothesis. The territories on the Sparse Area are much larger, which may equalize the resources available on the smaller Main Area territories. If so, then the relative fitness on the two areas may tend to be equalized, as suggested by the comparable reproductive success on a per nest basis and the degree of polygyny observed.

In addition to the potential effect of territoriality of excluding some individuals from breeding, the reduction in territory size at high population densities could also depress reproduction. Lack (1966) observed a reduction in clutch size of the Great and Coal Tits and Kluijver (1951) also observed a lower percentage of female Great Tits attempting second broods at high densities. They attributed the depressed reproductive effort to food abundance, although the expected increase in territorial conflicts at high population densities could be as important in reducing the energy available for reproduction. However, as Tompa (1962) observed for Song Sparrows, high densities do not necessarily cause lowered reproductive success. Such density effects were not apparent for the Ipswich Sparrow although it is quite possible that the breeding population did not become sufficiently large to cause depressed reproduction. The highest density of birds occurred on the Main Area in 1969, but no significant reduction in clutch size was observed. The reduction in third clutches, as compared with other years, has already been attributed to weather effects and the high success rates do not suggest density dependent effects.

SUMMARY

1. The territories and breeding success of 72 male and 89 female Ipswich Sparrows were examined from 1968-70. All territorial birds were color-banded, and plumage-marked for identification purposes. In 1971 additional territorial work was conducted and a count of the total number of adults on Sable Island was made. From 1968-72 selected plots were censused for population estimates.

2. A rich habitat (8.5 ha.) was examined from 1968-70; in addition, a sparse dry habitat (15 ha.) was examined in 1970 for a consideration of habitat effects.

3. Birds arrived in the area from mid-April to early May on the Main Area and many females were incubating clutches by the end of May. On the Sparse Area territorial establishment occurred later and some females did not complete their first clutches till late June.

4. Weather appeared to have a definite effect on breeding, affecting the commencement of nesting, and the duration of the nesting season. This effect was most notable in 1969 with poor weather and a low level of production.

5. A total of 98 territories was examined from 1968-71. Territories on the Sparse Area (1970: 1.09 ha.; 1971:1.18 ha.) averaged over three times the size of the Main Area. On the Main Area, territories were significantly larger in 1968 (0.42 ha.) than in 1969 (0.30 ha.) and 1970 (0.31 ha.) but not in 1971 (0.37 ha.). The number of males on the study areas appeared to be related to overall population size.

6. Some of the males are polygynous, but the amount of polygyny varied from 47% in 1968 to 5% in 1970. On the Sparse Area in 1970, 23% of the males were polygynous. Polygynous males have significantly larger territories only at certain population densities; in other years all territories are large enough to accomodate more

than one female.

7. One male had 3 females but usually the maximum is two. Successive polygyny is practised, with the second female commencing to nest after the first has begun incubating the eggs. Females built the nest and incubated the young alone, but both parents fed the young. The asynchronous nesting allowed the male to assist in feeding the young of all nests without division of effort.

8. Females appear to select a nesting site rather than a male directly. At low population levels, the females disperse randomly such as in 1968, but at higher levels such as in 1969 or 1970, they disperse in an even, or non-random pattern. Thus at the higher population levels, with the accompanying small territory size, to be polygynous a male's territory will have to be large enough to contain 2 repulsed females - significantly larger than those of monogamous males.

9. Nests were built of grass and other materials, and were well concealed on the ground. Although few predators exist on Sable Island poorly concealed nests produced fewer young than well concealed nests.

10. A total of 232 nests were found from 89 females. There was no significant differences in the number of nests initiated per female between years, study areas, or mating status of the female.

11. As many as 4 clutches were brought off during the nesting season. First females of polygyncus males and monogamous females generally attempted at least 3 nests, but second females brought off a maximum of 2 nests.

12. Usually one egg a day was laid after completion of the nest. Clutch size ranged from 2 to 6 eggs, with 4 and 5 eggs being common. The size of the clutch and the size of the eggs in the clutch, decreased toward the end of the season.

13. Incubation time ranged from 9-15 days and averaged 12.5. Over 85% of the eggs hatched in all years and areas. Nestling time ranged from 10-12 days and averaged 10.9. Nestling success was also high with over 77% of the eggs hatching and leaving the nest as juveniles in all years.

14. Polygynous males produced significantly more fledgings than monogamous males in all years (15.5 as opposed to 9.7). First females of polygynous males and monogamous females had similar production levels in all years. But second females produced considerably fewer fledgings than first and monogamous females.

15. The lower production by the second females of polygynous males is due only to fewer nests initiated than the other females, since reproductive success per nest is similar for all three classes of females.

16. Population estimates indicated that the breeding population was low in all years, ranging from 2042 to 4294. Production was high however, and the autumn population size ranged from 8422 to 14310 birds. Winter estimates in 1968 and 1970 were 755 and 627 respectively.

17. The percentage of adults returning in subsequent years varied from 24-42% on the study areas, and is comparable to the percentage returns (27-42%) estimated for the whole population. Very few banded juveniles returned to the study areas, nor were they seen elsewhere.

18. The concept of territoriality and its relation to polygyny was discussed. It was concluded that territoriality is due to sexual selection in males as a result of males attempting to maximize their reproductive output. As such they try to secure as large a territory as possible to increase the possibility of obtaining more than one female. Since females select a nesting site rather than a mate, a large territory increases the chance of more than one

female finding a suitable nesting site there.

19. Since females do not appear to suffer from a polygynous relationship, there appear to be no forces selecting against polygyny. Also it may be advantageous for some females to be second females on superior territories since they may still be more successful than being a monogamous female on a poor territory.

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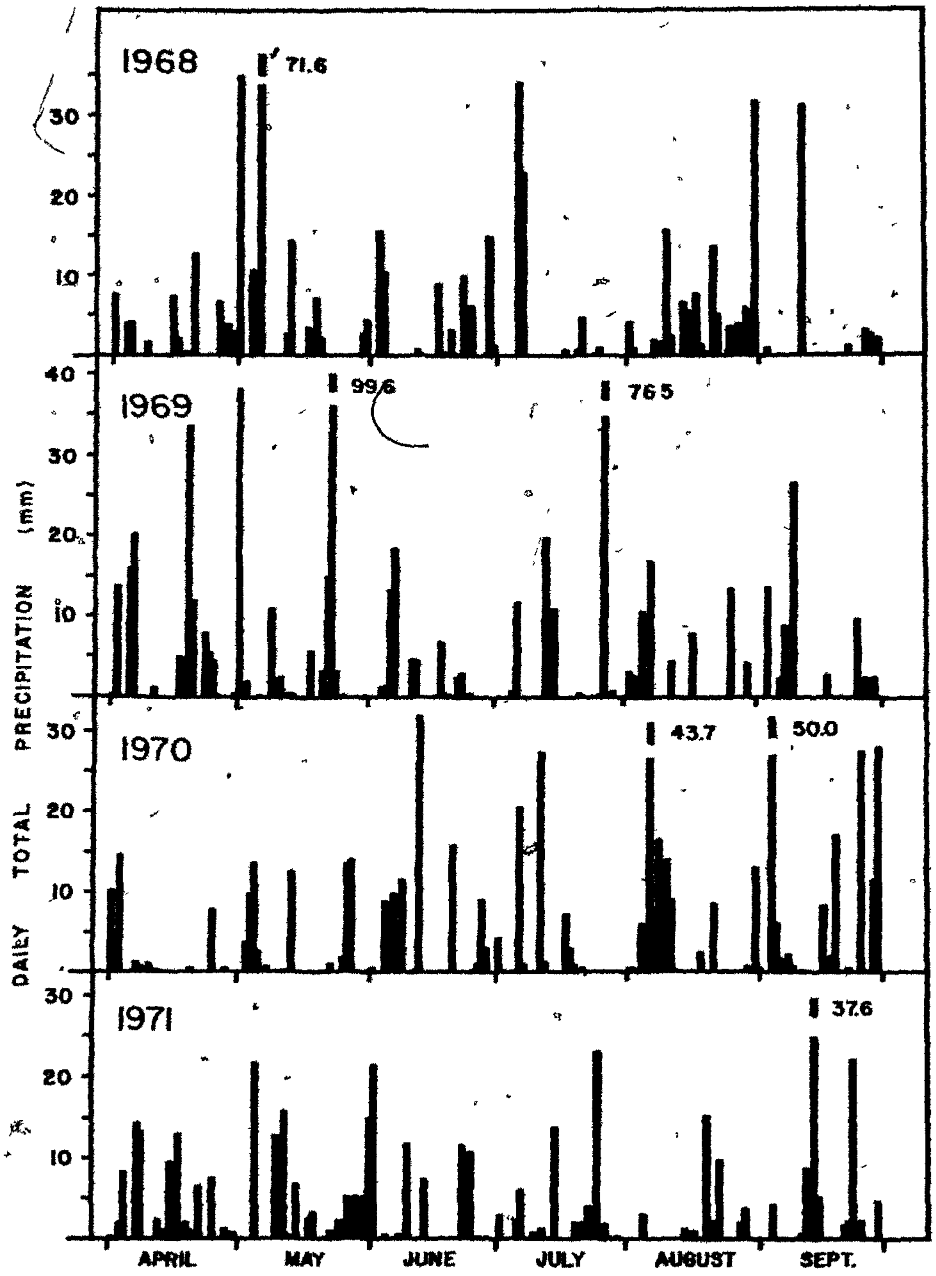
Appendix 1. Precipitation on Sable Island given as daily totals (mm) between April and September from 1968 to 1971.


1968
71.6
1969
99.6
76.5
1970
43.7
50.0
1971
37.6
DAILY TOTAL PRECIPITATION (mm)
0
10
20
30
40
APRIL
MAY
JUNE
JULY
AUGUST
SEPT.

Appendix 2. Successive returns of territorial birds to the Main Area are presented with reference to the mating system (polygamy indicated by *) and territory position (return to essentially the same territory in subsequent years indicated by +). Reproductive success is also presented as the number of young to leave the nest. For comparison the data for their first year as known territorial birds are also given. Data on mating and reproductive success are available only for 1968-70. The success of male 37 was not followed in 1969, but he occupied essentially the same territory in 1970. Females 14 and 46 nested adjacent to, but outside of, the study area in 1969 and 1971 respectively, so no mating or success data are available.

	1968	Number of Young	1969	Number of Young	1970	Number of Young	1971	1972
Males banded in 1968	1	14	1*+	20	1+	13		
	3	9	3	7				
	4*	16	4*	13	4+	11		
	6*	12	6+	7	6+	13		
	12	12	12	8				
banded in 1969			17*	10	17	12		
			22*	4	22*+	16	22+	
			23	6	23+	13	23+	
			25	8	25+	8	25+	25+
			26	9	26+	8	26+	
			27	8	27+	11		
			29	9	29	12		
			32	10	32+	17	32+	
			37	-	37+	8		
							41	41+
Females banded in 1968	1	14	1*+	8				
	3	9	3	9				
	6*	4	6*	0				
	8*	9	8+	7	8+	5		
	11*	8	11*+	9				
	13	9	13*	8				
	14	11	14	-	14	11		
	15*	8	15+	8				
	18	10	18*	7				
banded in 1969			23*	12	23+	13		
			24	7	24+	12		
			26*	5	26	11	26+	
			27*	7	27	12		
			28*	6	28+	17		
			30*	3	30+	16	30+	
			36	8	36	13	36+	

Appendix 2 (con't).

	1968	Number of Young	1969	Number of Young	1970	Number of Young	1971	1972
Females (con't)								
banded in 1969			39	8	39	13		
			41	7	41	7		
banded in 1970					46	8	46	46
					47	8	47+	47+
					50	8	50+	
					52	8	52+	52+

Appendix 3. The data used, and the results, of chi-square tests comparing the number of nests initiated by females using the null hypothesis that there is no difference between classes on the average number of nests initiated per female. The production of two females which, in 1969 switched mating systems, are not included in the comparisons.

A. The number of nests per female per year.

	1968	1969	1970	
Number of females	22	29	22	$\chi^2 = 2.793$
Number of nests	54	67	67	df. = 2, $p > 0.1$

B. The difference between the Main and Sparse Areas in 1970.

	Main Area	Sparse Area	
Number of females	22	16	$\chi^2 = 0.269$
Number of nests	67	44	df. = 1, $p > 0.5$

C. The difference between monogamous and polygamous females.

1968	Polygamy	Monogamy	
Number of females	14	8	$\chi^2 = 0.461$
Number of nests	32	22	df. = 1, $p > 0.1$
1969			
Number of females	12	13	$\chi^2 = 0.033$
Number of nests	29	30	df. = 1, $p > 0.5$
1970 - Sparse Area			
Number of females	6	10	$\chi^2 = 0.218$
Number of nests	15	29	df. = 1, $p > 0.5$

D. The difference between first and second females in polygynous matings.

1968	First	Second	
Number of females	7	7	$\chi^2 = 1.125$
Number of nests	19	13	df. = 1, $p > 0.1$
1969			
Number of females	6	6	$\chi^2 = 0.862$
Number of nests	17	12	df. = 1, $p > 0.1$
1970 - Sparse Area			
Number of females	3	3	$\chi^2 = 0.600$
Number of nests	9	6	df. = 1, $p > 0.1$

Appendix 3 (con't).

E. The difference between monogamous females and first females of polygynous matings.

1968	First	Monogamous	
Number of females	7	8	$\chi^2 = 0.001$
Number of nests	19	22	df. = 1, $p > 0.9$
1969			
Number of females	6	13	$\chi^2 = 0.477$
Number of nests	17	30	df. = 1, $p > 0.1$
1970 - Sparse Area			
Number of females	3	10	$\chi^2 = 0.006$
Number of nests	9	29	df. = 1, $p > 0.9$

F. The difference between monogamous females and second females of polygynous matings.

1968	Second	Monogamous	
Number of females	7	8	$\chi^2 = 1.250$
Number of nests	13	22	df. = 1, $p > 0.1$
1969			
Number of females	6	13	$\chi^2 = 0.186$
Number of nests	12	30	df. = 1, $p > 0.5$
1970 - Sparse Area			
Number of females	3	10	$\chi^2 = 0.708$
Number of nests	6	29	df. = 1, $p > 0.1$

G. The difference between monogamous females at the Main and Sparse Areas in 1970.

	Main Area	Sparse Area	
Number of females	20	10	$\chi^2 = 0.050$
Number of nests	61	29	df. = 1, $p > 0.5$

Appendix 4. Descriptions are given, and the importance of the vegetation categories are discussed. The numbers of birds on the census areas during the spring and autumn censuses from 1967 to 1972 are given along with the methods used to estimate the population size.

Vegetation Categories

In comparing the 1971 full island census subdivisions with the subsequent analysis, the most common discrepancy during the island census was in combining the "heavy beach pea" areas with "heavy marram grass" areas containing substantial quantities of beach pea. In such cases, the census values were prorated on the basis of the distribution found elsewhere in those categories.

Marram grass (A. breviligulata) is the most abundant plant on the island and has been divided into two classes: heavy and sparse. Areas of heavy marram grass contain less than 20% beach pea (Lathyrus japonicus) and other forbs. The lack of ground litter in the spring because of removal by winter winds and grazing horses may delay the commencement of nesting in many grassy areas; the vegetation cover appears to be adequate for nesting in mid-summer. Few birds are found in the areas of "sparse marram grass". These areas are usually newly colonized dunes or areas frequently inundated with sand. Few plants other than marram grass occur there.

The "composite" category refers to the most consolidated areas, often around ponds or in low areas. These areas contain a mixture of shrubs, forbs, grasses, sedges, and clumps of heath plants. The subdivision into sparse and heavy groupings is somewhat arbitrarily ascribed to the cover. In the "heavy composite" areas, the shrubs are usually in small clumps, surrounded by forbs and grasses. This provides excellent nesting habitat for the birds. Early nesting is possible since the consolidated areas retain litter over the winter and, with the woody shrubs, provide concealed nesting sites. The sparse areas have considerable amounts of exposed sand, but also have small clumps of dense vegetation which provide good nesting cover.

Although beach pea (L. japonicus) is abundant on the island, there are relatively few areas where it is the dominant plant. Since beach pea is not prominent until July, it is of doubtful value to breeding birds. It appears, however, to be an important congregating place for the birds in the autumn.

The "juniper" category refers to areas consisting of the two species of juniper, and crowberry (Empetrum nigrum). There are few relatively pure "juniper" areas, but most of the "composite" areas contain small patches of the junipers or crowberry. The birds are abundant in these "juniper" areas, but tend to occupy the peripheral portions. The center of such areas contain few birds. The dense growth provides concealed nesting sites, but the lack of plant diversity may limit other nesting requisites such as food abundance or availability.

Seaside sandwort (Arenaria peploides) is abundant only at the eastern end of the island. Although of little importance to the birds, it is the first colonizer of the shifting sand deposited on the eastern spit. This category is not considered in the population estimates since only 2 birds were found there.

Census Areas

Modifications were made in the size and location of some census areas since 1967 as knowledge of the vegetation structure of the island increased. The position of the 1972 plots are shown in Fig. 1 (the "ponds" and the "paddock" plots were located between the Main Study Area and the Meterological Station). Table 17 presents the census results. From 1968 to 1972, spring and autumn censuses were taken for estimates of the number of breeding birds and of production. Early winter censuses were also taken in 1968 and in 1970.

The most dramatic numerical increase in the autumn occurred in plot 1 which measured 13.7 hectares and appeared to be a congregating place for the birds at that season. Beach pea was a predominant plant in the area late in the summer (Table 18) and may have been a prime reason for this concentration of birds. Generally census areas with an appreciable beach pea component exhibited greater numerical increases in birds than did the other vegetation types. Beach pea is not a dominant plant form until July. At this time it is tall and dense and probably harbors more readily available food, with fewer territorial defenders, than do the more stable areas.

Preferred nesting areas such as the Main Study Area (plot 14) were not preferred in the autumn and did not exhibit large increases of birds.

Table 17. Summary of census values obtained from selected plots on Sable Island between 1967 and 1972. The spring censuses were conducted between May 25 and June 9, except in 1971 when it was conducted during the full Island census. The autumn censuses were conducted between August 21 - 29 except in 1971 and 1972 when they were conducted between September 12 - 21. The winter censuses were conducted only in 1968 and 1970, from November 3 - 4 and 19 - 30, respectively. In the autumn of 1971, four new plots were added, two were dropped (the paddock and the ponds), and the size of area 12 was enlarged. The area of each census plot is given in hectares.

		Spring						Autumn					Winter	
Plot	Area	1967	1968	1969	1970	1971	1972	1968	1969	1970	1971	1972	1968	1970
1	13.7	32	29.8	27	17	12	27	190	159.5	171	71	48	12.5	6
2	7.6	24	14.5	10	15	15	19	93	48	110	149	73	2	6
3	3.2	11	13	11	7	10	7	24	28	56	49	28	0	1
4	4.1	10.5	7.8	4	6	9	8	53.5	25	77	147	93	1	0
5	3.6	8	6.8	15.5	8	8	6	24.5	21.5	13	92	54	0	0
6	3.9	—	—	—	—	—	4	—	—	—	16	7	—	—
7	2.6	—	—	—	—	—	1	—	—	—	13	23	—	—
8	3.2	—	—	—	—	—	6	—	—	—	54	18	—	—
9	7.1	—	—	—	—	—	12	—	—	—	53	38	—	—
10	5.5	—	9	8	7	7	8	21	27	42	71	45	3	0
11	10.4	—	9	9	8	15	8	26	34	16.5	41	33	0	0
12	(2.1)(4.9)	14.3	8.5	11.5	8.5	9	18	32	9.5	15	12.5	7	0	0
13	4.9	8	4.3	4	3	4	4	48	16	70	30	48	10	11
14	3.5	—	12	26	24	19	16	34	25.5	39.5	16	10	2	2
15	2.9	—	11	6	5	10	4	19	9	16	31	60	3	3
16	4.1	—	7.3	13	10.5	10	11	28	18	36	50	56	8	7
paddock	1.1	5.7	5	11	6.5	13	—	6.5	13.5	21	—	—	0	0
ponds	1.1	12	11.8	18	8	13	—	6.5	8	37	—	—	4	2

Table 18. The census plots are subdivided into the vegetation categories used for the full island census. The expected number of birds was calculated by multiplying the respective areas by the full island estimate of the number of birds per hectare, in each vegetation category. The expected proportion of birds was derived from the expected number. This proportion was used to subdivide the census values to estimate the whole island distribution and production of Ipswich Sparrows.

Plot	Vegetation Category	Area (ha)	Expected Birds	Expected Proportion Birds
1	56% pea	7.7	10.6	0.624
	44% heavy marram	6.0	6.4	0.376
2	50% pea	3.8	5.2	0.559
	50% heavy marram	3.8	4.1	0.441
3	33% pea	1.1	1.5	0.405
	67% heavy marram	2.1	2.2	0.595
4	32% pea	1.3	1.8	0.439
	47% heavy marram	1.9	2.0	0.488
	21% sparse marram	0.9	0.3	0.073
5	25% heavy marram	0.9	1.0	0.143
	40% sparse marram	1.4	0.4	0.057
	35% heavy composite	1.3	5.6	0.800
6	100% sparse marram	3.9	1.2	1.000
7	100% heavy marram	2.6	2.8	1.000
8	100% juniper	3.2	26.0	1.000
9	32% heavy marram	2.3	2.5	0.108
	68% heavy composite	4.8	20.7	0.892
10	100% heavy marram	5.5	5.9	1.000
11	18% heavy marram	1.9	2.0	0.080
	35% heavy composite	3.6	15.6	0.624
	47% sparse composite	4.9	7.4	0.296

Table 18 (con't).

Plot	Vegetation Category	Area (ha)	Expected Birds	Expected Proportion Birds
12	100% juniper	(2.1)(4.9)	(17.0)(39.7)	1.000
13	43% pea	2.1	2.9	0.617
	24% heavy marram	1.2	1.3	0.277
	33% sparse marram	1.6	0.5	0.106
14	100% heavy composite	3.5	15.1	1.000
15	100% heavy marram	2.9	3.1	1.000
16	78% pea	3.2	4.4	0.815
	22% heavy marram	0.9	1.0	0.185
paddock	100% juniper	1.1	8.9	1.000
ponds	100% heavy composite	1.1	4.8	1.000

"Juniper" areas which generally have the greatest density of birds in the spring (plots 8, 12, and the "paddock") also generally exhibited the smallest numerical increases in the autumn. Although the counts from plot 8 in 1971 seem to be contradictory to the above, the census in 1971, and 1972, were taken a month later than in previous years and the relative distributions on most census plots differed from those in other years. At this late date in 1971 and 1972, the birds may have been flocking prior to migration and their movements could have greatly affected the bird counts. Migrating Ipswich Sparrows began arriving on the Nova Scotia mainland in late September and the peak of migration occurred in mid-October (unpublished observations) in 1971.

The two November counts indicated that a small proportion of Ipswich Sparrows remain on the island over the winter. The majority of birds were found on plots 1, 2, 13, and 16. All of these plots were similar in that each possessed one or more central depressions where the birds were concentrated and probably were protected from the wind. It is doubtful that many of these birds survived. An early spring census by D. Welsh and I.A. McLaren (March 28 to April 1, 1972; not included in Table 17) gave a total count of 6 Ipswich Sparrows on all the plots censused in the fall of 1971.

A problem involved in taking counts early in the breeding season is that the birds on the census plots may be transients. If so, the estimates of the breeding bird population may not be valid. Consequently, in late April and again in mid-May, 1971, several days were spent on 12 census plots to determine the number of territories on each (plots 6, 7, 8, and 9 were chosen in the fall of 1971, and the "ponds" and "paddock" plots were being discarded so they were not examined). To avoid possible bias due to prior knowledge of bird numbers, the territorial work was conducted prior to the full island census. There were more territories on many of the census plots in May than in April. Census plots 1, 11, 13, and 15 showed the greatest differences in the number of territories, and in the density of vegetation, between April and May. A total of 62 territories were found on the census plots in May, corresponding to a total of 128 adult birds counted during the full island census in June and July. On most plots, the number of birds was equal to twice the number of territories, plus or minus one bird. On plot 15, the difference was 2 birds. Given the error inherent in any census technique, we can be reasonably confident that the count totals of the spring censuses are of territorial males and their females.

Population Estimates

Nine census areas contained more than one of the vegetation categories. Since the birds were unevenly distributed in these various categories, it was necessary to subdivide the census values to obtain the overall island distribution. On the assumption that the breeding birds would distribute themselves in similar proportions every year, the expected proportion of breeding birds found in each vegetation category on the census plots (Table 18) was calculated from the 1971 breeding bird distribution (Table 15).

It is possible that the bird distribution in the autumn differs from that of the breeding birds, especially since the birds appear to congregate in areas of "beach pea" during that season. The average number of birds per ha. in the autumn were calculated for the "heavy marram", "heavy composite", and "juniper" areas from the census plots containing only one vegetation category (Table 18). Unfortunately no plots contained only "beach pea", "sparse marram", or "sparse composite". However, four plots (1,2,3, and 16) contained only "beach pea" and "heavy marram" so the average number of birds per ha. in the "beach pea" was calculated using the known averages for "heavy marram" and the census values. Similar calculations could not be made for the "sparse marram" and "sparse composite" areas, so in these cases, the relative concentrations derived for the breeding birds were used for the autumn population estimates. In 1971 a "sparse marram" census plot was added and the number of birds per ha. in that category was calculated directly from the autumn census results.