

THE BREEDING BIOLOGY OF THE SAVANNAH SPARROW,
PASSERCULUS SANDWICHENSIS (GMELIN),
AT SASKATOON, SASKATCHEWAN.

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by
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TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS	i
TABLE OF CONTENTS	ii
LIST OF FIGURES	vi
LIST OF PLATES	viii
LIST OF TABLES	ix
1. INTRODUCTION	1
1.1 Introductory Remarks	1
1.2 Scope and Purpose	3
2. ENVIRONMENT	5
2.1 General Description	5
2.2 Summer Climate	6
2.2.1 Source of information	6
2.2.2 Temperature	6
2.2.3 Precipitation	10
2.3 Study Area and Habitats	10
2.3.1 Description and history	10
2.3.2 Geology and soils	12
2.3.3 Vegetation	13
2.4 Fauna	19
2.4.1 General	19
2.4.2 Competitors	19
2.4.3, Predators	20
3. METHODS	22
3.1 Census	22

3.2 Breeding Cycle	23
3.2.1 General	23
3.2.2 Nest location	24
3.2.3 Nest information	24
3.2.4 Timing of the breeding cycle	25
3.2.5 Nesting success	25
3.3 Trapping and Banding	26
3.4 Behavioral Observations	27
3.5 Growth and Development	27
3.6 Habitat	28
4. BREEDING CYCLE	29
4.1 Arrival	29
4.1.1 Chronology and pattern	29
4.1.2 Reproductive condition on arrival	31
4.2 Reproductive Biology	34
4.2.1 Chronology of the cycle	34
4.2.2 Clutch size	37
4.2.3 Incubation period	38
4.2.4 Hatching	38
4.2.5 Fledging	40
4.3 Breeding Behavior	41
4.3.1 General	41
4.2.3 Prenuptial stage	42
4.3.3 Preliminary stage	44
4.3.4 Building	45

4.3.5 Laying	47
4.3.6 Incubation	47
4.3.7 Care of young in the nest	48
4.3.8 Care of young out of the nest	49
4.4 Post-Breeding Dispersal	50
4.5 Breeding Success	52
4.5.1 Success	52
4.5.2 Causes of loss	54
4.5.3 Effects of cowbird parasitism	55
5. GROWTH AND DEVELOPMENT	61
5.1 Description of the Young	61
5.1.1 Plumage development	61
5.1.2 Juvenal plumage	63
5.1.3 Soft parts	67
5.2 Growth	70
5.3 Behavioral Development	79
5.3.1 Vocalizations	79
5.3.2 Fear and escape	79
5.3.3 Begging	80
5.3.4 Motor development and coordination	80
6. TERRITORY	82
6.1 Territory Establishment	82
6.2 Territory Size and Population	84
6.2.1 Territory size	84
6.2.2 Population	84

6.3 Territory in Relation to Reproduction	87
6.3.1 Nest placement	87
6.3.2 Territory and feeding	90
6.4 Territorial Behavior	92
6.4.1 Seasonal pattern	92
6.4.2 Components of territorial behavior	94
6.4.3 Patterns of territorial behavior and displays	96
7. HABITAT SELECTION	102
7.1 Territory and Habitat	102
7.2 Nest Placement	106
8. RELATIONS WITH BAIRD'S SPARROW	109
9. DISCUSSION	113
9.1 Breeding Cycle	113
9.1.1 Chronology	113
9.1.2 Pre-breeding behavior	116
9.1.3 Breeding behavior	118
9.1.4 Success	122
9.2 Growth and Development	126
9.3 Territory	133
9.4 Habitat Selection	147
9.5 Relations with Baird's Sparrow	154
SUMMARY AND CONCLUSIONS	157
BIBLIOGRAPHY	159
APPENDIX I	170
APPENDIX II	171

LIST OF FIGURES

FIGURE	PAGE
1. Minimum air temperatures at Saskatoon	7
2. Maximum air temperatures at Saskatoon	8
3. Mean air temperatures at Saskatoon	9
4. Monthly precipitation at Saskatoon during the study period compared to the long-term mean	11
5. Pattern of arrival of resident male Savannah Sparrows	30
6. Nest initiations by week for 1966 and 1967	36
7. Number of Savannah Sparrows recorded during censuses, late summer, 1967	51
8. Growth curve for nestlings in a nest with two Cowbird nestmates (67-1) compared to the growth curve for nestlings in an unparasitized nest (67-3)	60
9. Growth in weight of nestling Savannah Sparrows. Semi-logarithmic scale	74
10. Growth in weight of nestling Savannah Sparrows. Logarithmic scale	75
11. Growth of wing, third primary and central rectrix of young Savannah Sparrows	76
12. Growth of tarsus and exposed culmen of young Savannah Sparrows	77
13. Territory establishment by six male Savannah Sparrows, 1967.	83
14. Territory size in relation to the number of song perches recorded	86
15. Number of territorial males censused during the breeding season, 1967	88
16. Approximate territories of Savannah Sparrows on the study area in 1967.	89
17. Territorial interactions of male Savannah Sparrows, 1967	93

FIGURE	PAGE
18. Habitats on the study area	103
19. Placement of nests in relation to brushy habitat	108
20. Approximate territories of Baird's Sparrows on the study area, 1967	112
21. Hypothetical sequence of events in territorial encounters of the Savannah Sparrow	146

LIST OF PLATES

PLATE	PAGE
1. Aerial view of Kernen's prairie from the south	14
2. Aerial view of the study plot from the north	14
3. Open grassland habitat	16
4. Sparse brush habitat	16
5. Dense brush habitat	18
6. Dense brush habitat with <u>Elaeagnus commutata</u>	18
7. Egg of a Baird's Sparrow showing damage caused by predation by a small mammal	56
8. A Savannah Sparrow egg showing damage caused by a Brown-headed Cowbird	58
9. Plumage development of young Savannah Sparrows. Ventral view	64
10. Plumage development of young Savannah Sparrows. Lateral view	64
11. Plumage development of young Savannah Sparrows. Dorsal view	65
12. Plumages of the Savannah Sparrow. Ventral view	68
13. Plumages of the Savannah Sparrow. Lateral view	68
14. Plumages of the Savannah Sparrow. Dorsal view	69

LIST OF TABLES

TABLE	PAGE
1. Volumes of the largest testis of male Savannah Sparrows	32
2. Size of the cloacal protruberance of male Savannah Sparrows examined in 1967	33
3. Calculated first egg dates and full clutch dates, 1966, 1967	35
4. Hatching pattern as determined from observations of hatching and ages of nestlings	39
5. Stages in the reproductive cycle of emberizine finches	41
6. Cessation of song by 18 male Savannah Sparrows at pair formation	42
7. Dimensions of nests and scrapes	46
8. Survival of nests, eggs and young calculated from exposure	53
9. Survival of nests, eggs and young calculated from losses	54
10. Growth in weight of nestling Savannah Sparrows	70
11. Wing length of nestling Savannah Sparrows	71
12. Third primary length of nestling Savannah Sparrows	71
13. Central rectrix length of nestling Savannah Sparrows	72
14. Tarsus length of nestling Savannah Sparrows	72
15. Exposed culmen length of nestling Savannah Sparrows	73
16. Measurements of live adult Savannah Sparrows	78
17. Territory size of the Savannah Sparrow	85
18. Position of nests in relation to territory	91
19. Seasonal changes in territorial interactions in 1967	94

TABLE	PAGE
20. Extents of habitats on the study area	104
21. Extent and proportion of habitats on Savannah Sparrow territories	104
22. Vegetation of Savannah Sparrow song perches	105
23. Height of Savannah Sparrow song perches	107
24. Nest placement in relation to brush habitat	107
25. Vegetation and height of Baird's Sparrow song perches	110
26. Plumage development in three species of Emberizinae	123
27. Behavioral development in three species of Emberizinae	131
28. Population densities of Savannah Sparrows in various habitats	142
29. Breeding habitats of the Savannah Sparrow throughout North America	150

1. INTRODUCTION

1.1 Introductory Remarks

The Savannah Sparrow, Passerculus sandwichensis (Gmelin), is one of the most widely distributed of all the Nearctic Emberizinae. Its breeding range (A.O.U. Checklist, 1957) extends from the tundra of northern Alaska, Yukon, Mackenzie and Keewatin, south across the width of the continent to the Mexican provinces of Sinaloa and Oaxaca, and Guatemala. Sixteen geographic races are recognized in North America (A.O.U. Checklist, 1957). The race concerned in the present study is the Nevada Savannah Sparrow, P.s. nevadensis Grinnell.

Such a polytypic species has naturally been the object of a number of taxonomic papers (e.g. Grinnell, 1910; 1939; Bishop, 1915; Oberholser, 1919, 1930; Camras, 1928, 1940; van Rossem, 1930, 1947; Huey, 1930; Taverner, 1932; Swarth, 1933, 1936; Peters and Griscom, 1938; Willett, 1939; Aldrich, 1940; Duvall, 1943; Johnson, 1956; Norris and Hight, 1957; Dickerman and Parkes, 1960; and Norris, 1960). The validity of certain forms, especially in the western rostratus group is still questionable. The position of P.s. nevadensis is somewhat obscure as well (Peters and Griscom, 1938). Occupying the central plains of the continent, this form intergrades northeastward with P.s. oblitus, eastward with P.s. savanna and northward and westward with P.s. anthinus. It has a greater geographic variability in mensural characters and color than any other race.

The breeding biology of P.s. savanna has been briefly described by Shields (1935) and Sutton (1959); and Linsdale (1938) treated the breeding biology of P.s. nevadensis briefly as well. The only other major works

concerned with this species involved studies of the feeding habits (Dillery, 1962, 1965), the ecology of wintering populations (Quay, 1957, 1958; Norris, 1960) and the physiology of salt marsh forms (Cade and Bartholomew, 1959; Poulson and Bartholomew, 1962).

Thus the ecology and behavior of the Savannah Sparrow during the breeding season have largely been ignored, and offer a wide field of possible work in view of the broad range, many forms and varied habitats of this species.

There is, however, a wealth of material on the breeding biology and behavior of other North American emberizines. The most complete and best known of these studies is that of Nice (1937, 1943) on the Song Sparrow (Melospiza melodia). Among other life history studies are works on the Rufous-sided Towhee, Pipilo erythrophthalmus (Barbour, 1950, 1951; Davis, 1958); the Ipswich Sparrow, Passerculus princeps (Dwight, 1895); the Grasshopper Sparrow, Ammodramus savannarum (Walkinshaw, 1940; Smith, 1963); the Baird's Sparrow, A. bairdii (Cartwright, Shortt and Harris, 1937); the Leconte's Sparrow, Passerherbulus caudacutus (Walkinshaw, 1937); the Henslow's Sparrow, P. henslowii (Hyde, 1939); the Sharp-tailed Sparrow, Ammospiza caudacuta (Breckenridge, 1930; Woolfenden, 1956); the Seaside Sparrow, A. maritima (Tompkins, 1941; Woolfenden, 1956); the Tree Sparrow Spizella arborea (Weeden, 1965, 1966); the Chipping Sparrow, S. passerina (Walkinshaw, 1944); the Clay-colored Sparrow, S. pallida (Walkinshaw, 1939; Fox, 1961; Salt, 1966); the White-crowned Sparrow, Zonotrichia leucophrys (Blanchard, 1941; Banks, 1959); the Song Sparrow (Marshall, 1948; Johnson, 1956; Tompa, 1962, 1964); the McCown's Longspur, Rhynchophanes mccownii

(Mickey, 1943); the Lapland Longspur, Calcarius lapponicus (Grinnell, 1944; Sutton and Parmelee, 1955); and the Chestnut-collared Longspur, C. ornatus (Harris, 1944).

From an examination of these many studies it is possible to describe the breeding biology of a "typical" emberizine and to examine the information gathered in the present study for similarities and differences.

The "typical" emberizine is a ground-nesting species, the males of which defend a territory which is a mating area, a nesting area, and a foraging area for food for the young (Type A territory of Nice, 1941). The birds are monogamous, but the open-cup nest is built by the female alone, and the male does not share in incubation. A clutch of 3-5 eggs is typical and incubation often begins prior to the completion of laying. The incubation period is about 12 days. Care of the young after hatching is shared by both parents and continues until the young are almost a month old. The young leave the nest at the age of 8-10 days, about one week before they are capable of sustained flight. Most emberizines rear two or more broods during a single breeding season.

1.2 Scope and Purpose

This study was carried out during the summers of 1966 and 1967 near Saskatoon, Saskatchewan. In general, the purpose of the investigation was to describe the ecology of the Savannah Sparrow during the breeding season, and, since the possibility of interspecific interactions was present, to examine the territorial behavior of the species. The primary objectives of the investigation were as follows:

(1) To outline the chronology of the breeding cycle of the Savannah Sparrow in the Saskatoon area.

(2) To describe as many aspects of the breeding cycle as possible, including

(a) arrival

(b) events and behavior from pair-formation through fledging of the young

(c) post-breeding dispersal

(3) To describe the growth and behavioral development of the nestlings.

(4) To describe the territorial behavior of the Savannah Sparrow and to examine the territorial relationships with the Baird's Sparrow.

(5) To attempt to document the existence of habitat selection by the Savannah Sparrow.

2. ENVIRONMENT

2.1 General Description

Saskatoon, Saskatchewan (52°08'N, 106°38'W) is located in the Aspen Parkland Region (Bird, 1961). In the undisturbed condition this area consists of two major plant communities, forest and grassland, intermingled in a mosaic of isolated patches and more or less solid stands. The region is bounded on the north by the boreal coniferous forest and on the south by the grasslands of Central North America. The aspen parkland is a poorly drained region situated on relatively young glacial drift, and on the beds of large glacial lakes with incomplete drainage systems (Bird, *ibid*). The soils are generally of the black soil zone although the parkland extends into the dark brown soil zone in some areas including the Saskatoon area (Mitchell, Moss and Clayton, 1947). These soils are formed under a heavy grass and herbaceous vegetation whereas a gray type develops under forest. This suggests that the aspen parkland represents a recent invasion of Aspen poplar (Populus tremuloides) upon an area that had been grassland for a long time. Much of the aspen parkland region has been cultivated for the production of cereal grains, and most of the remainder utilized as grazing land.

The climate of the region is characterized by great extremes in temperature between summer and winter, and by a comparatively low annual precipitation. The mean monthly temperature for Saskatoon varies from -1°F in January to 65°F in July. Absolute extremes of -55°F in January to 104°F in July have been recorded (Kendrew and Currie, 1955). The annual precipitation at Saskatoon varies from 8.8 to 21.0 inches with a mean of 13.7 inches. About 30 percent of the annual total precipitation falls as snow, and summer (June to August) has a strong maximum (Kendrew and Currie, 1955).

2.2 Summer Climate

2.2.1 Source of Information.

Information on climatic conditions during the summers of 1966 and 1967 was taken from annual and monthly reports of the Department of Transport Meteorological Branch weather station at Saskatoon. The weather station is located at the Saskatoon Airport and is approximately six miles west of the study area.

2.2.2 Temperature

Minimum, maximum and mean temperatures for the months of April through August are shown in Figures 1-3. These are calculated as means for five day periods (six-day periods for the last period in May, July and August). Also shown are the mean minimum, mean maximum and mean mean temperatures for the period 1931-1960.

In 1966 April temperatures were at or above normal for the first half of the month. In the latter part of the month there were two cold spells from 17-20 April and from 27-30 April. After this the temperature rose rapidly to a higher than normal period at the end of May and then fluctuated near the long term mean for the remainder of the summer. In 1967 the spring was somewhat late; temperatures remained below normal until mid-May. Although temperatures were below normal there was not the marked fluctuation of temperature as noted in late April of 1966. Again in 1967 the temperature rose rapidly to an above normal peak at the end of May and then followed the long-term mean for the rest of the summer.

With the exception of the cool, late springs, temperatures during both study periods were average for the area.

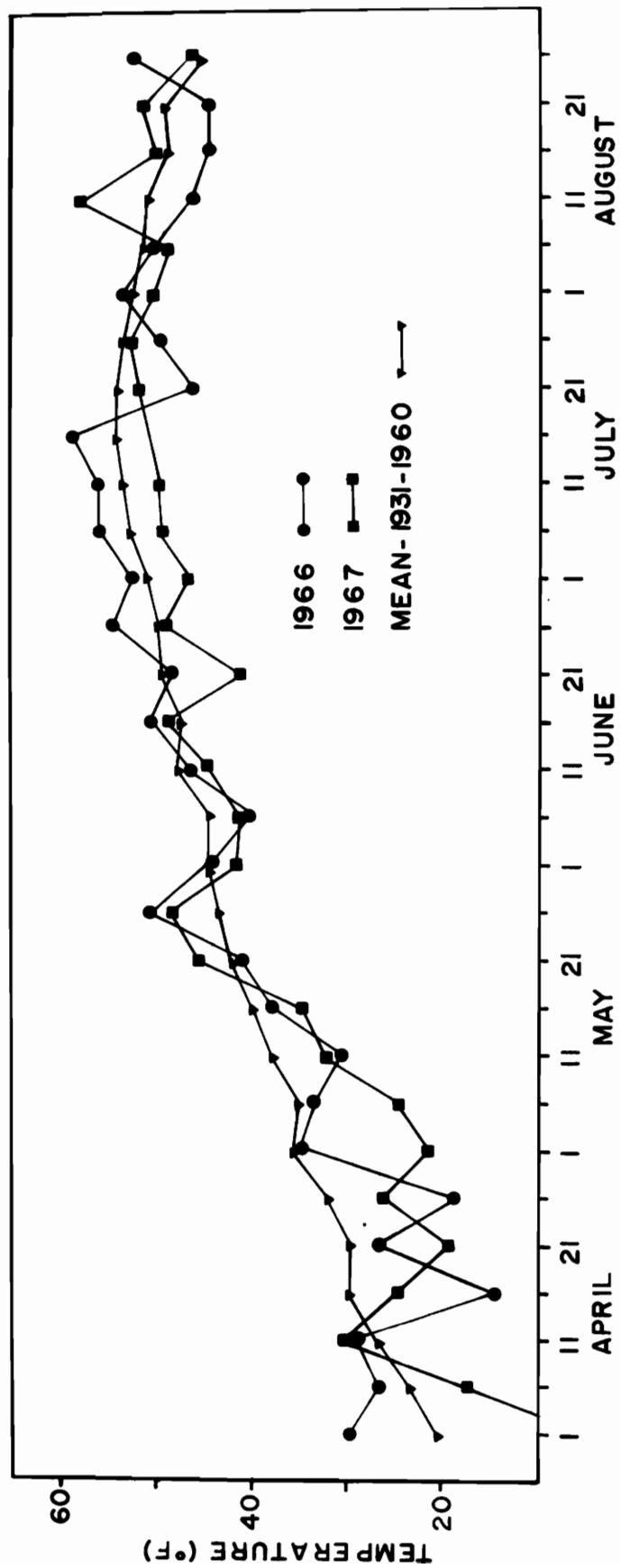


Figure 1. Minimum air temperatures at Saskatoon. Calculated as means for five-day periods beginning at date given.

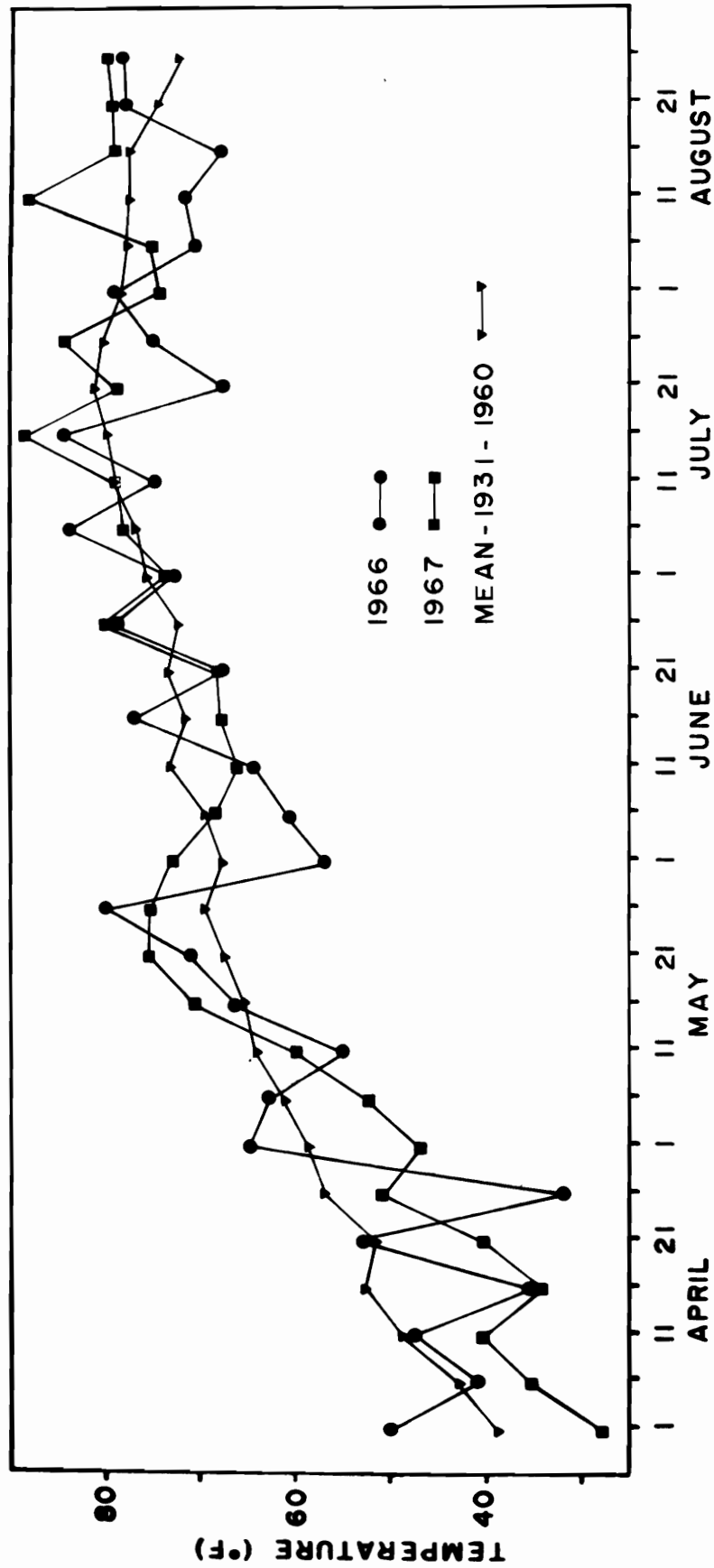


Figure 2. Maximum air temperatures at Saskatoon. Calculated as means for five-day periods beginning at date given.

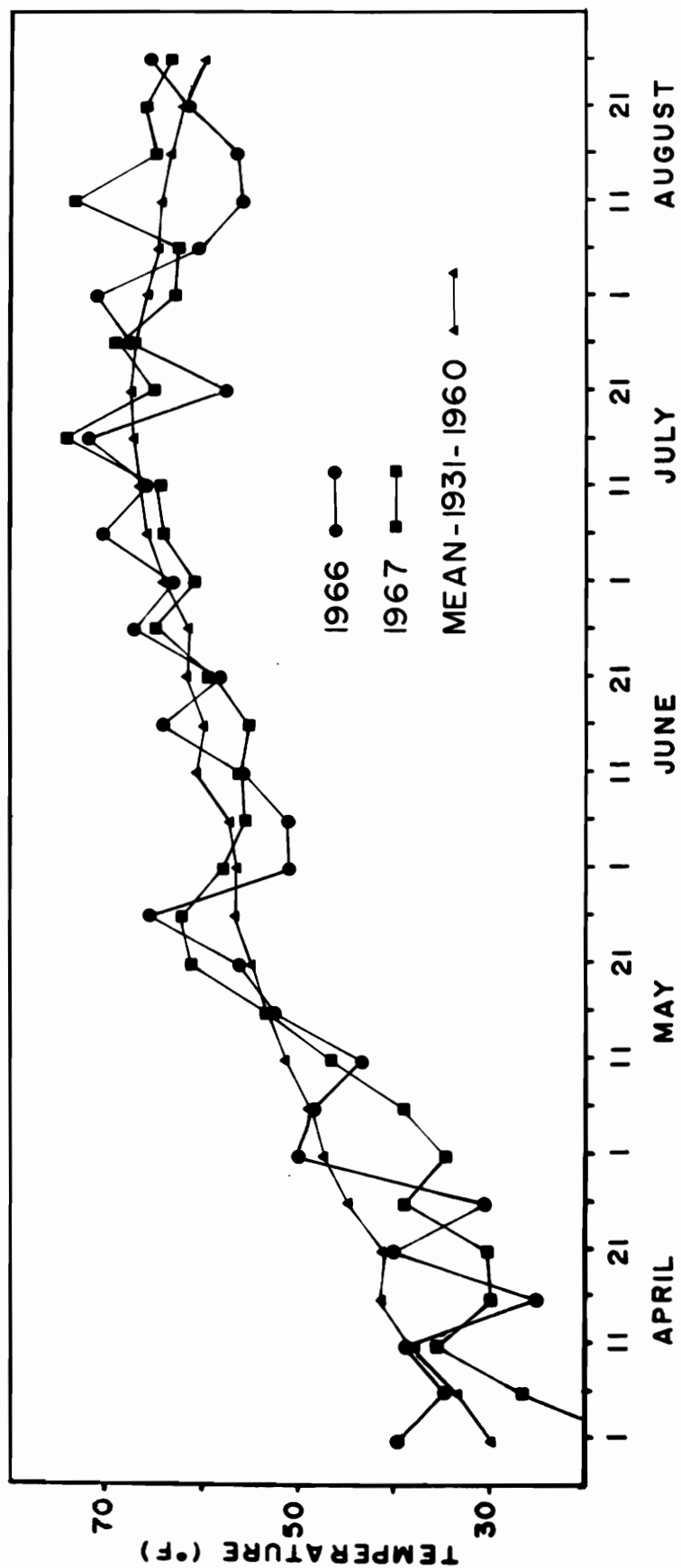


Figure 3. Mean air temperatures at Saskatoon. Calculated as means for five-day periods beginning at date given.

2.2.3 Precipitation

Figure 4 shows the monthly precipitation for Saskatoon from August 1965 to August 1967. The mean monthly precipitation for the period 1941-1960 is also shown for comparison. Total precipitation for the period August 1965-July 1966 was 13.78 inches and for the same twelve-month period in 1966-1967 was 10.88 inches. The mean annual precipitation for 1941-1960 is 13.86 inches. Figure 4 shows that the distribution of precipitation follows the mean figures with the exception of June, 1966. This was the wettest June since 1942 with a total of 5.38 inches (mean = 2.04 inches). This total was distributed throughout the month; there being measureable precipitation on 17 days, and a maximum of 1.54 inches on 25 June. This extremely wet month during the growing season was reflected in the lushness of the vegetation during the summer of 1966.

2.3 Study Area and Habitats

2.3.1 Description and History

The present study was carried out at Kernen's prairie, a 320 acre tract of grassland named for its owner. Situated at survey reference E $\frac{1}{2}$ 8-37-4-W3rd, the prairie is about three miles north-east of the City of Saskatoon.

The Saskatoon area was settled in 1883 and Kernen's prairie has been in the hands of the present owner's family since 1917. Regular, medium intensity grazing was carried out up until the 1930's. Since that time the only disturbances of this nature have comprised one summer of light grazing in 1948 and the mowing of some areas of the prairie in 1960 (Baines, 1964).

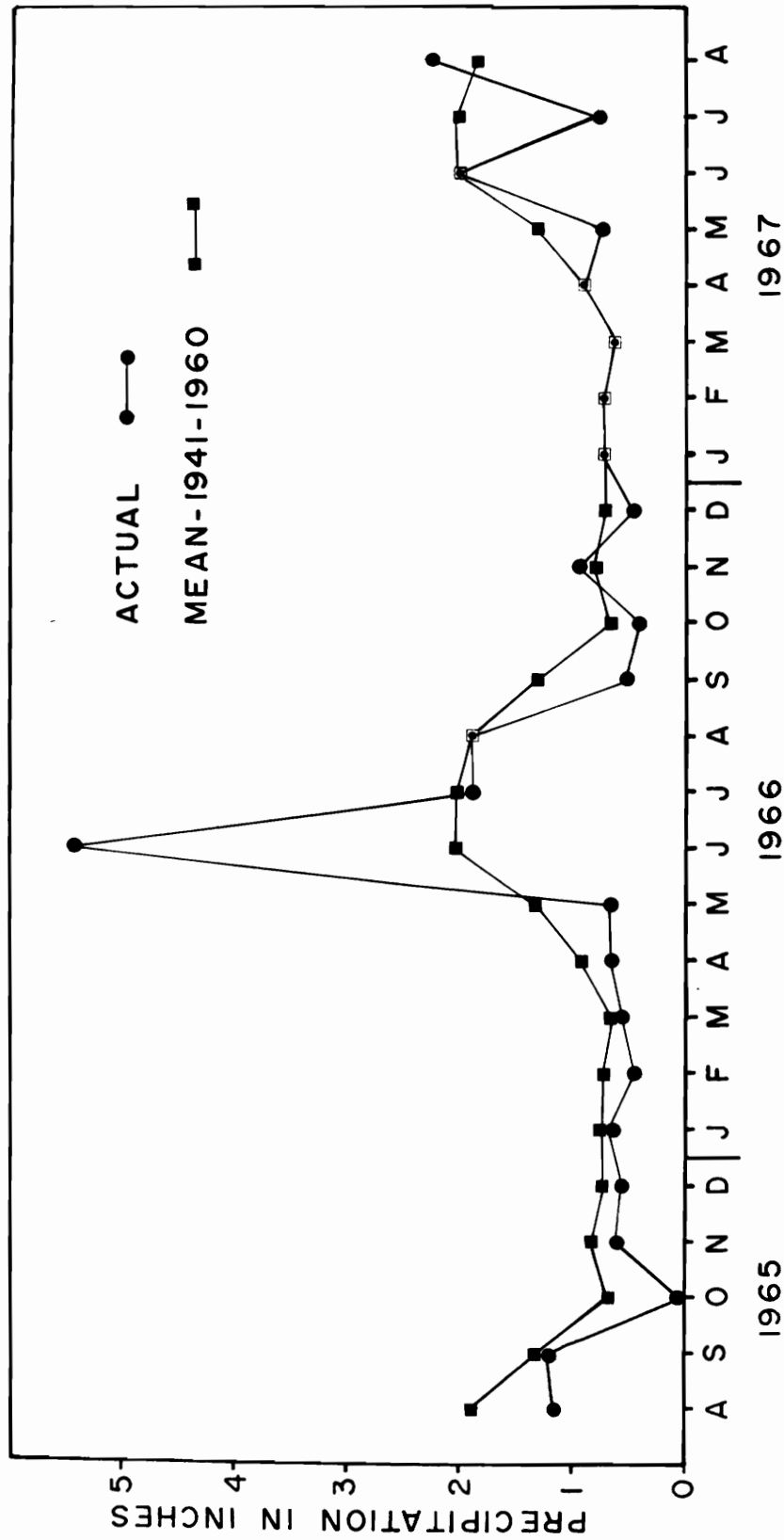


Figure 4. Monthly precipitation at Saskatoon during the study period compared to the long-term mean.

Mowing was again carried out on the east side of the prairie during the summers of 1965 and 1967 but did not affect the study area. The area therefore approximated the prairie habitat which was found in the area prior to settlement. It is the only sizeable tract of "virgin" prairie in the vicinity of Saskatoon.

The phytosociology of the prairie was the subject of a study by Baines (1964) and frequent reference to this work is made in the description of the vegetation.

In 1965 a plot was staked in the north-west corner of the prairie, to be used for long term studies of avian populations by W.J. Maher. The bulk of the present work was carried out on this plot. The plot measures 1000 by 2000 feet and is subdivided into a 200-foot grid. Each grid square has an area of 40,000 square feet (0.92 acre) and the plot has an area of 2 million square feet (45.91 acres). Throughout this study the term "prairie" refers to the entire 320 acre area, and the terms "study area" or "study plot" refer to the gridded area.

The north-south lines of the grid were lettered A to F and the east-west lines were numbered 0 to 10. This allows reference to any area on the grid with respect to a set of coordinates such as A0, E5.

2.3.2 Geology and soils

Kernen's prairie lies within the limits of glacial Lake Saskatoon, formed during the recession of the Wisconsin ice sheet about 10,000 B.P. (Edmunds, 1962). The soils have thus developed from glacial lacustrine deposits of fine texture. A north-south ridge extending the length of the prairie is basically a deposit of glacial till (Baines, 1964). This ridge

slopes gently ($1-1\frac{1}{2}^{\circ}$) on each side. The difference in elevation between the ridge crest and the lowest point on the prairie, in the south-east corner is about 30 feet. At various sites roughly circular glacial "kettles" occur. The extreme north-western corner of the study area shows a hummocky surface resulting from cracking of the soil during dry periods. These cracks form a polygonal network in which the hummocks have a mean diameter of 5.7 feet (Baines, 1964). These physiographic features are of importance to the distribution of soil moisture and thus to the distribution of the vegetation.

2.3.3 Vegetation

Kernen's prairie is located in the region of transition between the Mixed Prairie, or Stipa-Bouteloua Association of Clements (Clements and Shelford, 1939) to the south, and the Fescue Prairie (Festuca scabrella Association of Coupland and Brayshaw, 1953) to the north. Shrubs (Symphoricarpos occidentalis, Elaeagnus commutata, Spiraea alba, and Rosa acicularis) occur in all but the driest or saline habitats on the prairie (Baines, 1964). Several groves of aspen poplar (Populus tremuloides) are found at moister sites on the prairie, but none were located on the study area (Plates 1 and 2).

Baines (1964) has related the distribution of the vegetation types to soil moisture, and to the water retaining capacity of the soil. More definite species relationships were demonstrated in relation to slope position. Slopes were divided into upper, mid-, and lower slopes, with depressions as a fourth category.

Stipa spartea var. curtiseta and Agropyron dasystachyum occur as

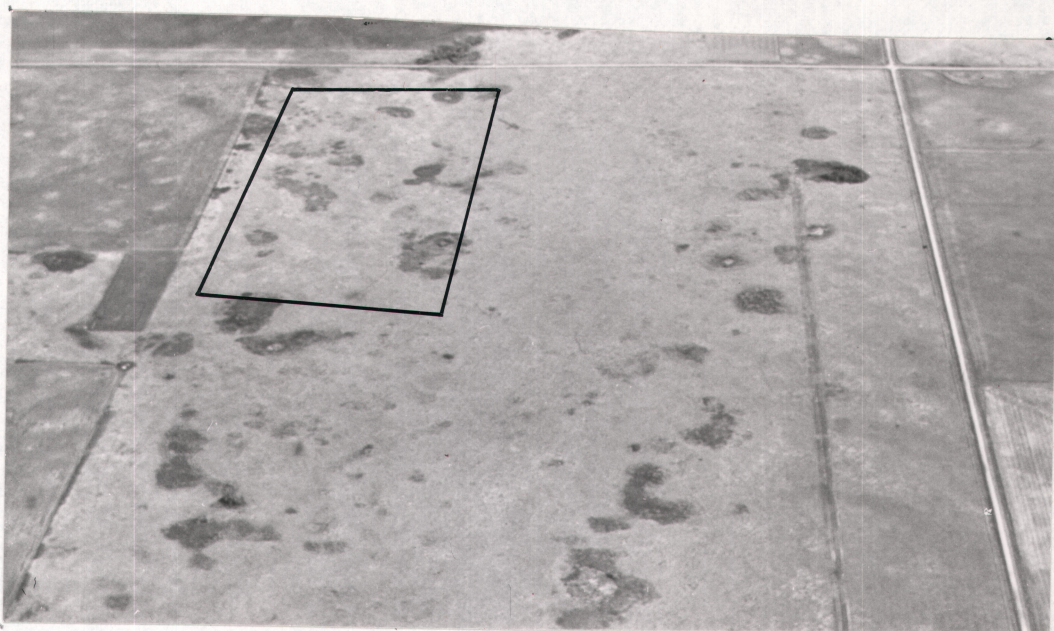


Plate 1. Aerial view of Kernan's prairie from the south. The study plot is outlined in the upper left hand corner. Note the mosaic of grassland and brush.



Plate 2. Aerial view of the study plot from the north. Brushy vegetation is mainly Symphoricarpos occidentalis, but an overstory of Elaeagnus commutata is apparent in the lower left corner. Three clumps of willows, Salix petiolaris can be seen in the upper left corner.

co-dominants on the upper and mid-slopes. This corresponds to the Stipa-Agropyron Association of Coupland (1961). On the lower slopes, these species are replaced by Festuca scabrella and Agropyron trachycaulum/A. subsecundum, which are components of the Festuca scabrella Association. Hordeum jubatum is virtually restricted to depressions, where it is ubiquitous (Baines, 1964).

Because these grasses have a similar physiognomic appearance it is unlikely that species differences are an important factor in habitat selection by the birds of the area. The distribution of the woody species is probably more important in this respect. All of the woody species on the study area (Symphoricarpos occidentalis, Elaeagnus commutata, Spiraea alba, and Rosa acicularis) attain maximum importance in the lower slope areas although not restricted to this section. Rosa acicularis is found in all four divisions and is the only woody species found in the upper slope section. Symphoricarpos occidentalis and Elaeagnus commutata often occur together in the field and show similar distribution on mid- and lower slopes. Spiraea alba extends further downslope, and is the only woody species found within the depressions.

With this vegetation distribution in mind it is possible to describe four avian habitats on the study plot, based on their physiognomic appearances.

Open Grassland: This habitat would correspond to the upper slopes of Baines (1964). The dominant grasses are Stipa spartea and Agropyron dasystachyum. Woody vegetation is virtually absent, although Rosa acicularis may occur as dwarf (less than 12 inches) individuals (Plate 3).



Plate 3. Open grassland habitat. C9 looking north-west.



Plate 4. Sparsh brush habitat. C4 looking south-east.

Sparse Brush: Stipa spartea and Agropyron dasystachyum are still the dominant grasses, with Festuca scabrella becoming more important (Plate 4). Symphoricarpos occidentalis is present as small (less than 18 inches) scattered plants, whose canopy has no noticeable effect on the understory vegetation. Canopy cover is less than 50 percent. This habitat would approximate the mid-slope region of Baines (1964).

Dense Brush: In this habitat the dominant vegetation is woody shrubs, primarily Symphoricarpos occidentalis. Canopy cover ranges from 50 percent to complete (Plate 5). The most important understory grass is Festuca scabrella, but in areas of complete canopy cover, no understory of herbaceous vegetation is found. Elaeagnus commutata often forms a layer above the Symphoricarpos and may reach a height of greater than six feet (Plate 6). In portions of this habitat bordering on depressions, the Symphoricarpos gradually gives way to virtually pure stands of Spiraea alba. This habitat would approximate the lower slopes of Baines (1964).

Grassy Depressions: This minor habitat is found in the depressions areas of Baines (1964). Hordeum jubatum is the dominant plant, although some small scattered plants of Spiraea alba may be present.

Four clumps of willows (Salix petiolaris), from three to eight feet in height and from four to six feet in diameter are located around a depression in the southeast corner of the study area. These have not been classed as a separate habitat but will be referred to separately.



Plate 5. Dense brush habitat. The species is Symphoricarpos occidentalis.



Plate 6. Dense brush habitat. The species is S. occidentalis with an overstory of Elaeagnus commutata.

2.4 Fauna

2.4.1 General

A variety of types of animals present on Kernen's prairie actually or potentially affect the success of the Savannah Sparrow. The most important of these are the invertebrates which form the bulk of the diet of the Savannah Sparrow during the breeding season. Animal material composes 74 percent of the diet of the adults during the months of June, July and August (Martin, Zim and Nelson, 1951) and is virtually the exclusive food of nestlings. The two most important food groups are Coleoptera and larval Lepidoptera (especially Noctuidae) (Judd, 1901; Dillery, 1965). Measurements of food habits and of the invertebrate fauna were not a part of this study, and the vegetational and climatic factors affecting populations of these food sources are complex and will not be considered here.

Birds and mammals could affect the Savannah Sparrow in three ways. Brood parasitism by the Brown-headed Cowbird (Molothrus ater) will be described in section 4.5.3. Interactions with other birds and mammals, either as competitors for resources or as predators are discussed below. A complete list of resident birds and mammals on the study area and in the vicinity is given in Appendices I and II.

2.4.2 Competitors

Eight species of birds which were resident on the study area are possible food competitors of the Savannah Sparrow. These include the Baird's Sparrow, the Clay-colored Sparrow, the Western Meadowlark (Sturnella neglecta), the Brown-headed Cowbird, and the Sprague's Pipit (Anthus spragueii) all of which were resident in some numbers. Other insectivorous birds such as the Brewer's Blackbird (Euphagus cyanocephalus), the Eastern Kingbird (Tyrannus tyrannus) and the Bobolink (Dolichonyx oryzivorus) were represented by one or two

pairs on the study area. A number of other species did not nest on the study area during the study period but were believed to do part of their foraging there. These include the Red-winged Blackbird (Agelaius phoeniceus), the Horned Lark (Eremophila alpestris) and the Vesper Sparrow (Pooecetes gramineus).

There is a possibility of overlap of food items between the Savannah Sparrow and certain small mammals on the study area. The Masked Shrew (Sorex cinereus) was present in low numbers and would not be a competitor for arthropod food. Meadow Voles (Microtus pennsylvanicus) and Deer Mice (Peromyscus maniculatus) were present in low numbers on the area. These species could be a factor if a cold spring, which forced the sparrows to rely heavily on seeds as a food source, were contemporary with a high small mammal population.

2.4.3 Predators

Several species of avian predators were resident on or near the study area. These include the Marsh Hawk (Circus cyaneus) (1966, 1967), the Short-eared Owl (Asio flammeus) (1966), the Burrowing Owl (Speotyto cunicularia) (1966, 1967) and the Loggerhead Shrike (Lanius ludovicianus) (1967). Actual predation by these species was not observed but it is likely that some loss of birds was due to their activities. Migrant or non-resident raptors recorded at the study area include the Cooper's Hawk (Accipiter cooperi), the Red-tailed Hawk (Buteo jamaicensis), the Swainson's Hawk, (B. swainsoni), the Sparrow Hawk (Falco sparverius) and the Great Horned Owl (Bubo virginianus). Losses to these species is probably negligible.

Mammalian predation is probably the most important factor in mortality of both adults and nests. Nest losses will be discussed in a later section. In both 1966 and 1967 a pair of Red Foxes (Vulpes fulva) raised litters on the south part of Kernen's prairie, about one-quarter mile from the study area. Remains of kills examined at the den included wings of Meadowlarks and sparrows (species unknown) and it seems likely that the Savannah Sparrow is subject to predation of both adults and young by foxes. The Least Weasel (Mustella rixosa) has been trapped on the prairie and the Long-tailed Weasel (M. frenata) has been seen in the area by the author. The extent of predation of these species on adults, eggs and young is not known, but could possibly be significant.

Rodent predation on nests will be discussed later. The Richardson's Ground Squirrel (Citellus richardsonii) and the Thirteen-lined Ground Squirrel (C. tridecemlineatus) were present on the study area at estimated population levels of one per five acres and one per two acres respectively. Ground squirrels, as well as the Meadow Vole, were implicated as a factor in nest loss.

3. METHODS

3.1 Census

During 1966, several censuses of the study area were carried out at irregular intervals during May and June. These gave an adequate estimate of population size, but did not allow a continuous record of territory histories or of population changes. In 1967, 14 censuses were carried out at regular weekly intervals from 2 May through 3 August. Savannah Sparrows were present on the study area for 15 weeks and the censuses covered the last 14 weeks. During the weeks of arrival of the birds, censuses were made two or three times a week, thus giving a total of 21 censuses of the plot in 1967.

The method of censusing the plot was for the observer to walk the plot along each grid line, either north and south or east and west. This meant that the observer should pass within 100 feet of any bird on the plot. Observations were mapped in the field on blank maps of the plot at a scale of 1 inch = 66.7 feet. Eight power binoculars and/or 25-power telescope were used during these observations. Although no standard observation period was set, each bird recorded was observed for a period of from two to ten minutes and its movements and activities during this time could be recorded. To allow comparisons of activities from week to week, all surveys were started one hour after civil sunrise time for that date.

Maps from each survey were compared and in this manner territories could be outlined and histories of individual birds and territories could be followed and correlated to known nests and other reproductive activities.

The territory size of 18 males was calculated in 1967 by plotting song perches mapped during the censuses. The song perches of an individual male showed a strong tendency to be grouped in a central core. Single observations which were isolated by more than 50 feet were omitted from calculations. Areas were measured with a polar planimeter. The habitats of these individual territories were also mapped and measured.

Most birds encountered during the census could be sexed with a degree of certainty. Banded birds and singing males posed no problem. Non-banded non-singing birds were sexed by behavioral means whenever possible. Females were much more shy and secretive than males. Two birds which were seen together on a territory, and which were not aggressive toward one another were assumed to be a pair.

3.2 Breeding Cycle

3.2.1 General

For convenience the period of residence of the Savannah Sparrow on the study area during 1967 has been divided into 15 weekly periods, designated Week 1, Week 2, etc. The actual dates covered by this designation are as follows:

Week 1	23 April - 29 April
Week 2	30 April - 6 May
Week 3	7 May - 13 May
Week 4	14 May - 20 May
Week 5	21 May - 27 May
Week 6	28 May - 3 June
Week 7	4 June - 10 June
Week 8	11 June - 17 June
Week 9	18 June - 24 June
Week 10	25 June - 1 July
Week 11	2 July - 8 July
Week 12	9 July - 15 July
Week 13	16 July - 22 July
Week 14	23 July - 29 July
Week 15	30 July - 5 August

These weekly intervals are arranged so that the regular censuses

fall at approximately the middle of the week.

3.2.2 Nest Location

Twenty-seven nests of the Savannah Sparrow were found during the two summers. Twenty-three of these were on the study area and four in adjacent areas. Seven of the nests were found accidentally in the course of other activities on the plot. However, several techniques proved effective in locating nests both before and after hatching.

During 1966 the author and an assistant used a 70 foot, 3/4-inch rope to drag the study area in an attempt to flush incubating birds from their nests. This proved ineffective and it was found that the rope could pass directly over an incubating bird without result. In 1967 this technique was modified by wiring tin cans, with several stones in each, at five foot intervals along the rope. This proved more effective and nine nests of the Savannah Sparrow were found using this method. Nine nests of three other species (Western Meadowlark, Clay-colored Sparrow and Baird's Sparrow) were also found in this fashion.

After eggs had hatched, nests were located by observing the adults carrying food to the young. After watching several trips to the nest, the general location could be determined and upon the next trip the observer would run in to the site, flushing the adult and locating the nest. Eleven nests were found in this fashion.

All nests were marked with a numbered 12-inch stake placed 10 feet to the south of the nest.

3.2.3 Nest information

The immediate cover and surrounding habitat were recorded for

all nests, along with the direction the nest faced and the precise grid location. The nest diameter and the diameter and depth of the cup were recorded for all nests. After the completion of nesting, seven nests were collected and the depth and diameter of the scrape under the nest were recorded.

Nests were visited at two-day intervals whenever possible. During the periods of expected hatching and fledging the nests were visited daily.

3.2.4 Timing of the breeding cycle.

Information on the timing of the breeding cycle was derived from nests found at all stages of the cycle. Eggs in those nests found before or during incubation were numbered with a felt marker to allow accurate determination of the incubation period and the hatching sequence. The date of initiation of nests found during incubation was calculated by back-dating once the date of hatching was known. Similarly, those nests found after hatching could be back-dated after determining the age of the young.

3.2.5 Nesting success.

Because of the nature of the data on many of the nests, success was calculated using the exposure method outlined by Mayfield (1961). This method allows the use of fragmentary data such as are obtained from nests found after hatching, or nests whose fate is unknown. Units of exposure are the nest-day (one nest observed for one day), the egg-day, and the nestling-day. Mortality rates and survival rates are calculated per nest-day, egg-day, or nestling-day. This method assumes that loss is

constant throughout the incubation period, and throughout the nestling period.

Nests from both years were considered together because of the small sample size. Those nests which were parasitized by the Brown-headed Cowbird (Molothrus ater) have been omitted from these calculations. Standard calculations of percentage of successful nests and percentage of eggs hatching and produced fledglings were also made for comparison.

3.3 Trapping and Banding

During 1966 all nestlings were banded shortly before leaving the nest, using a unique combination of color bands for each bird. Nestlings in 1967 were banded with one color combination per nest. In 1967, mist-netting of adults was carried out at dawn and dusk on calm days. Twenty-three adult male and six adult female Savannah Sparrows were captured in this manner and color-banded.

The color bands used were of the "bandette" type manufactured by the National Band and Tag Company. Since the smallest size available was too large, they were cut down and moulded to a suitable size. Red, green, and yellow bands in combinations of up to four bands per bird. The bands were read in the sequence top-bottom, left leg-right leg. Band retention was good; only one bird was known to have lost a band and others were observed up to 77 days without band loss.

Adult birds color-banded in 1967 were given code names which are used in discussing the results. Males were named M1, M2, M3 etc., and females

F1, F2, F3 etc. Females of known pairs were given the same numerical designation as their mate, for example, F3 would be the mate of M3. Non-banded birds mated to banded birds were given code names with a lower-case letter, for example, the mate of M7 would be f7.

3.4 Behavioral Observations.

Many of the behavioral observations, especially territorial behavior of males, were made by watching birds during the censuses. In addition, more intensive observations were made on territorial birds throughout the season. The birds did not seem to be alarmed by an observer watching quietly from more than 100 feet and a blind was seldom used.

Natural observations of territorial and sexual behavior were supplemented by the use of mounted dummies. Dummies of male Savannah and Baird's Sparrows in the singing posture and female Savannah Sparrows in the soliciting posture were constructed and used. A portable Uher 4000 Report-L tape recorder was used to record observations in rapid sequences of events.

3.5 Growth and Development.

Newly hatched birds were marked with colored wool tied around the tarso-metatarsus until the leg was large enough to retain a band. Nests were visited at a maximum of two-day intervals when possible.

Nestlings were weighed to the nearest 0.1 gram with an Ohaus Triple-beam Balance. In 1966 measurements were made of the third primary wing feather (counted from the outermost) and of the central rectrices. In 1967 these measurements were continued but additional measurements of

wing-length (chord), tarsus length and exposed culmen length were taken in the manner described by Godfrey (1966). Notes on changes in plumage and soft parts were made on each visit to a nest and the behavior of the young was recorded.

Young in those nests found after hatching were aged by comparison of their weights, wing lengths and third primary lengths to those of birds of known age.

Three nests in 1966 were enclosed to obtain information regarding development of the young after leaving the nest. The enclosures were constructed of 1/2-inch mesh screen and were about 12 inches in height and four feet by four feet in dimension. The presence of the enclosure did not seem to affect the parental behavior.

In the results the age of nestlings is given as the day of development; Day 0, Day 1, etc. Day 0 is the day of hatching, or birds classed as Day 0 are less than 24 hours old. Day 1 would include birds 24 to 48 hours old, etc.

3.6 Habitat

A detailed map of the brushy vegetation on the study plot was prepared in the summer of 1967. Each 200-foot grid square was temporarily divided with stakes into 50-foot squares and the vegetation was mapped by visual inspection. Vegetation was categorized on the basis of species composition, percent coverage of the canopy and height. The vegetation was mapped in the field at a scale of one inch = fifty feet with an estimated accuracy of ± 5 feet. The area of the different vegetation types was measured on the completed map with a polar planimeter.

4. BREEDING CYCLE

4.1 Arrival

4.1.1 Chronology and pattern.

In 1966 a single male Savannah Sparrow was recorded on the study area on 2 May. This was the first report for the species in the Saskatoon vicinity (Gollop and Gollop, 1966). In 1967 the first record for the species on the study area was three males on 27 April. No prior arrivals were reported in the Saskatoon vicinity (Gollop, 1967a). After these dates, the number of resident males (calculated from singing or known males) censused on the plot rose rapidly to approach the estimated peak resident population of approximately 32 birds as shown in Figure 5. This level was reached by the second week of May. Although the first arrival in 1966 was five days later than in 1967 it appears that peak population was reached at the same time.

Females appear to arrive at least a week after the males. In 1966, the first birds which behaviorally suggested females were recorded on 11 May. These birds were not singing and they did not appear to localize their activity to a particular area as did known males. On the same date, a female (MRL 488) was collected on the east side of the prairie. Significantly, all birds identified as Savannah Sparrows before this date were recorded as singing.

The first female collected in 1967 was taken on 29 May, although an effort had been made to collect females before this date. On the basis of behavior of observed birds, the first bird suspected to be a female was seen on 10 May. On this date a bird was seen during the census which, although watched for five minutes, showed no signs of territorial behavior

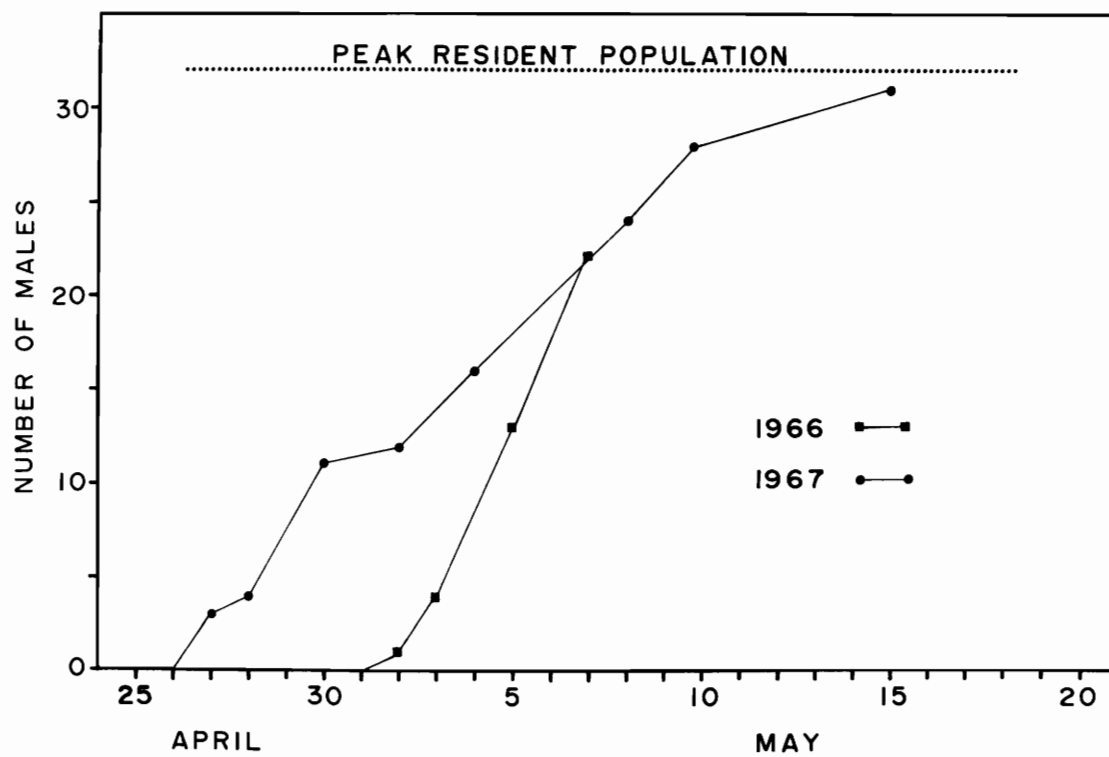


Figure 5. Pattern of arrival of resident male Savannah Sparrows.

and finally flew more than 400 feet off the prairie. Thus it would appear that the first females arrived 9 and 13 days after the first males in 1966 and 1967, respectively. At this time the arrival of the males is not entirely complete.

4.1.2 Reproductive condition on arrival

Males: Those males collected between the date of arrival and mid-May were not in full reproductive condition. Testes volumes of these birds average smaller than comparable figures for birds collected from mid-May to mid-July (Table 1). Individual measurements vary greatly however, and the difference between the means is not statistically significant.

The cloacal protruberance of male passerine birds, caused by a partial hernia of the seminal glomera and serving as a storage area for spermatozoa, may be used as an indication of reproductive condition (Wolfson, 1954 a, b; Salt, 1954). Variations in the fully developed structure within the species are minute (Salt, *ibid*). Therefore, birds having cloacal protruberances noticeably smaller than maximum size are probably not in full reproductive condition. Table 2 shows the progressive increase in the size of this structure in 1967.

Females: A female (MRL 488) collected on the presumed arrival date, 11 May, 1966, was not in full breeding condition. The largest ovarian follicle had a diameter of 2 mm and the oviduct was not enlarged. Follicle enlargement seems to occur in late May. MRL 599, collected 29 May, 1967 had a largest ovarian follicle of 3 mm diameter and some enlargement of the oviduct. MRL 603, collected 2 June, 1967 had a largest follicle of 7.9 mm

Table 1. Volumes of the largest testis of male Savannah Sparrows collected during 1966-67.

	Arrival - mid-May	Mid-May - mid-July
Number of specimens	17	10
Mean testis volume (mm ³)	182.5	241.1
Range (mm ³)	62.8 - 318.3	150.5 - 445.3

Table 2. Size of the cloacal protruberance in male Savannah Sparrows examined in 1967

Date	Specimen	Cloacal Protruberance	
		Diameter (mm)	Height (mm)
2 May	575	4	4
3 May	live	5	5
3 May	live	4	4
6 May	577	3	2
6 May	578	5	4
6 May	579	5	5
9 May	581	5	4
9 May	582	5	5
10 May	live	6	5
10 May	live	5	5
14 May	live	8	6
14 May	live	8	6
14 May	live	7	5
14 May	live	6	4
16 May	587	7	6
16 May	588	8	6
16 May	589	8	6
24 May	595	8	8
28 May	600	7	5
2 June	601	8	6
7 June	605	9	8
13 June	live	10	10
13 June	live	8	8
13 June	live	8	8
26 June	live	10	10
2 July	live	8	8
11 July	629	10	10

diameter, approximately maximum size. The oviduct of this bird was greatly enlarged. No post-ovulatory follicles were present.

4.2 Reproductive Biology

4.2.1 Chronology of the cycle

Only four nests were found in the laying stage in this study. The dates of initiation of these nests can be obtained by back-dating one day per egg. Nine nests were found in incubation and the remaining 14 were found in the nestling period. Nests found after laying was completed were back-dated to give a date of nest initiation which is estimated to be accurate \pm one day.

It is possible to calculate the date of laying of the first egg for 26 of the 27 nests. The other nest was found during incubation and was lost to a predator before hatching occurred. The calculated first egg dates and dates of full clutches for the remaining nests are shown in Table 3.

The five day difference between the earliest first egg dates for 1966 and 1967 is probably not significant in view of the low proportion of nests actually found and the similar climatic conditions during this period in the two years. For these reasons the figures for both years have been combined in Figure 6, which shows nest initiations by week.

From these figures, it would appear that the first nests are initiated during the last 10 days of May. The six nests initiated in Week 7 (June 4-10) are subject to two interpretations. Either they are nests of birds which began nesting later because of late arrival or other causes, or they are replacement nests of pairs which lost their first nests to

Table 3. Calculated first egg dates and full clutch dates, 1966, 1967,
in chronological order.

1966			1967		
Nest Number	First Egg	Full Clutch	Nest Number	First Egg	Full Clutch
66-3	22 May	25 May	67-3	27 May	31 May
66-1	24 May	26 May	67-5	27 May	30 May
66-2	24 May	28 May	67-1	28 May	30 May
66-5	8 June	12 June	67-9	4 June	8 June
66-4	9 June	12 June	67-4	7 June	10 June
66-7	18 June	22 June	67-2	8 June	-----
66-8	19 June	23 June	67-12	8 June	12 June
66-6	27 June	30 June	67-13	13 June	16 June
66-9	1 July	3 July	67-11	16 June	18 June
66-10	7 July	10 July	67-10	17 June	21 June
			67-6	18 June	22 June
			67-8	19 June	22 June
			67-14	19 June	22 June
			67-16	1 July	4 July
			67-15	8 July	10 July
			67-17	26 July	29 July

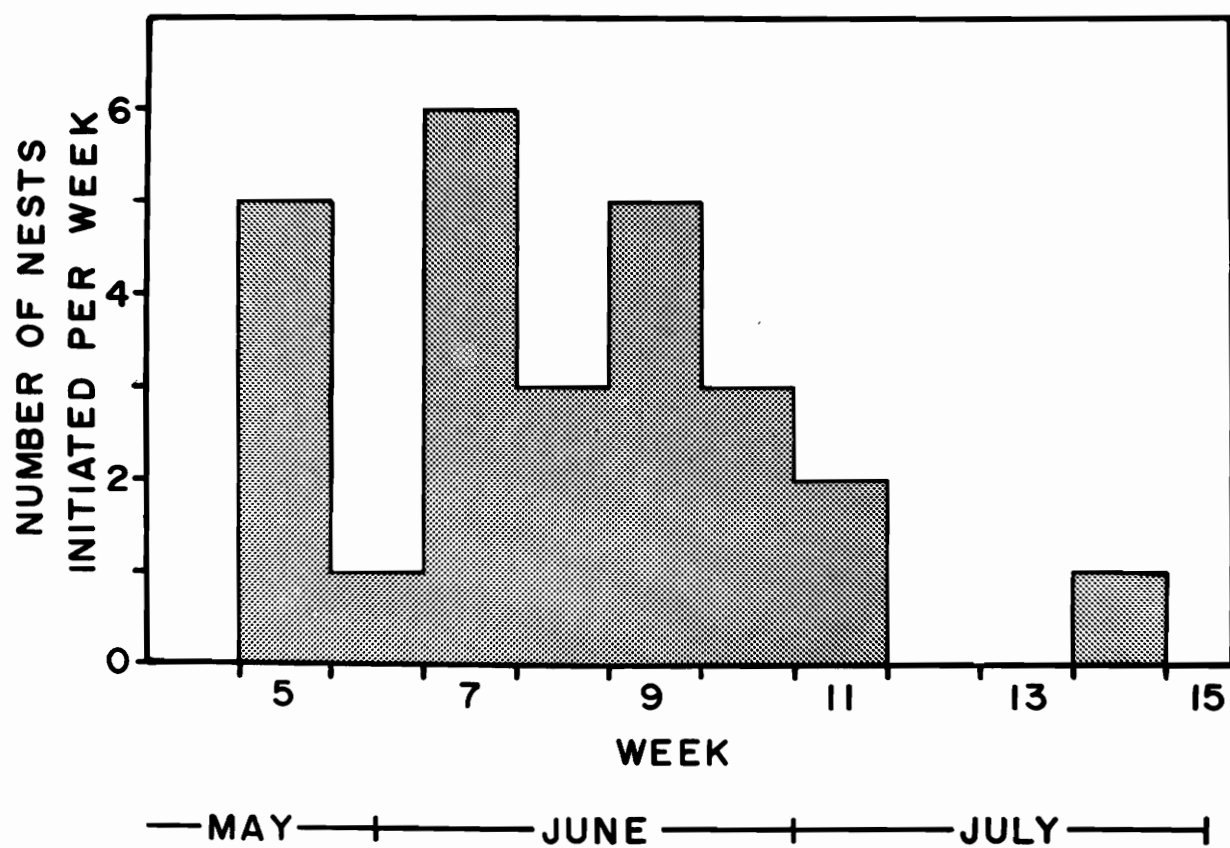


Figure 6. Nest initiations by week for 1966 and 1967 combined.

predators. Both explanations are probably correct. The nests initiated in Weeks 8 through 11 are probably a mixture of replacement nests and second nests.

It was not possible to ascertain that a pair which fledged a first brood renested, although this probably occurred. Nice (1937:133) states that for the Song Sparrow, 6-19 days elapse between fledging of the first brood and the first egg of the second brood. Using these figures for the Savannah Sparrow, second nests of pairs which initiated a successful first nest on 25 May would be initiated over a period of 23 June - 2 July, that is, in Weeks 9.- 11. The large number of nests found during this period (especially Week 9) suggests that a second nest is probable.

4.2.2 Clutch size

Information on clutch size is from nests found during laying or incubation. Individual egg loss during incubation is low (see Section 4.5.1) and the use of data from nests found late in incubation should not bias the figures greatly. Nests containing cowbird eggs have been omitted. This leaves ten nests for which the clutch size can be determined. Three nests had a clutch of three eggs, four had four eggs and three had five eggs, for a mean of 4.0 eggs per nest.

A minimum clutch size can also be given for those nests found after hatching. This was the number of young present plus the number of infertile eggs. The minimum clutch size for twelve nests found after hatching is known. A minimum clutch size of three was found in two nests, of four in four nests, and of five in six nests, for a mean minimum clutch

of 4.33 eggs per nest. This is larger than the mean figure for nests found before hatching. The population mean is probably approximated by both these figures.

Because of the small number of nests found, no attempt was made to look for seasonal differences in clutch size.

4.2.3 Incubation period

The accepted definition of the incubation period is the time from the laying of the last egg to the hatching of that egg. Only one nest was under observation for that period of time. This was nest number 67-8 in which the last egg was laid between 1410 hours on 21 June and 1040 hours on 22 June. This egg hatched between 1020 hours on 3 July and 1040 hours on 4 July. The egg was probably laid early in the morning of 22 June and one of the young was still damp on 4 July so that the incubation period can be considered to be 22 June to 4 July or 12 days.

4.2.4 Hatching

Six nests were observed during the hatching period. The pattern of hatching cannot be determined for one of these. Two of the remaining nests hatched over a two day period. In the remaining three nests, all young which hatched, hatched on the same day, but there was one egg in each nest which failed to hatch.

Further information on hatching pattern can be obtained from the calculated ages of nestlings. A number of nests contained one or more young which were developmentally a day younger than their nest mates. Of nine nests, excluding those in which hatching was observed, hatching was over a period of two days in five of the nests, and in one day in the

other four. This information on hatching pattern is summarized in Table 4.

It should be noted that the results of the two methods of determining hatching pattern do not conflict with one another and in all possible cases (Nests 66-6, 66-9, 67-1, 67-3 and 67-8) support each other. Summarizing the data from Table 4; of 13 nests whose hatching patterns could be determined, the eggs in seven hatched on one day, those in the remaining six, over a two day period.

Table 4. Hatching pattern as determined from observations of hatching and ages of nestlings.

Nest Number	Observation of hatching		Ages of nestlings		
	1 day	2 days	All same	One younger	Two younger
66-1				x	
66-2			x		
66-3			x		
66-5			x		
66-6		x		x	
66-7					x
66-9	x*		x		
67-1	x*		x		
67-3		x		x	
67-8	x*		x		
67-12					x
67-15		?		x	
67-16			x		

x* all hatch on one day but one egg failed to hatch

? hatching pattern not determined due to lack of observations.

4.2.5 Fledging

In this study the age of fledging is defined as the age at which a young bird leaves the nest, and a fledgling is defined as a young bird which has recently left the nest. It is necessary to define these terms to avoid confusion over the fact that the young leave the nest up to one week before they are capable of flight.

Nests which were enclosed to obtain information on growth and development of the young have been excluded from this section. From the remaining nests which were successful, it is possible to determine the age of fledging of 29 young. The distribution of fledging ages is as follows: 8 days- 7 birds, 9 days - 13 birds, 10 days - 6 birds, 11 days - 3 birds. The mean age of fledging is 9.17 days.

The effect of disturbance by the observer on the fledging of the young is difficult to determine. During the course of the study a fledgling from a nest which was not found was collected on 26 July, 1967. This bird was aged 8 days. On the other hand, birds which were being handled daily did not leave the nest until the age of 10 days (nest number 67-12). In one nest in which nestlings were not handled (nest number 66-6), the young fledged at the ages of 10 and 11 days. It appeared that human disturbance did not cause nestlings to leave the nest at ages younger than the natural fledging age of 8 to 11 days.

4.3 Breeding Behavior

4.3.1 General

The stages of the reproductive cycle of emberizines have been outlined by Nice (1943) for the Song Sparrow and by Tinbergen (1939) for the Snow Bunting (Plectrophenax nivalis) (Table 5). The stages in the reproductive cycle of the Savannah Sparrow parallel those of the Song Sparrow and Nice's divisions will be used. Stage 1, the proclaiming of territory, will be discussed in Chapter 6.

Table 5. Stages in the reproductive cycle of emberizine finches.

Song Sparrow (Nice, 1943)	Snow Bunting (Tinbergen, 1939)
	1. Males in flocks
1. Male proclaims territory	= 2. Males on territories
	3. Females present
2. Female arrives; prenuptial	= 4. Female on territory; preoestrus
3. Preliminary activities	} 5. Coition occurs
4. Building	
5. Laying	= 6. Laying
6. Incubation	= 7. Incubation
7. Care of young in nest	= 8. Nestlings
8. Care of young out of nest	= 9. Young have left

4.3.2 Prenuptial stage

This is the period between the arrival of the female and first copulation. During this period the females were more conspicuous than at any other time, except when feeding the young. Females were not noticeably localized in their activities on first arrival and moved freely around and off the study area. Shortly afterwards, however, they became paired and were usually seen in the company of a male. No special calls announcing the sex of females could be distinguished in the Savannah Sparrow.

From an examination of territory histories and observations on banded males it appears that a partial cessation of song by the male occurs upon pair formation. Actual counts of the songs per hour were not made but evidence is given by the presence or absence of individual males singing on their territories during the weeks prior to, during and after pair formation. Table 6 shows the observations on 18 individual males for the period 7 May through 10 June, 1967, divided into Weeks 3 to 7.

Table 6. Cessation of song by 18 male Savannah Sparrows at pair formation

Number of Males	Week				
	3	4	5	6	7
Recorded singing on territory	15	17	10	9	15
On territory, not singing	2	0	3	3	2
Not observed	1	1	5	6	1
Total	18	18	18	18	18

Since the chance of observation of a male is enhanced by song, it is likely that most of the males which were not observed during Weeks 5 and 6 (21 May - 3 June) were on their territories but were not singing.

It is difficult to observe pair formation or to ascertain whether it has occurred because of the secretive nature of the females. However, on a survey of the study area made on 25 May, 1967 there was evidence that at least 12 of 27 males recorded were paired, that is, they were in the company of a bird believed to be a female. Probably most birds were paired by this date. It was difficult to census females after late May as they were involved with nest building, laying and incubation and were even less conspicuous.

A probable male courtship display was observed on 25 May, 1967. A lone male gave this display while perched in a bush on his territory. The tail feathers were slightly spread and the wings were raised to a position near the horizontal and were quivered. Little or no extension of the carpal joint was noted. Some of the body feathers were raised, particularly the scapulars. The male gave "chip" call notes during this display. A female may have been in the vicinity but was not observed. This display was seen again on the same day. In this instance it was given by M14 to a female immediately after returning from a territorial fight. Shortly afterwards the female was seen in a weak precopulatory display, but no copulation took place. This display also occurred while the male was perched in a bush.

Sexual chases were recorded on a number of occasions. These are very similar to territorial chases and can only be distinguished by the

identity of the birds involved. During these chases the male sometimes gave a harsh, nasal call best described as a buzzing "wheent" or "wheenk". Normal flight was used during sexual chases.

The Buzzing Wheent call was also recorded in males prior to the arrival of females. It was noted to be given by two different males on 30 April, 1967. The call was accompanied by wing-quivering and sometimes progressed into a trill. It was given at a rate of approximately one call per second and would be given by a male as an interruption in a sequence of normal songs. In no case was this call recorded in connection with overt territorial defence, such as supplanting attacks, territorial chases or flights. The call was not heard after pair-formation.

Nice describes the "pounce" as the main element of male courtship in the Song Sparrow. Here the male "suddenly flies down to his mate, collides with her, and immediately flies away with a loud song"(1943:174). Nice states that pouncing is typically confined to the early stages of the nesting cycle and is probably analogous to the sexual chase of other birds. A similar behavior pattern was seen in the Savannah Sparrow. In all of these observations the male reacted to a movement of the female by flying to the position where she had landed, and pouncing on her. These observations took place after pair-formation and it is unlikely that the pounce is important in pair formation, as is the case in the Song Sparrows.

4.3.3 Preliminary stage

This stage is marked by the start of copulation. Complete copulation was not observed although soliciting by females and attempts to mount by males were both seen. The description of copulation is based on these observations plus observations made using a dummy mounted in the female precopulatory posture.

The female precopulatory display is typical of emberizine finches. The female perched in a bush with the body held horizontally. Both the head and tail were raised at angles of approximately 45° above the horizontal. The tail was not spread or vibrated. The wings were raised from the body by extension of the humeral joint and were quivered rapidly. If the male attempted to mount while the female was not responsive, she would peck at him as he hovered above her.

Males responded to a dummy in this position by approaching and mounting. The male sometimes sang in flight as he flew up to mount. The male landed on the back of the dummy and fluttered his wings, apparently to maintain balance as he shifted his footing and lowered his tail in an attempt to achieve cloacal contact. While mounted, males held the body very erect and the head was extended forward. The feathers of the crest were raised.

Copulation attempts with dummies were of very short duration but one male was observed to make four attempts in one minute, perching several feet away from the dummy between each attempt. On several occasions, copulation attempts by males were accompanied by a twittering call.

4.3.4 Building

Nest building behavior was not observed in this study but it is probably similar to that of other emberizines. In many cases the nests of known pairs of Savannah Sparrows were located outside the area defended by the male (see Section 6.3.1). The choice of the site is probably made by the female alone as is the case with most of the studied

Emberizinae (Nethersole-Thompson and Nethersole-Thompson, 1943).

Nest placement in relation to habitat will be discussed in Chapter 7. The actual nest site was similar in all cases. Nests were typically woven into the base of a clump of grass, or occasionally placed in a natural depression at the base of a clump of grass. Where a natural depression was not present, a scrape was excavated in which the nest was built. The nests were screened from view in all but one direction by overhanging grass. Because of the prevailing northwesterly winds of the area, the dead grass of previous years growth was bent over in a southeasterly direction and all nests found opened in a 135° compass arc from east through south-west. In some cases the overhanging grass formed a short tunnel through which the bird passed.

Nests were constructed entirely of grass. The grass of the outer cup was often woven into the grass clump in which the nest was placed. The linings of all nests were of finer grasses. Table 7 shows the dimensions of the nests, as well as the dimensions of scrapes under the nest.

Table 7. Dimensions of nests and scrapes

	Mean (mm)	Number in Sample	Range (mm)
Nest diameter	84.4	24	75-95
Cup diameter	62.7	24	60-75
Cup depth	39.2	24	25-50
Scrape diameter	75.7	7	65-85
Scrape depth	11.4	7	5-20

4.3.5 Laying

Only four of the 27 nests were found during the laying stage. In two of the nests it is possible to state that eggs were laid between mid-afternoon of one day and mid-morning of the next. In no instance did more than 24 hours pass between the laying of eggs.

The female must spend a certain portion of her time at the nest, other than when she is laying. All four of the nests found during laying were found by flushing the female from the nest and three of these occasions were in the mid-afternoon (1400-1600 hours).

4.3.6 Incubation

Incubation is performed by the female alone. No known male was ever flushed from a nest containing eggs and in this stage of the cycle the males appear to resume singing at a level comparable to that found before pair formation.

Incubation appears to start before the completion of the clutch in many cases. This is evidenced by the fact that the hatching of many nests extends over two days and in many nests one or two of the young appear to be younger than their nest mates.

During incubation the female sits very closely on the nest and it is necessary to pass within several feet of the nest in order to flush her. One female would not flush until an extended hand was within a foot of her. On some occasions birds would fly directly from the nest but more often they would give a distraction display upon leaving. Two types of displays were observed and a female would consistently give the same type of display.

Usually the female would flush from the nest, fly five to ten feet and then drop to the ground. She would then flutter along the tops of the bushes, or through the grass, with the tail spread and lowered and the wings raised and fluttered. No calls were noted. After this performance the female would perch, or flit nervously, 20 or more feet away from the observer, uttering alarm calls.

The second type of display is described as the "small mammal run" because of its similarity to a mouse moving through the grass. This display was given by the female from nest number 67-10 on three occasions. On June 22 this female flushed from the nest, landed five feet away and displayed. With the body held horizontal and the wings held close to the body, the bird ran for 20 feet, weaving through and under the grass. She then hopped up into the air, flew with a jerky flight for three feet, then dropped to the ground and ran on fluttering her wings in the more usual display. The female from nest number 67-17 gave a display described as a combination of the two types.

Distraction displays were common during incubation but declined in frequency after hatching when they occurred mainly in the first days of nestling life. On one occasion a female responded to the distress call of a nestling being banded by fluttering to within four feet of the observer in a very intense display.

4.3.7 Care of the young in the nest

During this stage of the cycle the activities of both birds of the pair are directed toward supplying food for the rapidly growing young. The male almost ceases singing and appears to do an equal share of the

feeding. Brooding of the young is suspected to be carried out only by the female, as is the case in the Song Sparrow (Nice, 1937: 130).

Time did not permit extended observation periods to allow accurate calculation of feeding rates. Birds which were observed while locating nests visited the nest at intervals of 5 - 10 minutes. The members of the pair appeared to alternate so that one adult was usually in the vicinity of the nest. All nests found in this manner were found at least several days after hatching.

Distraction displays may be given by the female if she is surprised on the nest while brooding. No known male gave a distraction display. When the birds were not on the nest, the typical reaction to an observer was for both adults to scold strongly. Two different notes are used in scolding. The first is the "chip" or "tsip" alarm call. This is the alarm note used by both females and males when closely approached by an observer at any stage of the cycle. The second call is louder, harsher, and may be described as "chep" or "clep". This appears to be a high intensity version of the first alarm call, since intergradation between the two notes was noted.

The "chep" or "clep" alarm call was never recorded during incubation. Both sexes were recorded giving it, primarily during the late nestling period and after the young fledged.

4.3.8 Care of the young out of the nest.

The young leave the nest at an age of 8 - 11 days (see section 4.2.5). Both parents appear to care for the young for at least 10 days after fledging. Whether both sexes take an equal share in this activity is

not known, but on at least one occasion, a banded female, F23, was seen in company with 18-19 day fledglings. No observations of parental care were made after the age of 20 days but fledglings were observed on what was believed to be the territory of their parents up to an age of 27 days. Young Song Sparrows become fully independent at an age of 28-30 days (Nice, 1937: 133).

4.4 Post-breeding Dispersal

The Savannah Sparrows dispersed from the study area gradually, beginning about the second week of July. The latest dates that Savannah Sparrows were recorded on Kernen's prairie were 8 August 1966 and 4 August, 1967. Figure 7 shows the results of censuses from 6 July through 10 August, 1967 and documents the pattern of departure. The population on 6 July (Week 11) is only slightly lower in numbers than earlier in the breeding season. It is similar to earlier surveys in the proportion of the sexes (approximately 75 percent males, 20 percent females). The population then decreased slowly until 20 July and then very rapidly until the last birds had left. This rapid drop in the population censused is due largely to emigration, but cessation of song by males made them less conspicuous and likely to be undercensused as was also true of females and juvenile birds. It appears possible that the males leave the breeding area before the females (Figure 7). This may be an artifact resulting from the cessation of singing by males, but the idea is supported by the fact that three birds randomly collected on 2 and 3 August, 1967 were all females. Random collecting earlier in the season resulted in the collection of predominantly male birds.

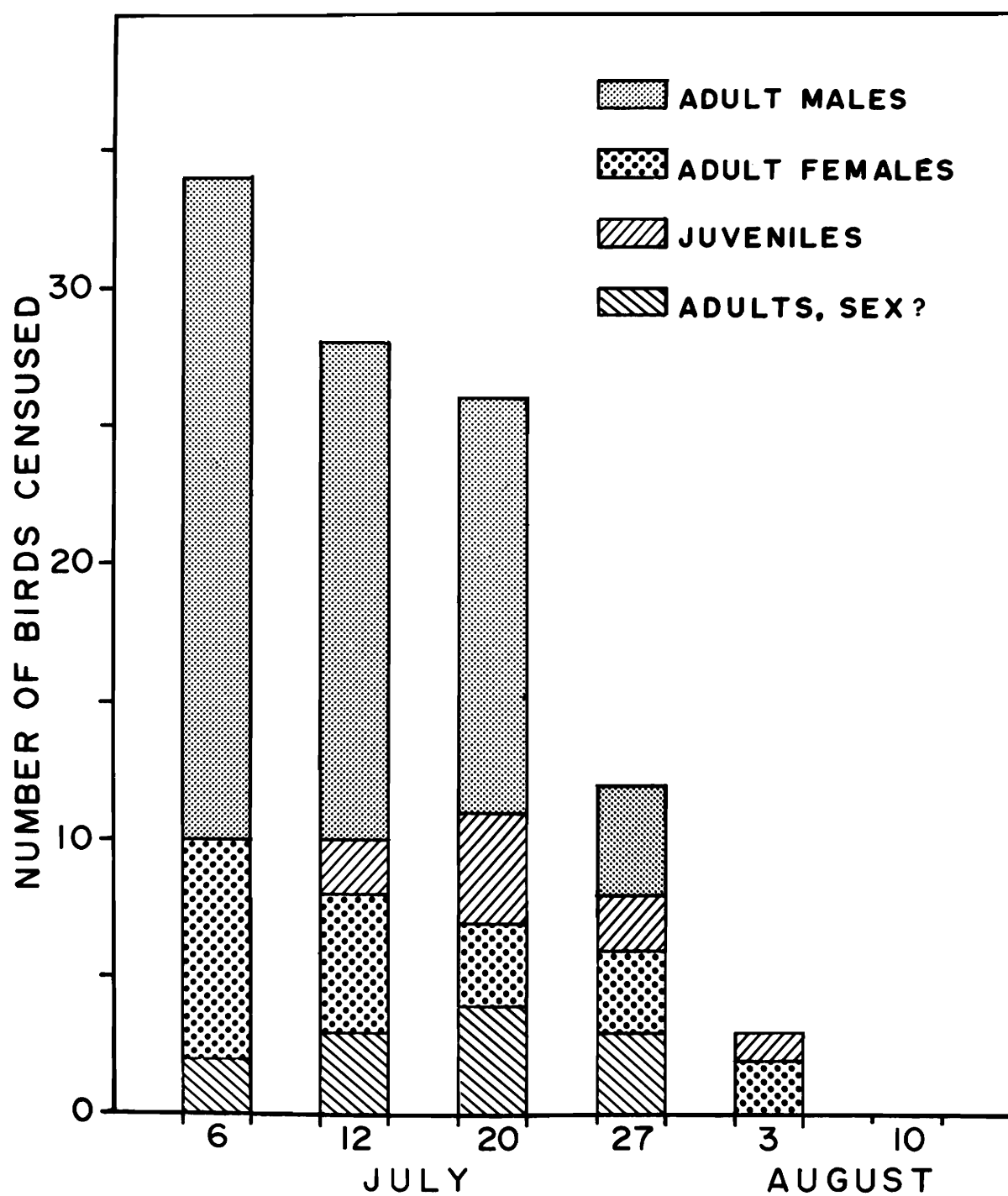


Figure 7. Number of Savannah Sparrows recorded during censuses, late summer, 1967.

After leaving the breeding grounds Savannah Sparrows were seen in the vicinity of Saskatoon for as long as two months. No collecting was done and it is not possible to state when the local residents left and were replaced by migrants from the north. During this period they were seen in weedy fields, along road sides and in other places with suitable cover and food. Flocks were seen around the margins of lakes and sloughs. On 10 September, 1967, the writer flushed approximately 25 Savannah Sparrows from one-quarter mile of shoreline vegetation at Rice Lake, 18 miles west of Saskatoon. The vegetation was primarily the bullrush Scirpus paludosus with traces of S. acutus and Typha latifolia. This density of birds is considerably higher than is found in local breeding populations. The latest dates for Savannah Sparrows in the Saskatoon area during the study seasons were 15 October, 1966 and 24 September, 1967 (Gollop, 1966; Gollop, 1967b).

4.5 Breeding Success

4.5.1 Success

Breeding success or survival as calculated from exposure (Mayfield, 1961) is shown in Table 8. When calculated in this fashion nest success was 24.2 percent, the product of survival of nests during incubation (41 percent) and of survival of nests during the nestling period (59 percent). However, when losses of individual eggs and nestlings were considered (omitting infertile eggs), the probability of survival of an individual egg from the start of incubation to the fledging of the young was 0.16 or 16 percent.

Table 8. Survival of nests, eggs and young calculated from exposure.

Survival of:	Number of day units	Losses	Losses per day	Survival per day	Probability of survival
Nests during incubation	56	4	0.07	0.93	0.41
Nests during nestling period	88	5	0.06	0.94	0.59
Individual egg during incubation	177	2	0.01	0.99	0.88
Individual egg during hatching	--	1/20	-----	-----	0.95
Individual nestling during nestling period	272	7	0.03	0.97	0.79
Total period	--	-	-----	-----	0.16

Conventional calculations of breeding success are in Table 9.

Nests which were lost during laying, and those found after hatching could not be used in these calculations. Four or 50 percent of the remaining eight nests were successful (i.e. fledged at least one young). Survival of eggs during incubation was 51.5 percent and survival of eggs to fledging was 39.4 percent. When all 27 nests found during the study are considered, 14 or 51.9 percent were successful.

Table 9. Survival of nests, eggs and young calculated from losses. Only those nests found during incubation are used (Total of 8 nests).

Survival of:	Number	Number lost	Percent lost	Percent survived
Nests	8	4	50.0	50.0
Eggs to hatching	33	16	48.5	51.5
Eggs to fledging	33	20	60.6	39.4
Young to fledging	17	4	23.5	76.5

All nests	27	13	48.1	51.9

4.5.2 Causes of loss

Causes of nest loss are generally difficult to determine. During the present study evidence was obtained which implicates several species of small mammals as important factors in nest loss of ground nesting birds. Nest number 67-4 was found predated on 12 June, 1967. A numbered egg shell from this nest was found at the entrance to the burrow of a Thirteen-lined

Ground Squirrel, about 10 feet from the nest. The lining of the nest was slightly torn. No egg shells were found at the nest. Many of the predated nests had no egg shells present and had torn linings, and it appears that ground squirrels were a cause of significant nest losses.

A Baird's Sparrow nest on the plot was predated on 11 June, 1967. One of the four eggs was whole and in the nest, one was broken in the nest and two were broken and empty near the nest. These last two eggs had small holes chewed in them (see Plate 7) and were in a small mammal runway. Fresh scats of mouse size were found with the eggs. The predator here was probably a Meadow Vole or a Deer Mouse, more likely the former in view of the habitat and relative abundance of the two species. Several Savannah Sparrow nests were also predated by predators who left egg shells in or near the nest and small mammals are a possible suspect in these cases.

A pair of Red Foxes, and subsequently their young, hunted the study area in both seasons. They were probably a factor in nest mortality after hatching but this was not documented.

4.5.3 Effects of cowbird parasitism

None of the ten nests found during 1966 were parasitized by the Brown-headed Cowbird (Molothrus ater). In 1967, however, six of the seventeen nests found were parasitized. Cowbirds were much more conspicuous on the study area during that year and other species of birds were also heavily parasitized. A description of the parasitism and the results in parasitized nests follows:

67-1: Found on 5 June when it contained 3 host and 2 parasite eggs. Two host eggs and both parasite eggs hatched on 11 June. The nest



Plate 7. Egg of a Baird's Sparrow showing damage caused by predation by a small mammal, probably a Meadow Vole.

was predated on 15-18 June.

67-2: Found on 8 June when it contained one cowbird egg. A punctured Savannah Sparrow egg was found six inches from the nest (see Plate 8). This nest was abandoned immediately.

67-3: This nest contained five Savannah Sparrow eggs, all of which hatched. On 18 June, when the young were 7 days of age, a fresh cowbird egg was found in the nest. This egg remained after the young sparrows fledged.

67-4: This nest was found on 9 June when it contained three sparrow eggs and one parasite egg. The clutch was complete by 11 June with four host and one parasite eggs. The nest was predated before hatching.

67-6: This nest contained two host eggs and three cowbird eggs on 19 June. Subsequently three more host eggs were laid to give a full clutch of five sparrow eggs and three parasite eggs on 22 June. This nest was also predated before hatching.

67-13: On 3 July, this nest contained a three-day old host nestling, a cowbird nestling and an infertile cowbird egg. Both young fledged successfully.

Summarizing the effects of brood parasitism, it is possible to say that parasitism early in the laying period may possibly cause desertion (nest number 67-2), but that later in the laying period it apparently has no effect on abandonment. It appears that cowbirds frequently remove a host egg from the sparrow nest when laying one of their own (nests number 67-1, 67-2) but this does not always seem to be the case; it is unlikely that eight host eggs were laid in nest number 67-6. Eggs of the parasite



Plate 8. Savannah Sparrow egg from nest number 67-2 showing damage caused by a Brown-headed Cowbird during removal of the egg from the nest.

are normally deposited during the laying period of the host, but in one case an egg was laid after the host young had hatched.

The effect of cowbirds on success after hatching was variable. The one host nestling in nest number 67-13 grew normally but it is possible that other host nestlings had starved before the nest was found. In nest number 67-1 with two young of both the host and parasite species, growth of the host species was affected. Figure 8 compared the growth in weight of the host young in this nest to the growth in weight of five Savannah Sparrow nestlings in nest number 67-3 which hatched on the same date as the young in 67-1. It is apparent that the two cowbird nestmates had a detrimental effect on their growth.

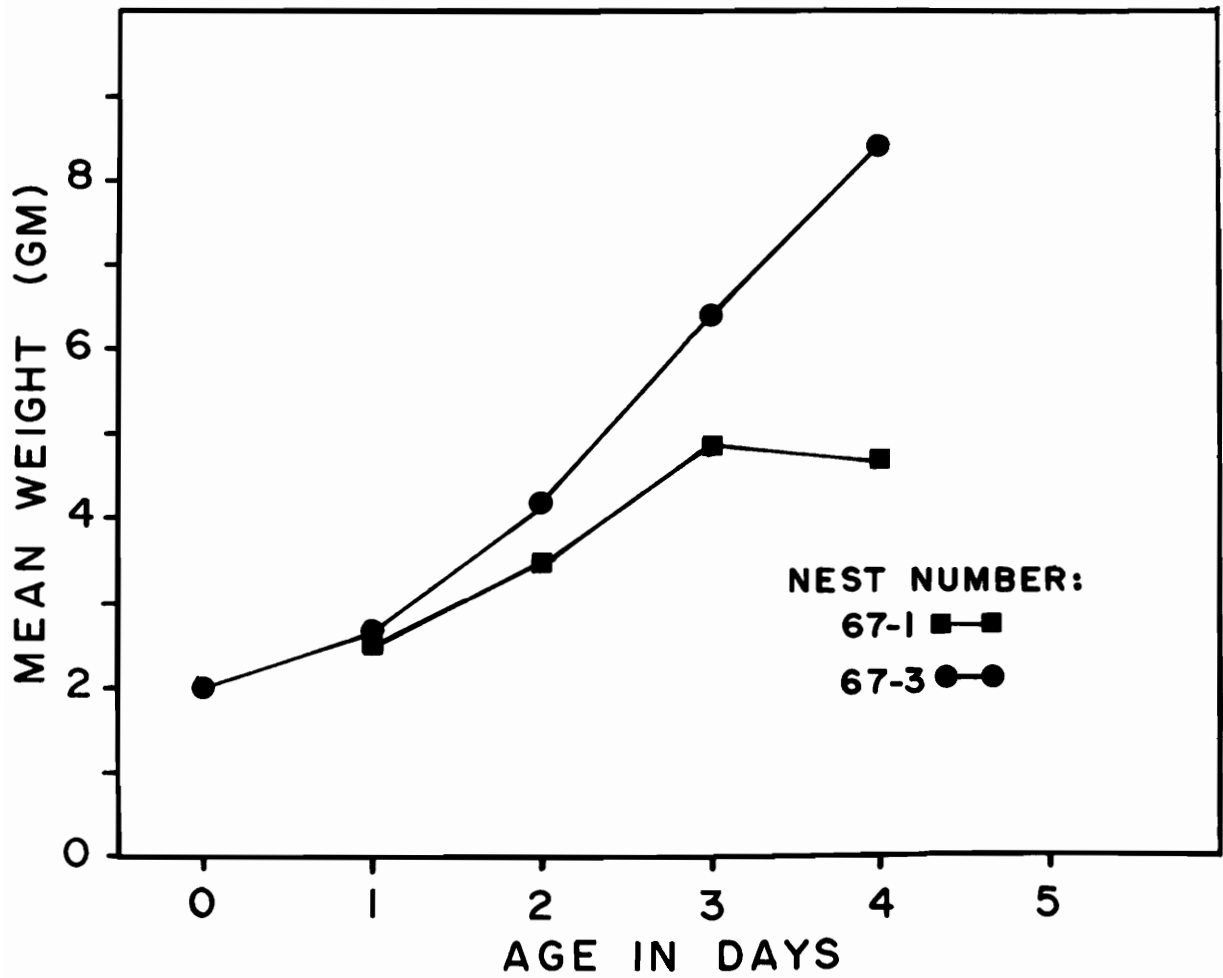


Figure 8. Growth curve for nestlings in a nest with two Cowbird nestmates (67-1) compared to the growth curve for nestlings in an unparasitized nest (67-3).

5. GROWTH AND DEVELOPMENT

5.1 Description of the Young

5.1.1 Plumage development

Terminology used in the description of the feather tracts is taken from Van Tyne and Berger (1959: 88-91)

Day 0: The newly hatched young were partially covered with dark gray down about 6 mm in length. This was found on the coronal and frontal regions of the capital tract, the dorsal and interscapular regions of the spinal tract, and on the alar, femoral and humeral tracts. The papillae of the primary and secondary remiges of the alar tract were seen faintly through the skin.

Day 1: The plumage was similar to that of Day 0 birds, but the feather papillae of the incoming juvenal plumage were seen through the skin on the spinal tract (dorsal and interscapular regions) and on the humeral tract.

Day 2: Pigmentation of the papillae in the alar, humeral, spinal, and capital tracts made them much more conspicuous. Papillae were faintly visible beneath the skin on the pelvic and femoral tracts, on the cervical region of the spinal tract, on the occipital and auricular regions of the capital tract, and on the sternal region of the ventral tract. The quills of the primary remiges had begun to protrude through the skin.

Day 3: Papillae were pigmented and readily visible on all previously mentioned tracts. On this day papillae were seen faintly on the caudal and crural tracts. The quills of the primary and secondary wing feathers and those of the primary and secondary coverts had broken through the skin.

Day 4: The quills of feathers of many of the tracts had begun to protrude through the skin on this day. These included the alar, humeral, capital (frontal, coronal and occipital regions), spinal (cervical, dorsal and interscapular regions), femoral and central tracts. The quills of the crural tract were still beneath the skin.

Day 5: This day marked the first emergence of feathers from their sheaths. This occurred on the spinal, ventral, pelvic and femoral tracts. Quills of the crural tract and of the rectrices were protruding through the skin.

Day 6: Feather emergence continued. It was now noticeable on the spinal, ventral, femoral, crural, and alar tracts. The quills of the capital tract and those of the primary and secondary remiges had not split. The third primary now measured about 10 mm and the central rectrices about 1 mm.

Day 7: The nestlings appeared to be well feathered and thermoregulation appeared to have begun. Nestlings of this age were noted to shiver and fluff their feathers on a cool day. Both the remiges and the rectrices had begun to emerge from their sheaths, as had the feathers of the coronal region of the capital tract. The anal circlet was noticeable as the feathers had broken their sheaths. The nestlings still showed tufts of the natal down on the tips of the feathers of all tracts which had borne down at hatching.

Day 8: The only quills which had not yet broken through their sheaths were those of the frontal, loreal, auricular and superciliary regions of the capital tract and the interramal region of the ventral tract. Plates

9, 10, and 11 show a nestling at this stage of feather development.

Day 9: All feathers had broken out of their sheaths, but sheaths remained on the bases of the remiges and coverts of the alar tract, the frontal, loreal, superciliary and auricular regions of the capital tract, and the interramal region of the ventral tract.

Day 10: Young birds of this age were tailless and short-winged, but well feathered. All down was lost except for some slight tufts on the feathers of the capital and spinal tracts.

Day 12: All natal down was gone. The tips of the rectrices were visible beyond the coverts above and below them. Feather sheaths were not openly visible but could be found at the bases of the rectrices and remiges. Plates 9, 10 and 11 show a fledgling of this age.

Day 16: Young of this age were flying strongly. They were still bob-tailed and the wings had not reached full length but otherwise the birds had the full juvenal plumage. A bird of this age is shown in Plates 9, 10 and 11.

5.1.2 Juvenal plumage

The juvenal plumage of the Eastern Savannah Sparrow (Passerculus sandwichensis savanna) has been described by Dwight (1900) and by Sutton (1935). That of P.s. nevadensis is basically similar. Capitalized color names are those of the Villalobos color chart (Palmer, 1962).

The juvenal plumage is acquired by a complete postnatal moult. The development of this plumage has been described in Section 5.1.1. Development begins at hatching and is complete, except for final growth of the remiges and rectrices by the age of 15 days.



Plate 9. Plumage development of young Savannah Sparrows, Ventral view.
Left to right: Day 8, Day 12, Day 16.



Plate 10. Plumage development of young Savannah Sparrows. Lateral view.
Left to right: Day 8, Day 12, Day 16.



Plate 11. Plumage development of young Savannah Sparrows. Dorsal view.
Left to right: Day 8, Day 12, Day 16.

The feathers of the dorsal plumage are Black edged with pale Buffy Yellow. The edgings become Buffy Brown on the feathers of the crown (except on the median stripe) and on the wing coverts. The margins of both the remiges and the rectrices are a pale Chestnut. Below, the color shades from pale Buffy Yellow anteriorly to White posteriorly. The feathers are finely streaked with Black to Blackish Gray on the upper breast, sides and flanks. The facial pattern is dominated by creams and buffs. The superciliary line is pale Cream with fine Black streakings. There is a Black eye-stripe of variable extent and two diffuse Black stripes in the malar region. The plumage of the auricular area is Buffy Yellow to Buffy Brown in different specimens.

Sutton (1935) believes that there are two color phases in the juvenal plumage of P.s. savanna. He states (p.19):

"In the series of fourteen juvenal specimens at hand five are distinctly dull colored in general appearance, the underparts being quite without any suggestion of yellow or buffy-yellow. All others are much more colorful both above and below".

During the present study an attempt was made to ascertain the presence of these phases in P.s. nevadensis. Variation in the color of the underparts was recorded, but this was a highly variable character and did not seem to fall into two distinct "phases". The upper breast was uniformly Buffy Yellow but the color of the belly varied from pale buffy yellow to cream to white in different individuals. Differences could be typified only by comparison to nest mates. Of 18 young approaching fledging 15 were characterized as "white phase", two as "yellow phase" and one as intermediate.

A partial postjuvenal (prebasic I) moult replaces the body plumage and the wing coverts but not the remiges and rectrices (Dwight, 1900).

In P.s. savanna this begins in late June or early July and is complete by early to mid-September (Sutton, 1935). In birds which hatch later in the season, this moult is undoubtedly later. No birds known to have hatched near Saskatoon were collected in the first winter (basic I) plumage. Other Saskatchewan specimens show that this plumage is found in birds collected as early as 2 September. It is easily distinguished from the juvenal plumage by the lesser extent of black on the dorsal areas due to the narrower medial streaks, and by the absence of the plumulaceous nature of the juvenal feathers. Plates 12, 13 and 14 compare the juvenal, first winter (basic I) and nuptial (alternate) plumages of the Savannah Sparrow.

5.1.3 Soft parts

The skin of newly hatched nestlings was orange-yellow or salmon in color. By Day 3 the skin was less orange in color and the exposed skin of older nestlings was yellowish-pink in color. The bill was yellowish-pink at hatching and gradually darkened to a blackish-pink by Day 15. The hinge of the mandibles was pale yellow in color and was still prominent at Day 15. The lining of the mouth was a bright pinkish-red. The feet were a yellowish-pink in color, somewhat lighter than the skin. The egg tooth was still present on nestlings when they fledged but was subsequently lost between the ages of 12 and 16 days.

The eyes, which were closed at hatching, began to open on Day 3. By Day 5 the eyes were completely open and on Day 6 a nestling was noted to sit up and peer around intently.

The feces were enclosed in a fecal sac up to the age of 8 days. On Day 8 some individuals no longer produced fecal sacs and by Day 9 they

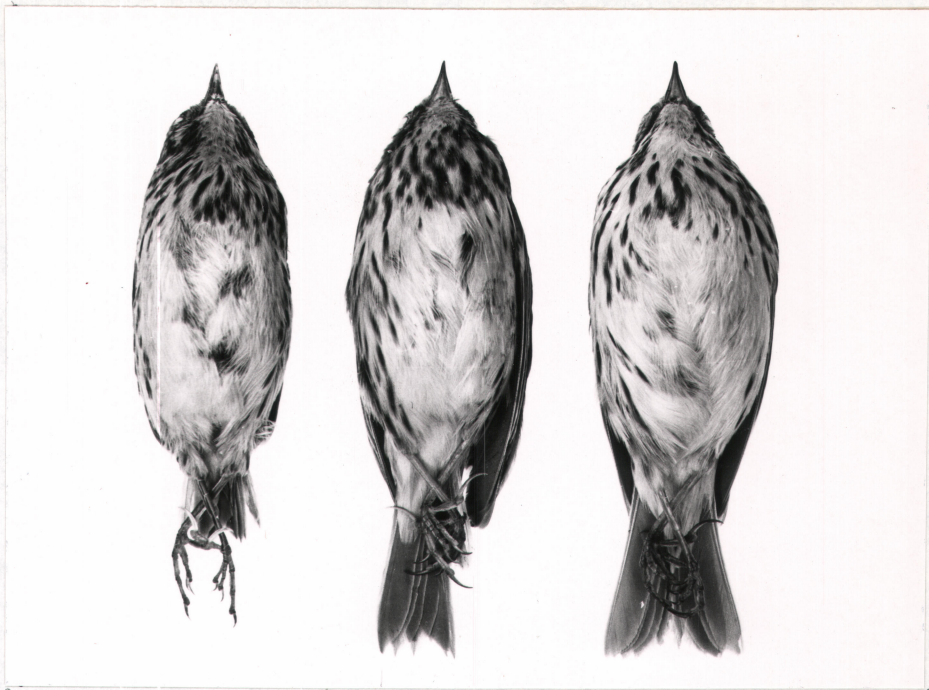


Plate 12. Plumages of the Savannah Sparrow. Left to right: Juvenal, First Winter (Basic I), and Nuptial (Alternate). Ventral view.

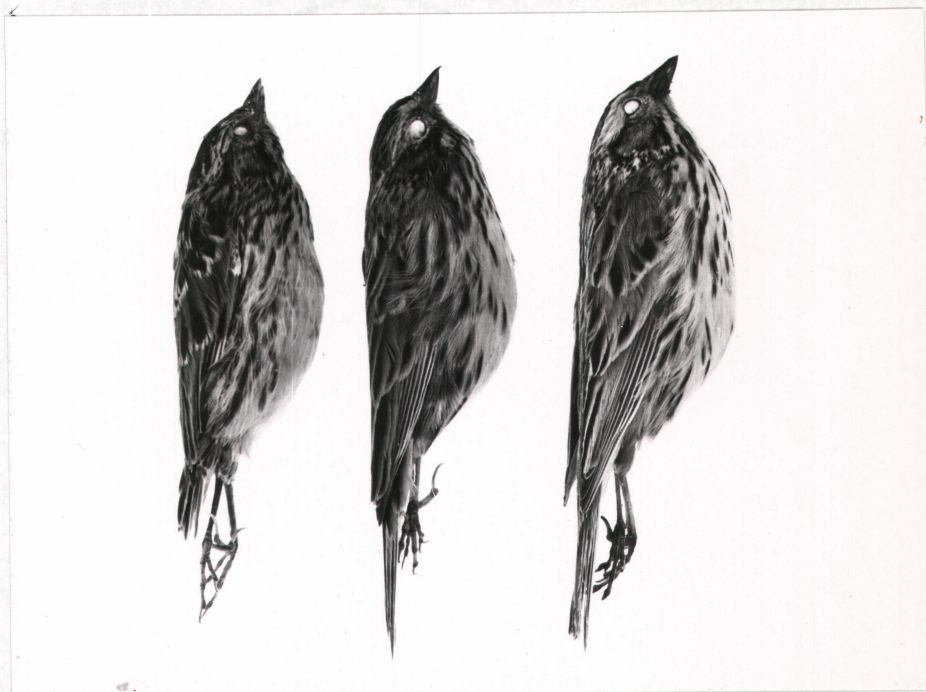


Plate 13. Plumages of the Savannah Sparrow. Left to right: Juvenal, First Winter (Basic I), and Nuptial (Alternate). Lateral view

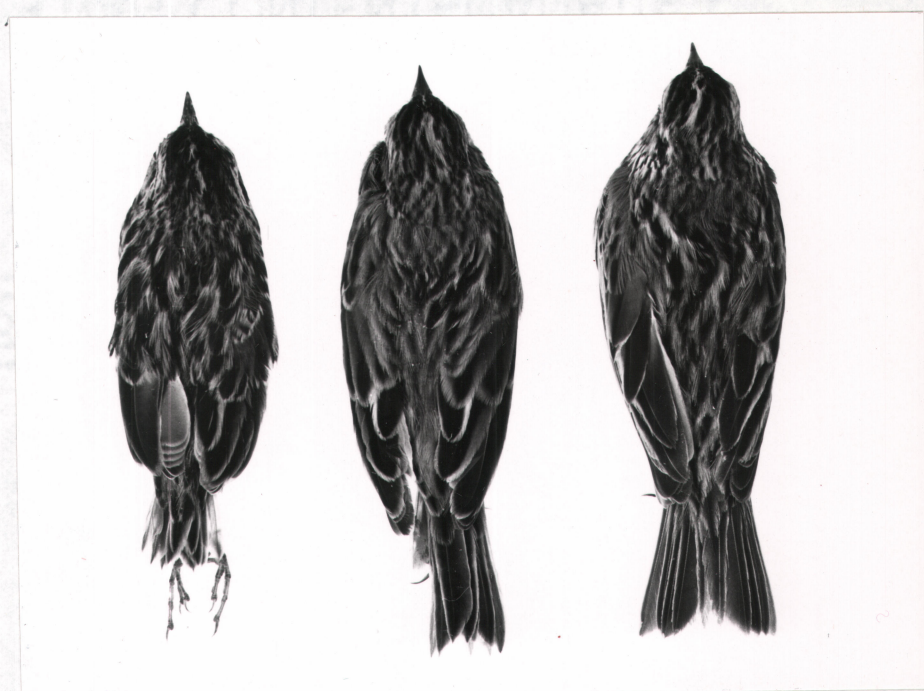


Plate 14. Plumages of the Savannah Sparrow. Left to right: Juvenal, First Winter (Basic I), and Nuptial (Alternate). Dorsal view.

were not recorded.

5.2 Growth

The growth of six different characters was measured during the present study (Section 3.5). The results of these measurements are shown in Tables 10 through 15, and are graphically displayed in Figures 10 through 13. For comparative purposes, the corresponding measurements of 21 adult male and 6 adult female Savannah Sparrows are given in Table 16 (except third primary length). These measurements were taken on live birds at the time of banding in the same fashion that the nestlings were measured.

Table 10. Growth in weight of nestling Savannah Sparrows.

Day	Mean weight (gm)	Range (gm)	N
0	1.62	0.8 - 2.5	5
1	2.77	2.5 - 3.2	7
2	4.23	3.2 - 5.3	12
3	5.67	3.1 - 7.2	16
4	8.08	4.5 - 10.1	20
5	9.98	8.8 - 11.4	20
6	11.77	10.3 - 13.6	13
7	13.44	11.8 - 16.5	25
8	14.06	12.5 - 15.3	13
9	15.26	13.1 - 16.1	10
10	14.33	13.7 - 15.0	3
11	15.43	14.1 - 16.9	3
12	15.55	14.7 - 16.4	2

Table 11. Wing length of nestling Savannah Sparrows

Day	Mean wing length (mm)	Range (mm)	N
0	6.5	6.0 - 7.0	4
1	7.3	7.0 - 8.0	6
2	8.7	8.0 - 9.5	11
3	11.3	10.0 - 13.0	6
4	15.6	14.0 - 19.0	8
5	19.0	---	1
6	23.2	22.0 - 25.0	5
7	28.5	25.0 - 32.0	14
8	32.3	30.0 - 34.0	6
9	36.6	35.0 - 38.0	5
15	52.0	---	1

Table 12. Third primary length of nestling Savannah Sparrows

Day	Mean primary length (mm)	Range (mm)	N
3	0.9	0.5 - 1.5	7
4	3.1	1.0 - 5.0	12
5	5.9	3.0 - 9.0	13
6	10.2	7.0 - 12.0	13
7	14.7	11.0 - 17.0	26
8	19.2	15.0 - 22.0	16
9	23.6	22.0 - 25.0	8
10	27.7	27.0 - 28.0	3
11	30.7	30.0 - 31.0	3
12	34.0	---	2
15	39.0	---	1

Table 13. Central rectrix length of nestling Savannah Sparrows.

Day	Mean rectrix length (mm)	Range (mm)	N
4	trace	---	5
5	0.8	trace - 1.5	9
6	1.1	0.5 - 2.0	13
7	2.6	1.0 - 4.5	26
8	4.2	3.0 - 6.0	16
9	5.8	5.0 - 7.0	8
10	10.3	9.0 - 11.0	3
11	12.0	10.0 - 13.0	3
12	16.5	16.0 - 17.0	2
15	24.0	---	1

Table 14. Tarsus length of nestling Savannah Sparrows.

Day	Mean tarsus length (mm)	Range (mm)	N
0	6.0	5.5 - 6.5	4
1	7.8	7.5 - 8.0	6
2	9.5	8.5 - 10.0	11
3	11.5	11.0 - 13.0	6
4	14.4	13.0 - 16.0	8
5	15.0	---	1
6	17.1	17.0 - 17.5	5
7	19.5	18.0 - 21.0	14
8	18.9	18.0 - 19.5	6
9	19.8	19.0 - 20.5	5
15	19.0	---	1

Table 15. Exposed culmen length of nestling Savannah Sparrows.

Day	Mean culmen length (mm)	Range (mm)	N
0	4.0	3.5 - 4.5	4
1	4.4	4.0 - 5.0	6
2	4.5	4.0 - 5.0	11
3	5.1	4.5 - 5.5	6
4	5.6	5.0 - 6.0	8
5	6.0	---	1
6	6.9	6.5 - 7.0	5
7	7.3	7.0 - 8.0	14
8	7.7	7.5 - 8.0	6
9	7.6	7.5 - 8.0	5
15	8.0	---	1

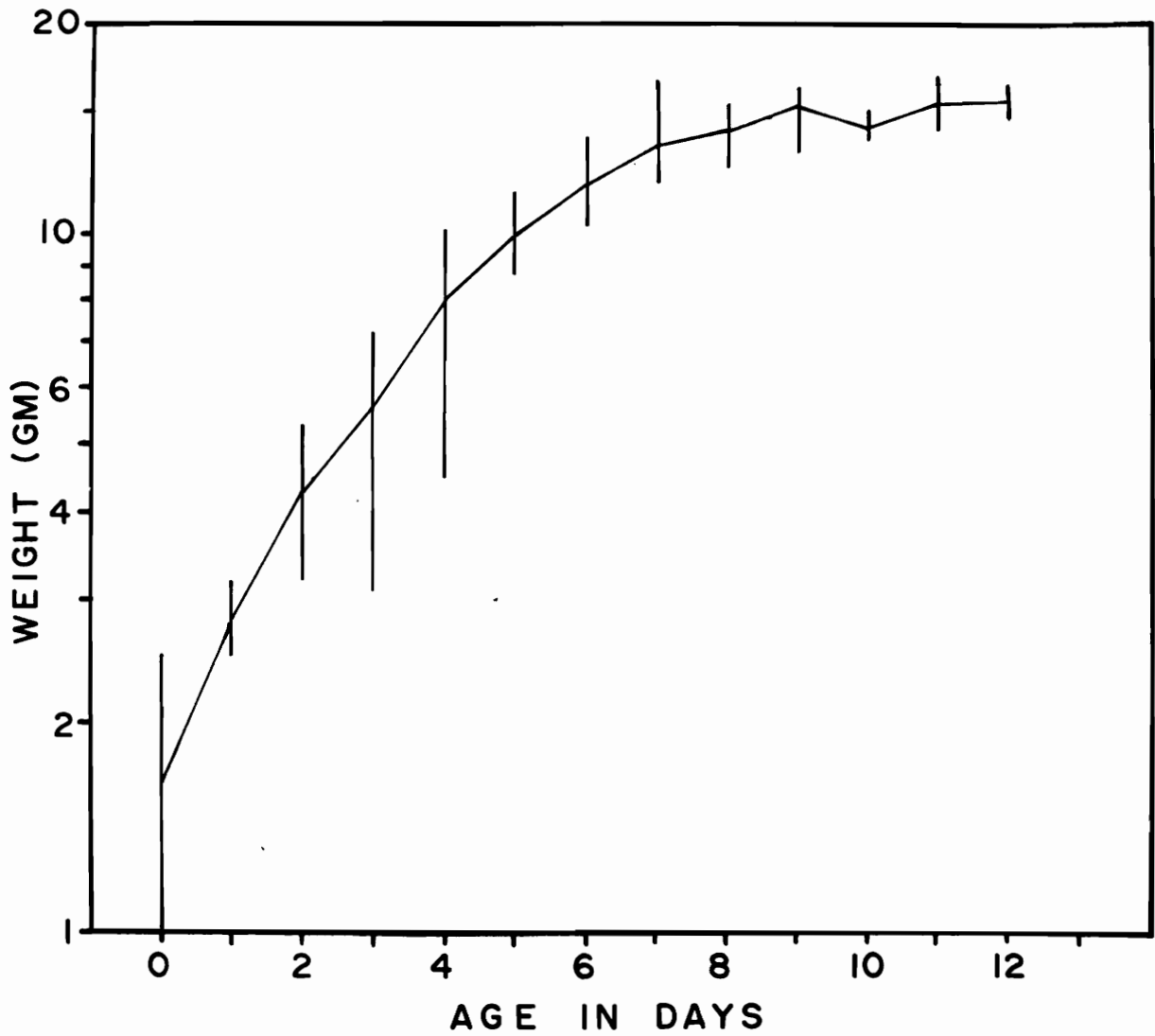


Figure 9. Growth in weight of nestling Savannah Sparrows. Vertical lines indicate range of daily weights. Semi-logarithmic scale.

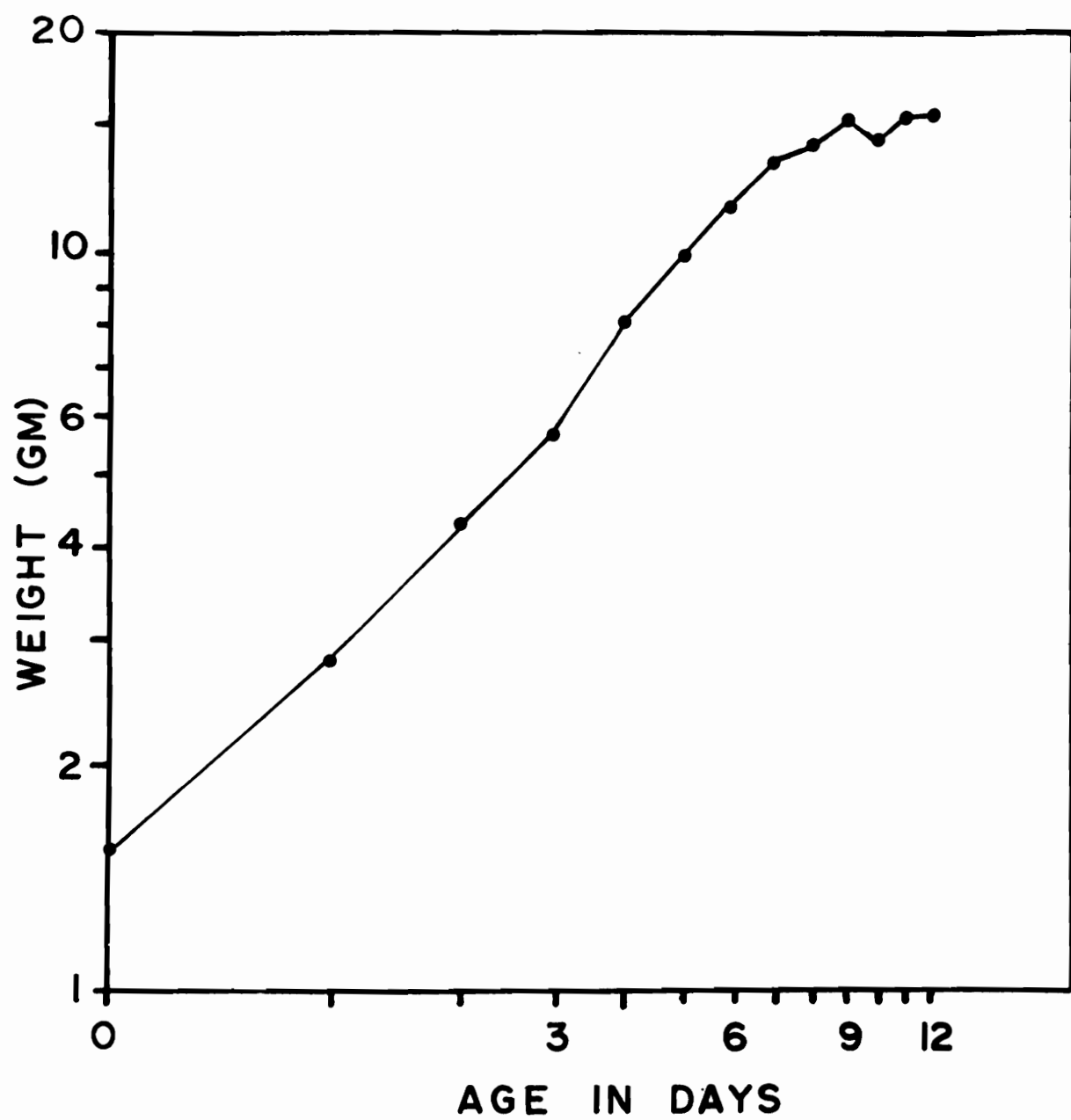


Figure 10. Growth in weight of nestling Savannah Sparrows. Logarithmic scale.

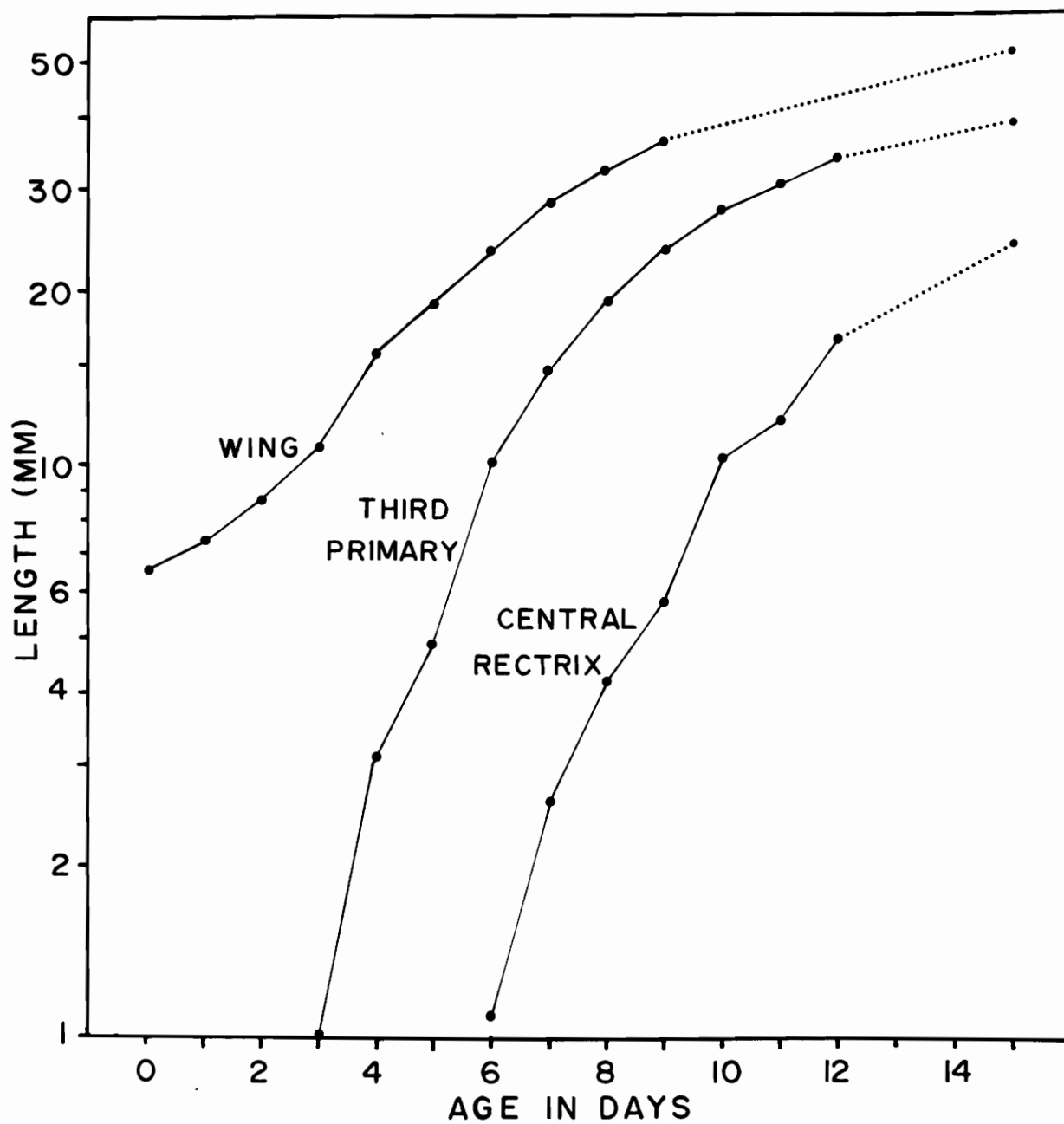


Figure 11. Growth of wing, third primary and central rectrix of young Savannah Sparrows. Semi-logarithmic scale.

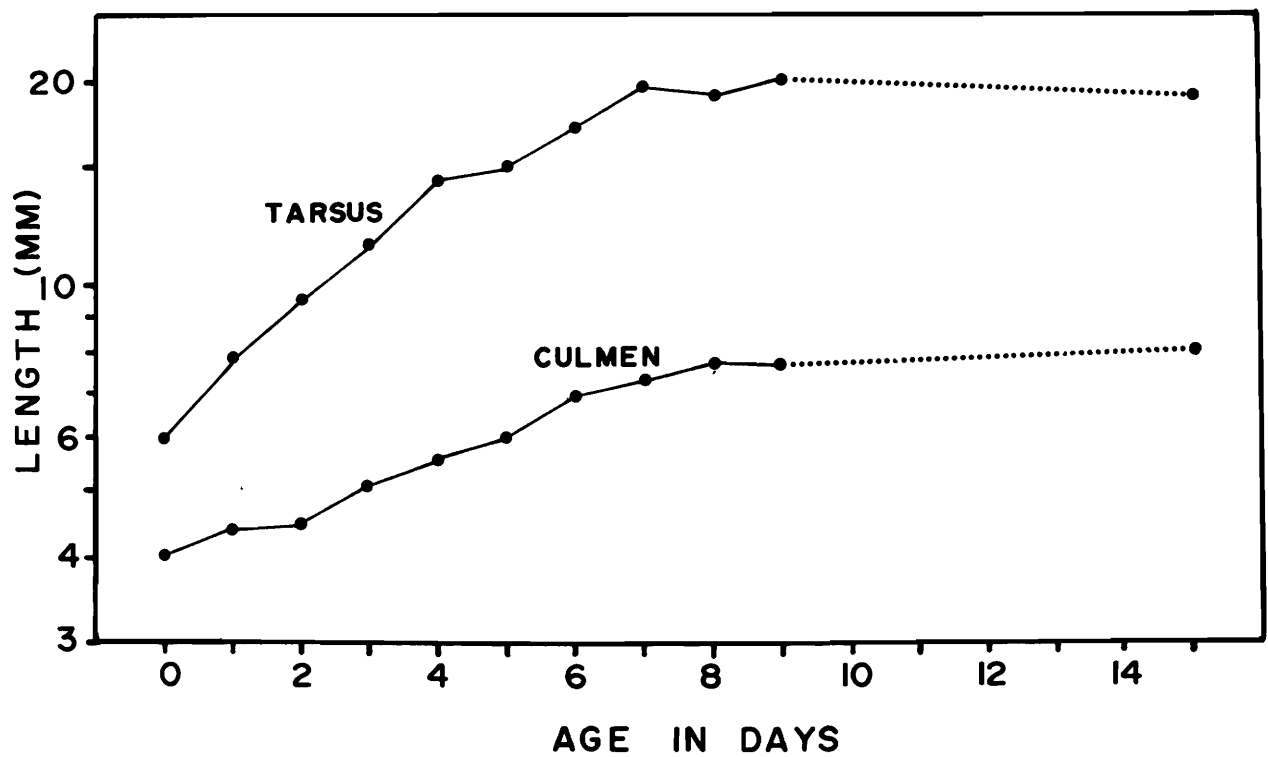


Figure 12. Growth of tarsus and exposed culmen of young Savannah Sparrows. Semi-logarithmic scale.

Table 16. Measurements of live adult Savannah Sparrows

Character	Males			Females			Combined
	Mean	Number	Range	Mean	Number	Range	Mean
Weight (gm)	19.1	19	17.2 - 21.3	18.3	6	15.7 - 21.9	18.9
Wing length (mm)	71.1	21	69.0 - 74.0	67.4	6	66.5 - 69.0	70.3
Rectrix length (mm)	50.1	21	48.5 - 52.0	48.6	6	47.0 - 51.0	49.8
Tarsus length (mm)	20.8	21	20.0 - 22.0	19.8	6	19.0 - 20.0	20.6
Exposed culmen (mm)	10.9	19	10.0 - 11.5	10.8	6	10.0 - 11.3	10.9

5.3 Behavioral Development

5.3.1 Vocalizations

Newly hatched young (Day 0) were silent. After this time three distinct vocalizations were recorded.

Begging Call: This call was best described as a buzzing or wheezing "peep" or "seep", given while the young birds were gaping for food. It was first recorded on Day 1. At that age it was very weak and faint, but it became louder, until Day 4 when it was very audible. It was not recorded after Day 6 except in one nest where it was given on Day 9 in response to the location call of a nest mate. This call was always given in conjunction with begging and its disappearance after Day 6 accompanied the cessation of indiscriminate gaping.

Distress Scream: This call was given by birds that were handled roughly or restrained during banding or weighing. It may be described as a shrill "wheep" or "wheenk". It was first given on Day 7 and continued until at least Day 15. Its effect on parental behavior was described in Section 4.3.5

Location Call: This call is a loud sharp "chep". It was first given by a Day 9 bird. It was also heard from fledglings in company with their parents.

5.3.2 Fear and escape

No signs of fear of the observer were noted until Day 4, when the birds occasionally struggled when held. Until Day 7 the birds were generally quiet when held. From Day 7 onward the young struggled very vigorously when held or confined. The development of this behavior coincided with the first record of the distress call. Day 8 young sometimes

fled the nest when replaced, but this was not general until Day 9 or 10.

5.3.3 Begging

No gaping or other begging activity was noted in Day 0 birds. Beginning on Day 1 they gaped and called indiscriminately at disturbances such as a whistle or a vibration of the nest. Gaping was accompanied by the begging call. Gaping was directed straight upward from Day 1 to Day 3. After this age (and coinciding with the opening of the eyes) gaping was directed in the direction of a finger, pencil or other object held near the nest.

On Day 1 the body was held horizontal and the head was only slightly raised during gaping. The gaping motion was very wobbly. On Days 2 and 3 the birds began to hold their bodies more vertically using the legs and wings as props. On Day 3 the complete begging pattern of older nestlings was established. The body was held vertically and the neck was stretched fully.

Discrimination in gaping began to develop at Day 6 and was complete by Day 8. At Day 8 the nestlings would no longer gape at disturbances, even if their bills were actually touched with a pencil. Gaping was observed in Day 9 young but this was in response to the location call of a nest mate, and was directed toward the nest mate.

5.3.4 Motor development and coordination

Movements of the Day 0 young were restricted to grasping motions of the feet when the young were picked up. These grasping motions developed until the age of Day 6 or 7 when the young could perch on a finger or other object.

Day 1 young, when placed on a flat surface, could crawl after a fashion with "swimming" motions of the wings and legs. This type of movement continued until Day 6 when the young sat up and hopped. The first attempt to fly from the hand was noted in a Day 9 young. Flights of one foot were accomplished on Day 11 and of five feet on Day 12. No altitude could be gained until Day 13 when the young were apparently able to fly over the 18 inch walls of the enclosure confining them. By Day 15 they were flying strongly and were capable of flights of at least 100 feet. It was possible to run down and capture young of this age, but only with considerable effort.

6. TERRITORY

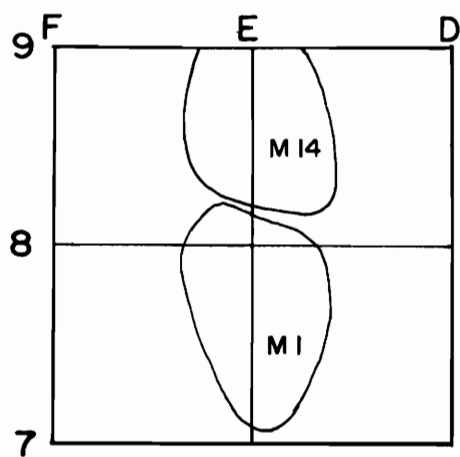
6.1 Territory Establishment

The pattern of arrival of male birds on the study area has been described in Section 4.1. Territorial establishment appears to begin immediately. The first birds recorded in both 1966 and 1967 were singing and they appeared to remain on the territory where they were first seen. In other cases birds, which were believed to be newly arrived, were noted in an area, silent or singing weakly, on one day, then singing strongly on the next. These cases were after the first arrivals and may have reflected the influence of other males who were established and singing.

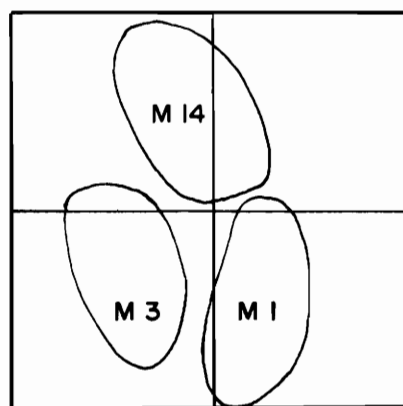
The size of the territories was calculated during 1967. During the period of establishment (27 April-15 May) the territories of individual males as outlined by song perches were larger than those defended later in the season. The mean area of six territories during establishment was 0.39 acres while the mean of 18 territories later in the season was 0.17 acres (see Table 17). The mean area after establishment of the six territories which were measured during establishment was 0.14 acres. Even in the period of 27 April-15 May it was possible to trace the gradual shrinkage of individual territories.

Six males eventually held territories near E8 in 1967. Five of these males were colorbanded shortly after their arrival. They presented an excellent example of the shifting and shrinkage of territory which occurred as more males arrived on the study area. The approximate territory boundaries as determined by observations of song perches and territorial conflicts are mapped for six dates from 27 April to 15 May in Figure 13.

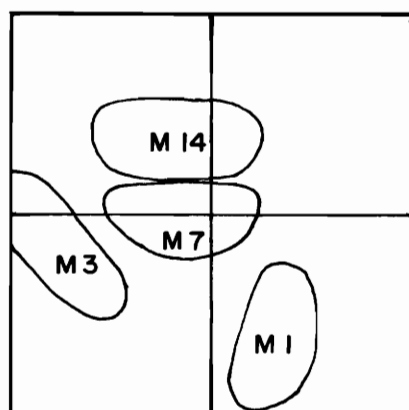
On 27 April two males (M1 and M14) were defending large territories north and south of E8. On 28 April a third bird was singing to the east of



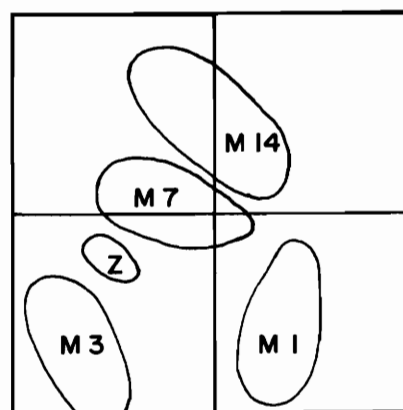
27 APRIL



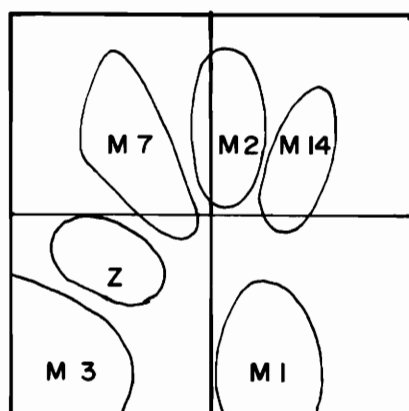
4 MAY



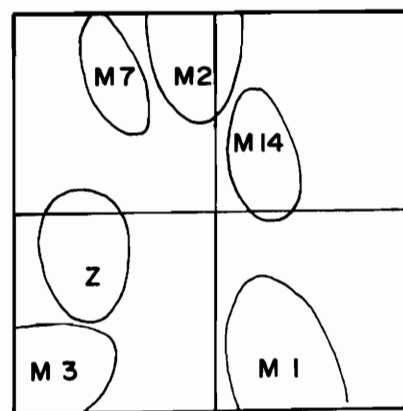
8 MAY



10 MAY



12 MAY



15 MAY

Figure 13. Territory establishment by six male Savannah Sparrows, 1967.

E8 and by 4 May this male (M3) was firmly established. On 8 May, a fourth male (M7) was proclaiming territory in the central area around E8 and had usurped areas formerly defended by M1, M3 and M14. Another male, who was never banded, was on territory Z, wedged between M3 and M7 on 10 May. The final male, M2, who had been banded on 3 May, began proclaiming his territory between M7 and M14 on 12 May. Some further contraction and separation of the territories took place but by 15 May they had reached the size and area that was maintained for the remainder of the season.

6.2 Territory Size and Population

6.2.1 Territory size

It is possible to outline the areas defended by 18 individual males from data obtained during the censuses of the plot in 1967. For six of these males it is also possible to determine the areas originally claimed, as well as the areas defended after establishment (Table 17). It should be stressed that these territory sizes are minimal and that the "sphere of influence" of a male singing in this minimum area might be considerably larger. Although some of these areas are based on as few as five song perches, these have been included because there appears to be no correlation between the number of song perches observed and the size of the area outlined by the song perches (Figure 14). Mean territory size during establishment was 0.38 acres and after establishment was 0.17 acres. This halving of territory size conforms to the pattern of territory establishment described in Section 6.1.

6.2.2 Population

Only the population of territorial males can be determined accurately, because of the secretive nature of females and non-territorial

Table 17. Territory size of the Savannah Sparrow as determined by song perches, 1967

	During Establishment	After Establishment
Number of territories	6	18
Mean area (acres)	0.39	0.17
Range (acres)	0.23 - 0.68	0.05 - 0.32
Mean number of song perches	11.7	10.3
Range of number of song perches	7 - 17	5 - 19

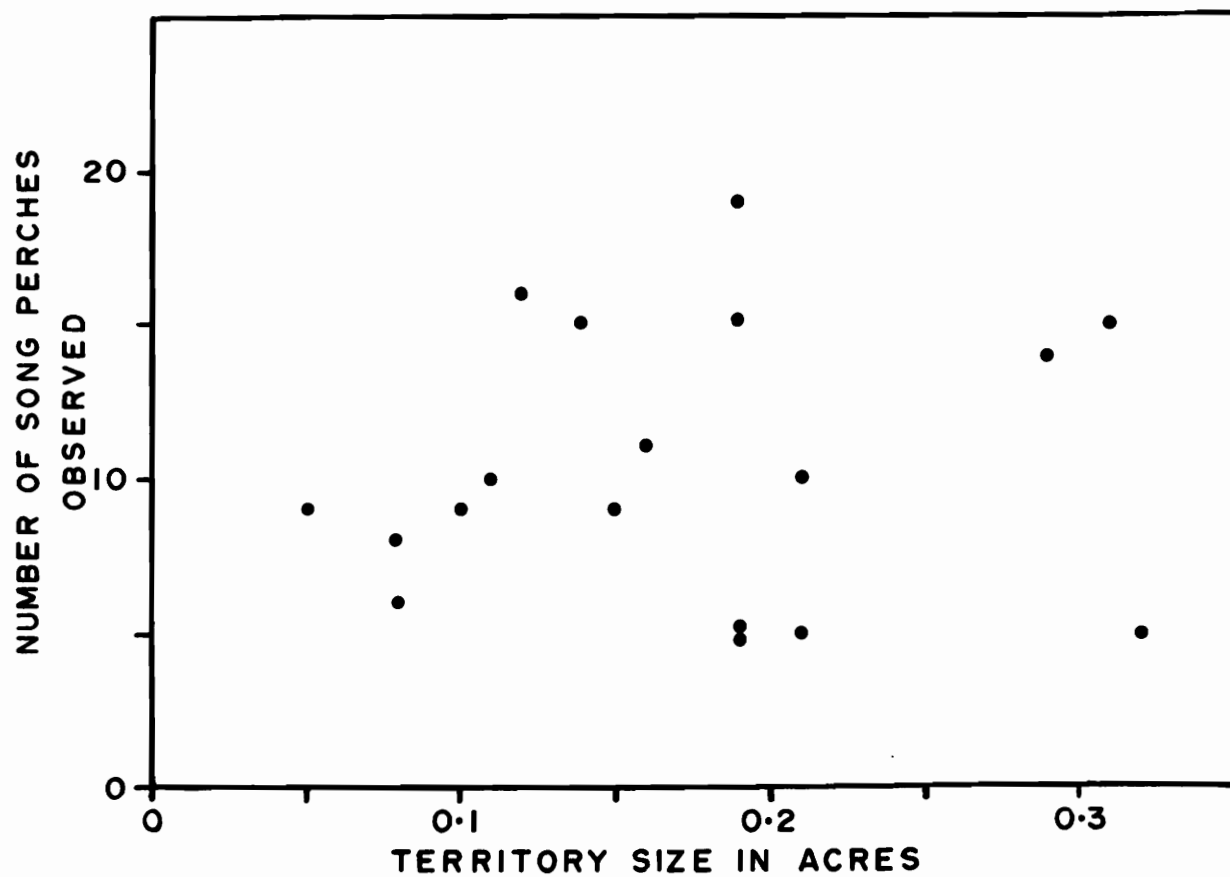


Figure 14. Territory size after establishment in relation to the number of song perches recorded, 1967.

males. Population build-up and decline have been described in Sections 4.1 and 4.4 respectively. The mean number of males recorded on censuses during the breeding season in 1967 was 25.6, the maximum was 30 (Figure 15). From comparison of maps made during different censuses, it appears that 38 different territories were entirely, or partly on the study area (Figure 16). Twenty-five were entirely on the plot and approximately 1/4 to 3/4 of the remaining 13 territories was on the plot. The study area had an estimated 31.5 territories in 1967 if the 13 partial territories are considered to average half on the plot. This gives an estimated population level of 68.6 territories per 100 acres or 439 territories per square mile of similar habitat.

6.3 Territory in Relation to Reproduction

6.3.1 Nest placement

It is possible to relate the position of 12 of the 17 nests found in 1967 to the territories of the parental male. The distance of the nest site from the territory is shown in Table 18. Seventy-five percent of the nests were on, or extremely close to, the area circumscribed by the song perches of the parental male. Many of these nests within fifty feet of the territory were actually within twenty feet of it. The one nest which was 200 feet from the territory of the male was nest number 67-13. This nest was rather unusual. The nest was initiated on approximately 12 June about 50 feet east of co-ordinates D6, within the area defended by M17 up until 25 June. M17 and his mate had nested 100 feet west-southwest of D6. This nest (67-7) was initiated in the period 10 - 15 June and was predated on

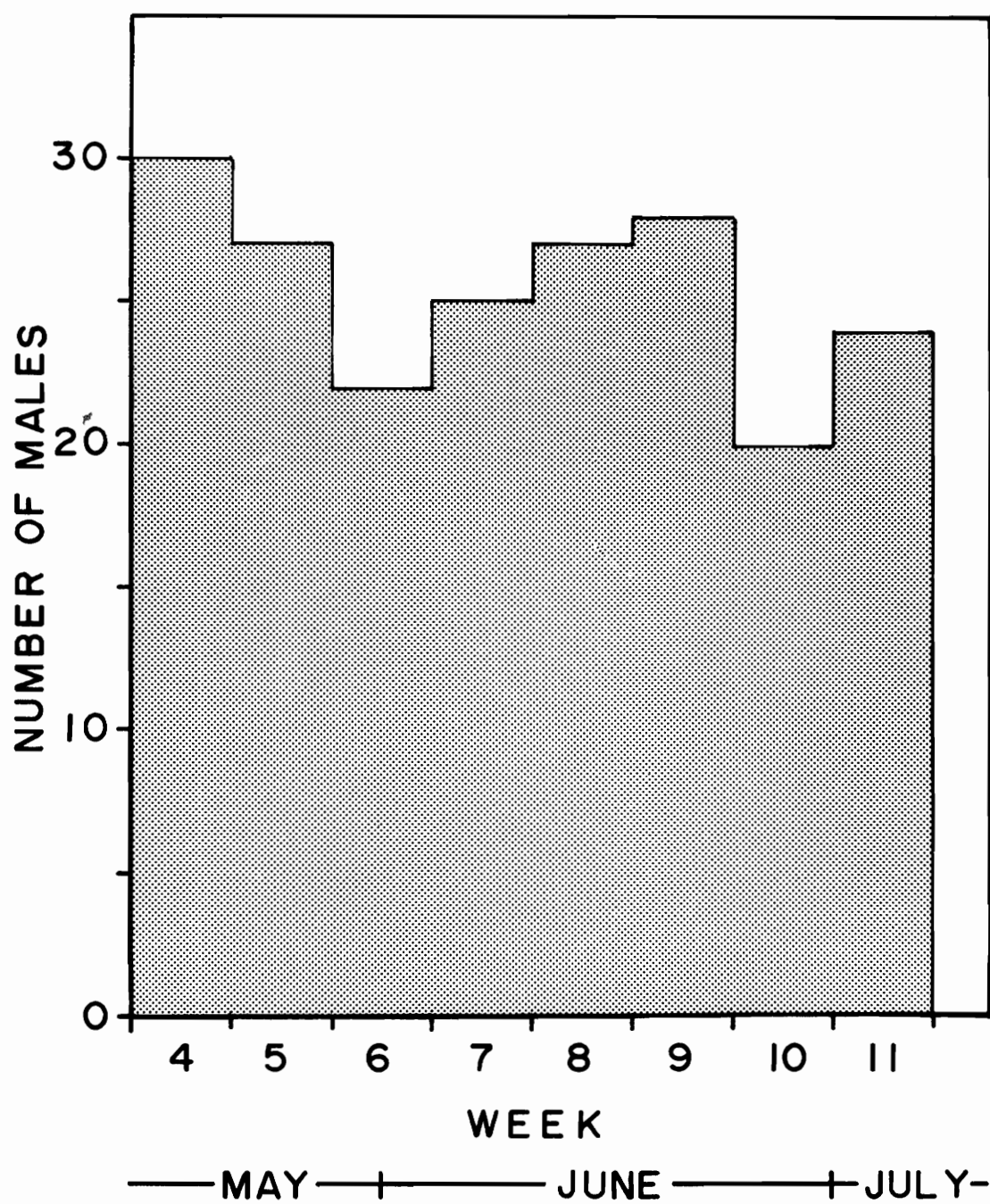


Figure 15. Number of territorial males censused during the breeding season, 1967.

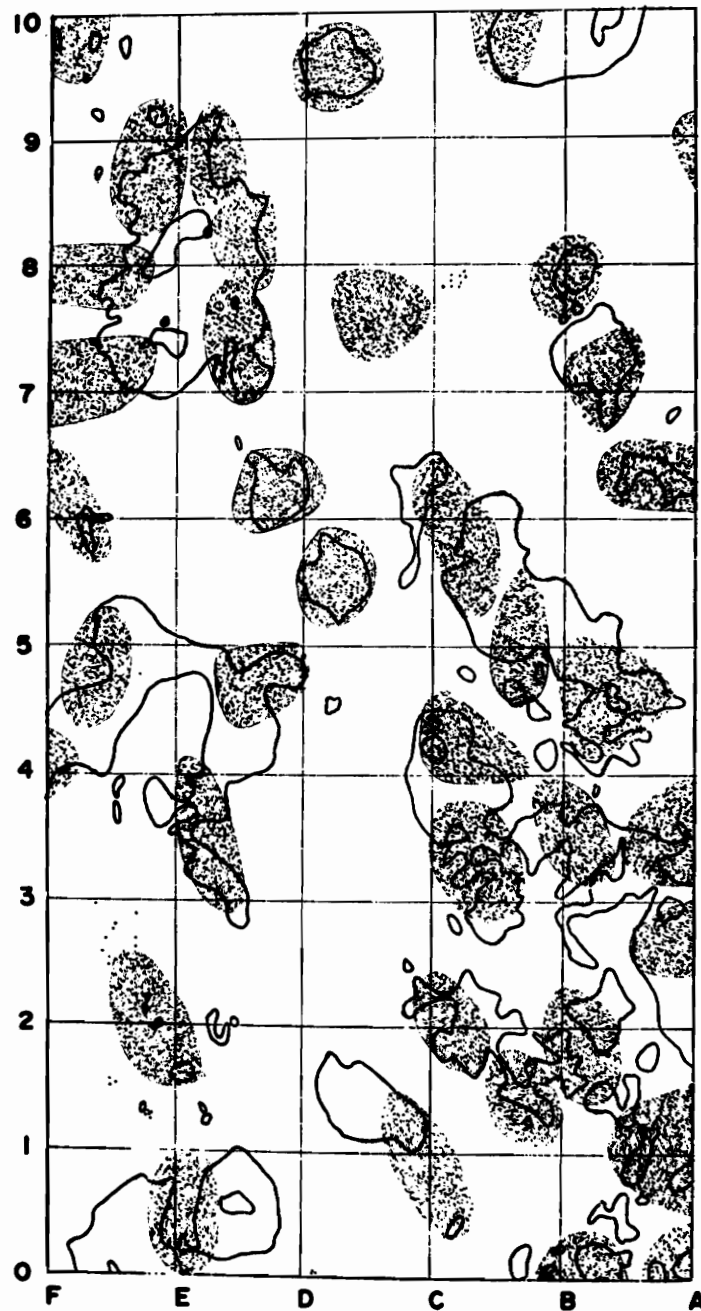


Figure 16. Approximate territories of Savannah Sparrows on the study area in mid-June, 1967 (stippled). Brush habitat outlined in black.

22 June. M17 was last seen on 25 June. Nest number 67-13 hatched on approximately 28 June and was then cared for by M1 and his mate. Up until the time of hatching, M1 had defended an area 200 feet south-southeast of the nest site. It is apparent that nest number 67-13 was initiated on the territory of a male other than the mate of the female.

63.2 Territory and feeding

Males were observed feeding on their territories, between song bursts, on fourteen occasions in the two seasons. On four occasions they were observed foraging outside of their territory. On one of these four occasions, a non-territorial male (M6) was observed feeding on an area defended by M10, and was ignored by M10 who was present. The other three cases involved territorial males. On 1 June, 1967 an unbanded male was seen foraging at the edge of M13's territory. This intruder was immediately chased by M13 and returned to his territory 100 feet to the west, where he resumed singing. The other two cases involved banded males, M3 and M2, who were seen foraging in neutral grassland, 150 and 300 feet from their territories respectively.

On two occasions two males were seen foraging peacefully on their respective sides of a territorial border. These cases involved M14 and M2, and M1 and the nonbanded male from territory Z.

No information is available on the foraging of females.

Some information was obtained on the source of food brought to nestlings. The distance from the nest to the foraging area is known only

Table 18. Position of nests in relation to territory

Distance from territory (feet)	Number of nests.
On territory	2
0 - 50	7*
50 - 100	1
100 - 150	1
150 - 200	1

* Two of these nests (67-1 and 67-3) belonged to males whose territories were not mapped. They may have been on the territory.

in one case -- nest number 67-12 where the adults were foraging in grassland 200 - 300 feet north of the nest site. The female of this pair (F23) was observed foraging within 20 feet of a singing male without reaction.

Other distances must be given as minimum distances as only the food-carrying flight was observed. Six observations show flights of 100+, 400+, 100+, 100+, 300+ and 600+ feet.

Savannah Sparrows appear to be somewhat opportunistic in foraging. On 28 July, 1966, a pair were observed carrying food to a nest near C4. They were observed for one and one-half hours in which time each adult made four or five trips to the nest. On several flights they were observed to fly distances of at least 600 feet to the wheat field west of the study area. Again on 8 August, 1966, an adult was observed returning from the wheat field with its bill full of insects. This flight had a minimum distance of 300 feet although neither its origin nor end point were observed.

6.4 Territorial Behavior

6.4.1 Seasonal pattern.

Territorial aggressiveness showed a marked seasonal pattern in the Savannah Sparrow, when measured by the occurrence of overt territorial aggressiveness such as territorial chases, fights, and supplanting attacks. During the censuses of the study area in 1967 all such territorial interactions were recorded. The results are shown in Table 19 and graphically shown in Figure 17.

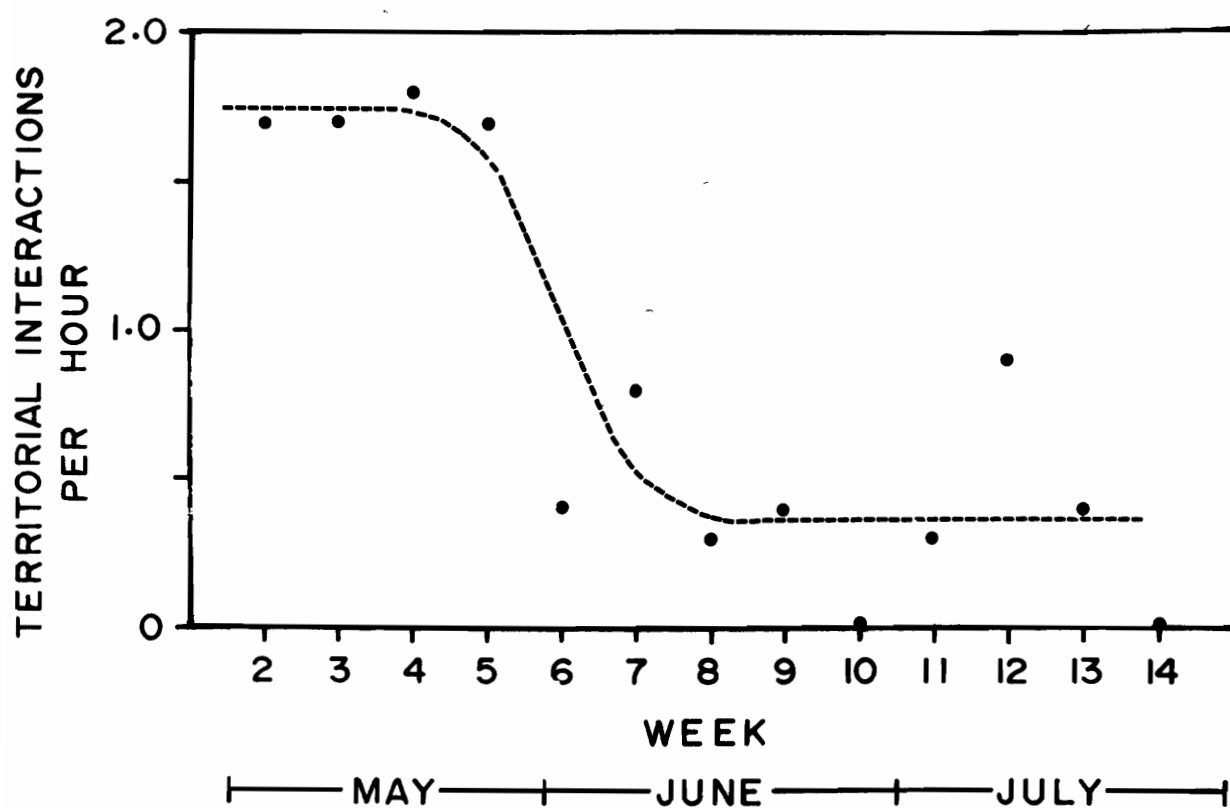


Figure 17. Territorial interactions of male Savannah Sparrows, 1967.

Table 19. Seasonal changes in territorial interactions of male Savannah Sparrows. 1967.

Week	Time Observed (minutes)	Numbers of				Interactions per hour
		Chases	Fights	Supplants	Total	
2	344	9	0	1	10	1.7
3	287	5	3	0	8	1.7
4	394	10	1	1	12	1.8
5	213	2	4	0	6	1.7
6	142	1	0	0	1	0.4
7	156	2	0	0	2	0.8
8	195	0	0	1	1	0.3
9	150	1	0	0	1	0.4
10	152	0	0	0	0	0.0
11	187	0	1	0	1	0.3
12	196	1	0	2	3	0.9
13	150	1	0	0	1	0.4
14	96	0	0	0	0	0.0

It is easily seen from Figure 17 that the initial high level of overt territorial defence dropped off rapidly between Week 5 and Week 6 (25 May - 1 June) and remained at about one-fourth the former level until the birds left the breeding grounds (Weeks 13 - 15). It is interesting to note that the time of this drop in territorial aggression coincided with the time of nest initiation., (see Figure 6).

6.4.2 Components of territorial behavior.

In this section the individual behavioral components will be described. In the following section their organization into display patterns will be described. Names given to components or displays are capitalized.

Vocalizations: Territorial song will be described in the following section. Typical song was also recorded during aerial chases (Flight Song). During some chasing a twittering call was also heard, although it could not be determined whether this was given by the pursuer or the pursued.

Wing movements: Two extremes of wing movements during territorial encounters can be described although there appears to be a complete gradation between the extremes. Wing Flicks may be described as very narrow amplitude movements of the wing out from the body, in which the wing-tip moves a distance of up to one inch. This movement is very rapid and is effected by extension of the humerus. There is no extension of the carpal joint. The second type of movement is the Wave, where the wing is raised very noticeably from the body and the carpal joint is extended, opening the wing. In the extreme case the wing is held high over the body for a short period of time. Wing Flicks are always bilateral; there is a tendency for Waves to be unilateral.

Tail movements: Tail Flicks; rapid, short movements in the vertical plane were often recorded as part of territorial encounters. A second type of tail movement was also recorded. This was the Tail Waggle in which the tail was wagged back and forth rapidly in a horizontal plane. During this movement the tail described an arc of approximately 60° and the tip a chord of approximately two inches.

Plumage movements: During territorial encounters between two males several plumage movements were observed. Crest raising was the most common of these, but was not restricted to territorial encounters. Puffing

of the body feathers, particularly those of the flanks and breast was recorded in aggressive males. A third plumage movement; sleeking of the body feathers, was observed in subordinate males.

Gaping: The presentation of the open bill toward an opponent was recorded on several occasions.

Head Forward: The Head Forward Threat posture of the emberizine finches (Andrew, 1961) was recorded in the Savannah Sparrow. It was sometimes accompanied by Gaping.

Displacement activities: This type of behavior was noted in males which were presented with a male dummy on their territories. Under these circumstances they would often peck at the branches of the bush in which they perched between attacks on the dummy. On no occasion were they observed to capture any food item. One bird was also noted to wipe its bill on a branch under similar circumstances.

6.4.3 Patterns of territorial behavior and displays.

The behavioral components described in the previous section were often seen grouped into patterns or displays. These are described below.

Territorial song: The proclaiming of territory occupied most of the time of males prior to the formation of a pair bond and during incubation. Although no measurement of the diurnal pattern of singing was made it is possible to state that there were two peaks of singing activity during the day. The greatest of these was in the early morning, with a lesser peak in the late afternoon and evening. Singing was noted to begin as early as one and one-quarter hours before civil sunrise on 16 June, 1966.

The time of last song in the evening was recorded on 6 occasions in 1967. The times averaged 35 minutes after civil sunset and ranged from 25 to 49 minutes after.

The song of the Savannah Sparrow consists typically of a number of short, introductory notes which are followed by a buzzing trill which first rises and then falls. Peterson (1961) describes it as "a dreamy lisping 'tsit-tsit-tsit, tseeee-tsay'". Godfrey (1966) describes it as "a lisping 'tsip'tsip'tsip'tsip'tse-whEEEEEEEEEE-you', the 'whEEEE' being trilled, and the final 'you' being abrupt and much lower". Both of these descriptions agree on the lisping nature of the song and on the basic pattern. During the present study a considerable amount of individual variation in song was noted. The variation was between individuals rather than within individuals. The songs of different males would vary noticeably in the number of introductory notes and in the phrasing of the trill. The final note of the song as mentioned by Godfrey was present in the songs of only some individuals. Individual males sang songs of one type only. For example the male on territory A sang a song which may be described as "tsip-tsip-tsip tseee-tsit-seee" which was easily recognizable from the songs of other males. This male was never heard to sing any other song during the season.

Territorial song is typically given from a conspicuous, elevated perch. An analysis of the height and type of song perches used is given in Section 7.1. The rate of song delivery was measured on 32 occasions by determining the time required for five complete songs by a male who was singing steadily. The mean rate of song delivery was 4.6 songs per minute

(range of 3.2 - 10.0 songs per minute). No attempt was made to analyse diurnal or seasonal patterns.

While singing a bird may alternate bouts of song with bouts of maintenance behavior such as feeding or preening. Typically a male moved about his defended area between song bouts. On 20 May, 1966, a male who was singing steadily changed position 11 times in 36 minutes. In contrast, a male on 15 June, 1966 sang from the same perch for a full hour.

As was described in section 4.3.2 the singing of males appeared to almost cease during the period between pair formation and nest initiation. During incubation the male resumed singing at the previous high level. Singing declined again during the feeding of young, but many males sang between trips to the nest with food.

Countersinging, the regular alternate delivery of songs by two males, apparently in response to each other, was commonly noted.

Supplanting attack: The Supplanting Attack was the usual reaction to an intruding male on the territory. The resident male flew toward the intruder, who would usually fly away before the territory holder arrived. In some cases this led to a chase; in others, the resident male would land at the position or on the perch that the intruder had vacated. During the flight toward the intruder the resident often used the Vibrating Flight in which the wings were moved in very rapid, narrow amplitude beats near the horizontal plane. This type of flight was easily distinguishable from normal flight and was confined to aggressive encounters.

Supplanting attacks were also observed in birds perched on the ground. In this case the attacker would run rapidly toward the other, with

the body horizontal using the Head Forward Threat posture. Gaping was not observed in these attacks.

The use of dummy males allowed description of the behavior preceeding attacks by the territorial male. The male typically sang strongly and showed a number of various movements. Puffing of the body feathers, particularly those of the breast and flanks were almost invariably observed. The crest feathers were often raised. Tail Flicks, Tail Waggles, and wing movements varying in degree from Flicks to Waves were given. On one occasion a Head Forward Threat with Gaping was observed, directed toward the dummy.

When the attacking male arrived at the position of the intruder he would attempt to land on the same perch. The intruder would leave the perch at this time, if he had not already done so. In the case of attacks on dummies the attacking male would hover jerkily above and behind the dummy, with the Head Forward and bill open. The legs were dropped during this hovering. At this point the male either attacked the dummy or returned to a perch nearby. In the attack, the male attempted to land on the dummy's back, and attempted to bite and peck it. These attacks were very vigorous; the attacker would often pull feathers from the dummy and on one occasion an attacking bird broke a wing and the tail off the dummy.

Chases: When the object of a supplanting attack fled, the attacking male would often pursue him, leading to a chase. Chases were of varying duration, with the birds twisting and turning as they flew around the area. Two bird chases were common, but upon occasion three birds were seen in one chase.

Chases appear to be more persistent and more numerous early in the season (Table 19). On 5 May, 1966, two males were noted chasing almost continuously for ten minutes. Between chases they would land on the ground or in bushes three to four feet apart and the pursuing male would sing strongly. Later in the season chases were brief, with the attacking male ending pursuit as soon as he left his defended area.

During the aerial chase, the attacking male occasionally sang. More often a twittering call would be heard, although it was not determined which bird gave this call. The twittering call was also given by some attacking males after returning from a chase.

Males returning to their song perch after a chase often flew with the same Vibrating Flight which was given during supplanting attacks. Almost invariably the male sang very strongly upon his return.

Fights: Physical contact between chasing males was rare. On one occasion (17 May, 1967) when a fight was observed closely it was recorded as follows:

"An unbanded male near C2 was involved in a fight with M4 at 0749. The birds mounted in the air to a height of 20 feet, bill to bill, fluttering against each other, then dove to the ground. Fighting continued on the ground for a few seconds, then the birds mounted again and finally broke off."

The total time involved in this encounter was probably less than 30 seconds. This type of behavior was typical of other fights observed.

Puff-Sing-Wave display: On a number of occasions the three elements, Puffing, Singing and Waving were recorded at the same time and warrant description as a display. The name of the display is taken from Nice (1942: 154) who described a similar display, which she also calls the "challenge", for the Song Sparrow.

This display was first seen on 12 May, 1967, while watching M2 and M7 who were contesting a portion of a brush patch near E9. M2 was noted to fly up and land in a 12-inch Symphoricarpos bush and give the display. The call given was not the typical song, but the twittering call given during or after territorial chases. Both wings were spread out from the body, one out slightly to the side and the other fully raised over the back. Both wings were quivered. The body feathers were fluffed during this action. The display continued for approximately 15 seconds, during which time the male alternated the waved wing; right - left - right. M2 was seen to give this display twice on this date; unfortunately the position of M7 could not be determined at the time.

This was the only occasion on which this display was recorded under natural conditions. However, in experiments with dummies, the combination of feather puffing and wing waving was the commonest type of display pattern preceeding attack. This was often, although not invariably, accompanied by normal song. Both the Puff and Wave elements were also seen individually as well.

7. HABITAT SELECTION

7.1 Territory and Habitat

The habitats of the study area have been described in Section 2.3.3. The extent of each of these habitats was mapped and is shown in Table 20 and illustrated in Figure 18.

The habitats found on 17 individual territories were also measured (Table 21). The results are expressed in two ways. First, the total areas of each habitat on all territories are compared, and second, the mean percentage areas of each habitat on individual territories are compared. This second method, where percentages of each habitat on each territory are averages (thus giving unequal sized territories equal weight) compares rather closely to the calculation of the percentage of each habitat in the total of the 17 territories.

A comparison of the proportions of available habitats on the study area and those measured on the individual territories gives a Chi square value of 98.48. The probability of this large a chance deviation from the expected values (if territories were random in respect to habitat) is very much less than 0.001. It is apparent from Tables 20 and 21 that this deviation is caused by an avoidance of open grass areas by the birds and a distinct preference for both sparse and dense brush.

One of the most important features of the territories of male Savannah Sparrows was the song perches. During the course of field work in 1967 information on the height and type of vegetation of 438 song perches was recorded. The type of vegetation for these perches is shown in Table 22 and their heights are shown in Table 23.

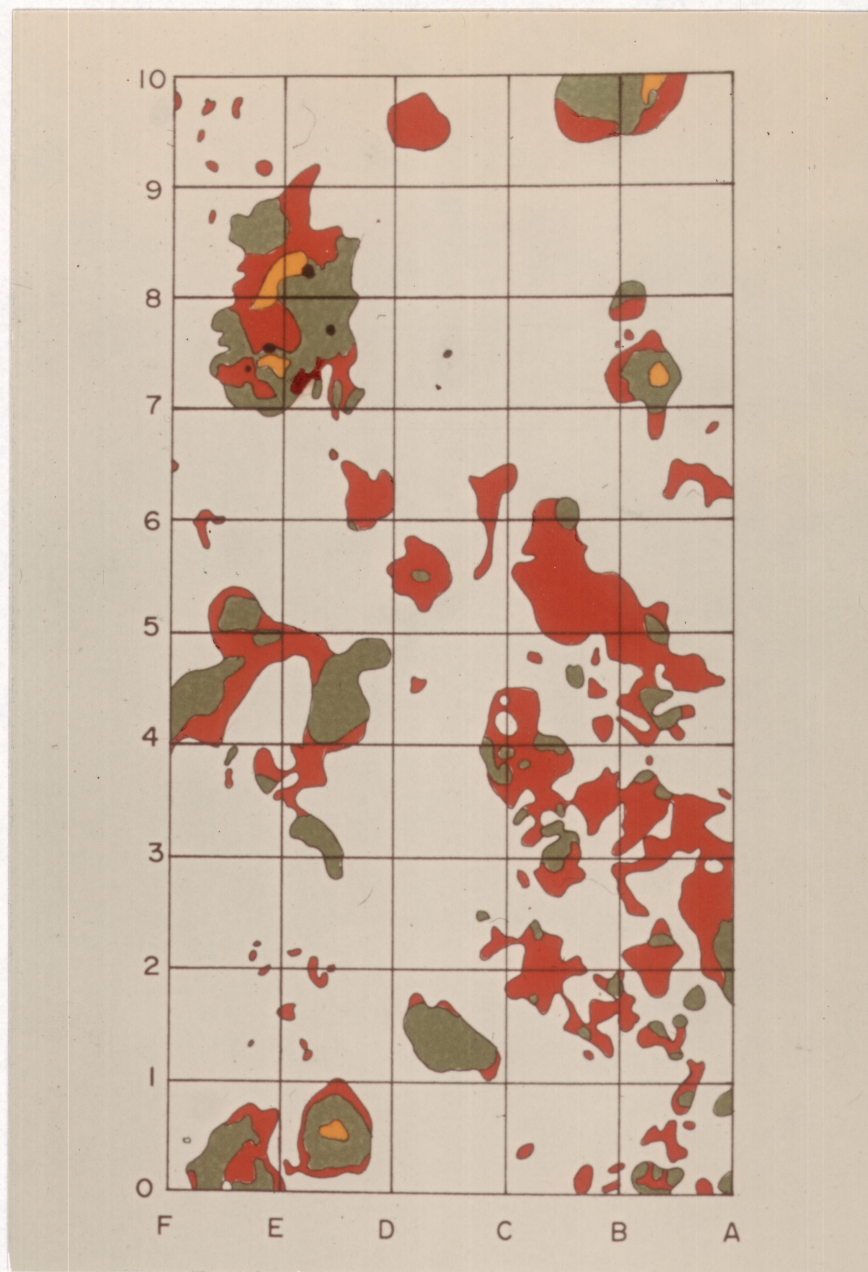


Figure 18. Habitats on the study area

Open grassland --- Uncolored
 Sparse brush --- Red
 Dense Brush --- Green
 Depressions --- Yellow
 Willows --- Black

Table 20. Extents of habitats on the study area

Habitat	Area (ft ²)	Area (acres)	Percent of Total
Open grass	1,558,250	35.77	77.9
Sparse brush	268,350	6.16	13.4
Dense brush	163,325	3.75	8.2
Depressions	9,675	0.22	0.5
Willows	400	0.01	trace
Total	2,000,000	45.91	100.0

Table 21. Extent and proportion of habitats on Savannah Sparrow territories

	Habitat type				
	Open grass	Sparse brush	Dense brush	Depression	Willows
Total area on seventeen territories (ft ²)	47,150	51,850	26,175	925	25
Percent of total area	37.4	41.1	20.8	0.7	trace
Mean percentage of individual territories	39.8	34.3	24.6	1.3	trace

Table 22. Vegetation of Savannah Sparrow song perches

Type of vegetation	Number of song perches	Percent of total	Percent of natural perches
<u>Symphoricarpos</u>	215	49.1	58.3
<u>Elæagnus</u>	73	16.7	19.8
<u>Spiraea</u>	22	5.0	6.0
<u>Salix</u>	15	3.4	4.1
Herbaceous forbs	13	3.0	3.5
Grass (tufts)	12	2.7	3.3
Ground	10	2.3	2.7
<u>Rosa</u>	9	2.1	2.4
Unnatural (posts, stakes)	69	15.6	----
Total	438	99.9	100.1

Although it is not possible to compare the song perches recorded with those actually available, the figures in Table 22 show a distinct preference for perches on bushes as contrasted to those on grass tufts or on the ground. Similarly the figures in Table 23 show a preference for elevated perches. The low numbers of perches higher than 48 inches are undoubtedly due to the scarcity of tall vegetation on the study area. The low numbers of perches under 12 inches in height can only be due to avoidance of such positions by the birds.

The use of artificial perches (fence posts and stakes) should be noted. These perches make up 15.6 percent of the total perches.

7.2 Nest placement.

The actual situation of the 27 nests found during the present study was similar in all cases (Section 4.3.4), although there were differences in the surrounding habitat. All nests were in sparse brush, at the edge of brush (sparse or dense) or in open grass. No nests were located in dense brush habitat. Their distribution in relation to brushy habitat (Table 24 and Figure 19) shows that over half the nests were in brush and another 30 percent were located within 20 feet of brush. Only one nest was more than 50 feet from brush.

Table 23. Height of Savannah Sparrow song perches

Height class (inches)	Number of perches	Percent of total
0	10	2.3
6	12	2.7
12	94	21.5
18	143	32.7
24	74	16.9
36	50	11.4
48	46	10.5
60	3	0.7
72	2	0.5
84	3	0.7
96	1	0.2
Total	438	100.1

Table 24. Nest placement of Savannah Sparrows in relation to brush habitat

Distance from brush (ft)	Number of nests	Percent of nests
0	14	51.9
0 - 10	5	18.9
10 - 20	3	11.1
20 - 30	2	7.4
30 - 40	1	3.7
40 - 50	1	3.7
80 - 90	1	3.7
Total	27	100.0

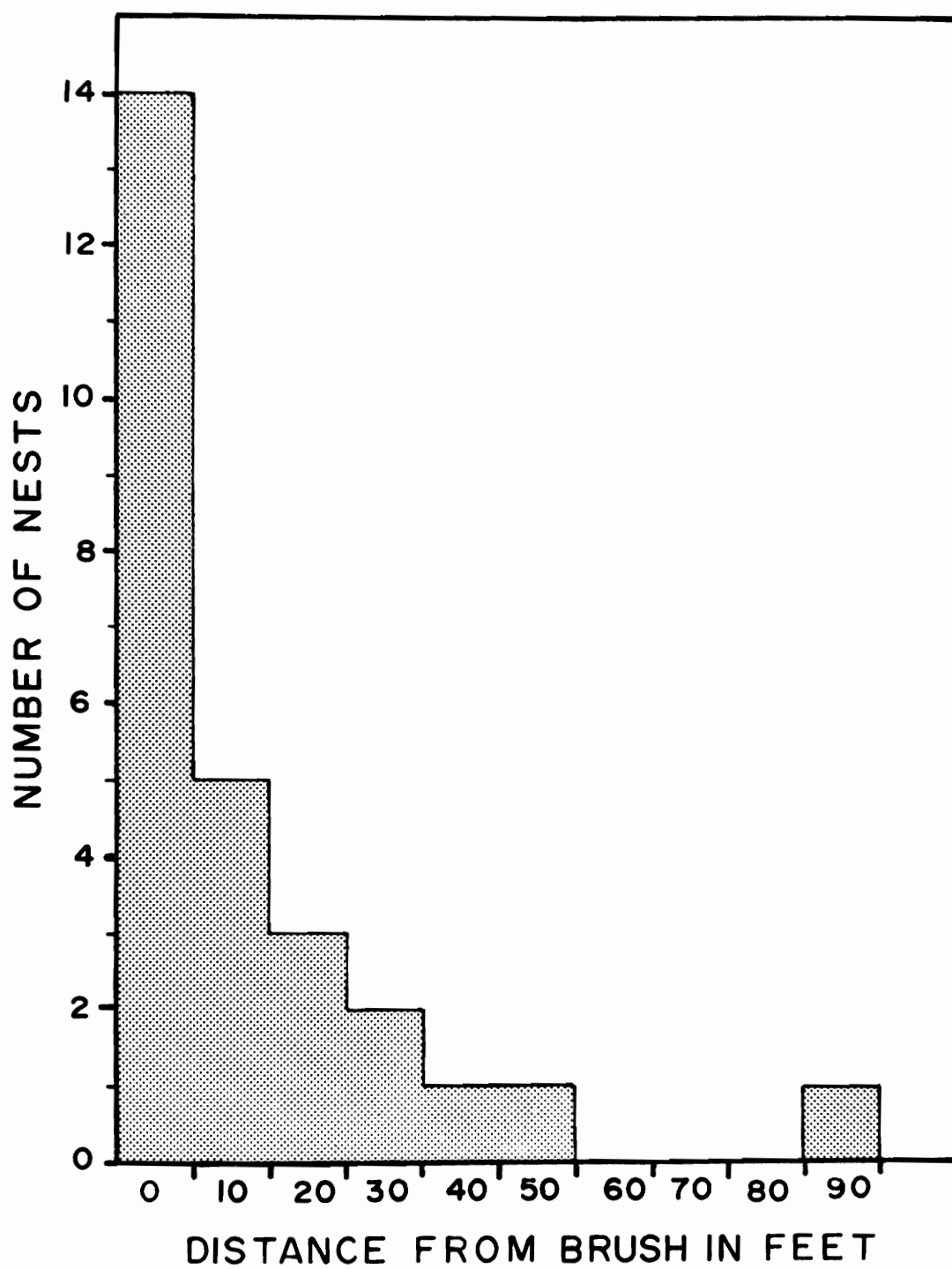


Figure 19. Placement of nests in relation to brush habitat.

8. RELATIONS WITH BAIRD'S SPARROWS

Baird's Sparrows were present on the study area in much lower numbers than Savannah Sparrows. During 1967, four pairs were resident on the plot, and another pair bordered on the plot. They were more numerous on the prairie east of the plot.

Savannah and Baird's Sparrows do not exhibit interspecific territoriality. On only three occasions in the two seasons were any interactions noted. This is no more frequent than interactions between Savannah Sparrows and other species such as Clay-colored Sparrows or Western Meadowlarks.

On 24 June, 1966, a male Savannah Sparrow was observed to make three unsuccessful attempts to supplant a Baird's Sparrow from a stake at the edge of its territory. On 13 June 1967, M13 flew to investigate a Baird's Sparrow which had landed near his perch. He flew with the Vibrating Flight, gave one Puff-Wave upon landing and immediately returned to his former position. The male Baird's Sparrow remained where he had landed and sang. On 6 July, 1967, a Baird's Sparrow (female?) was flushed by the observer and landed 40 feet from a singing male Savannah Sparrow. The Savannah pounced on the Baird's Sparrow but immediately broke off and returned to his perch.

Experiments with dummies on 25 June, 1967 demonstrate the absence of interspecific hostility. M13 was presented with a male Savannah dummy on his territory. He displayed to the dummy and attacked it for nine minutes. At this time the Savannah dummy was replaced with a male Baird's Sparrow dummy. M13 returned and landed 5 feet away from the dummy with Crest Raised and giving Tail Flicks. Within 15 seconds he began to move away from the

dummy and within five minutes had resumed normal singing and feeding. However, when the male Savannah dummy was replaced he returned and attacked and displayed to the dummy for 12 minutes.

The territories of the Baird's Sparrow are much larger than those of the Savannah Sparrow. Two territories on the plot in 1967 measured 1.4 and 0.8 acres. These territories were 3 to 5 times the size of the largest Savannah Sparrow territories. Very little territory overlap between the two species was recorded. This is related to the nature of the vegetation utilized.

Table 25. Vegetation and height of Baird's Sparrow song perches.

Vegetation	Height (inches)					Total
	0	6	12	18	24	
Grass (tuft)	14	-	-	-	-	14
Ground	-	16	-	-	-	16
<u>Symphoricarpos</u>	-	3	-	-	-	3
Artificial	-	-	-	3	1	4
Total	14	19	0	3	1	37

Table 25 shows the vegetation and heights of 37 Baird's Sparrow song perches recorded in 1967. A striking preference for perches in open grassland (on the ground or on tufts of grass) is shown. Only three song perches were in brush and all three of these were very low, although taller brush was available nearby. On no occasion was a Baird's Sparrow seen singing from any habitat other than open grassland or very sparse brush. This selection of the open grassland habitat is also shown by the habitats of the two measured territories. One of these contained grassland habitat exclusively; the other contained 84.1 percent open grassland, 12.7 percent sparse brush and 3.2 percent dense brush.

Baird's Sparrows set up territories on the plot only where there were large, continuous stretches of open grassland habitat (see Figure 20). This also relates to their abundance on other parts of the prairie, particularly the ridge to the east of the plot, where brushy habitat was virtually absent (see Plate 1).

Four nests of the Baird's Sparrow were found during the two seasons. The nest construction and actual nest sites were essentially identical to those of the Savannah Sparrow but the placement of the nests with relation to habitat differed. Two of the nests were 100 - 150 feet from brush and the other two were over 500 feet from the nearest brush. This sample is very small but is strikingly different from the results for the Savannah Sparrow (see Table 24).

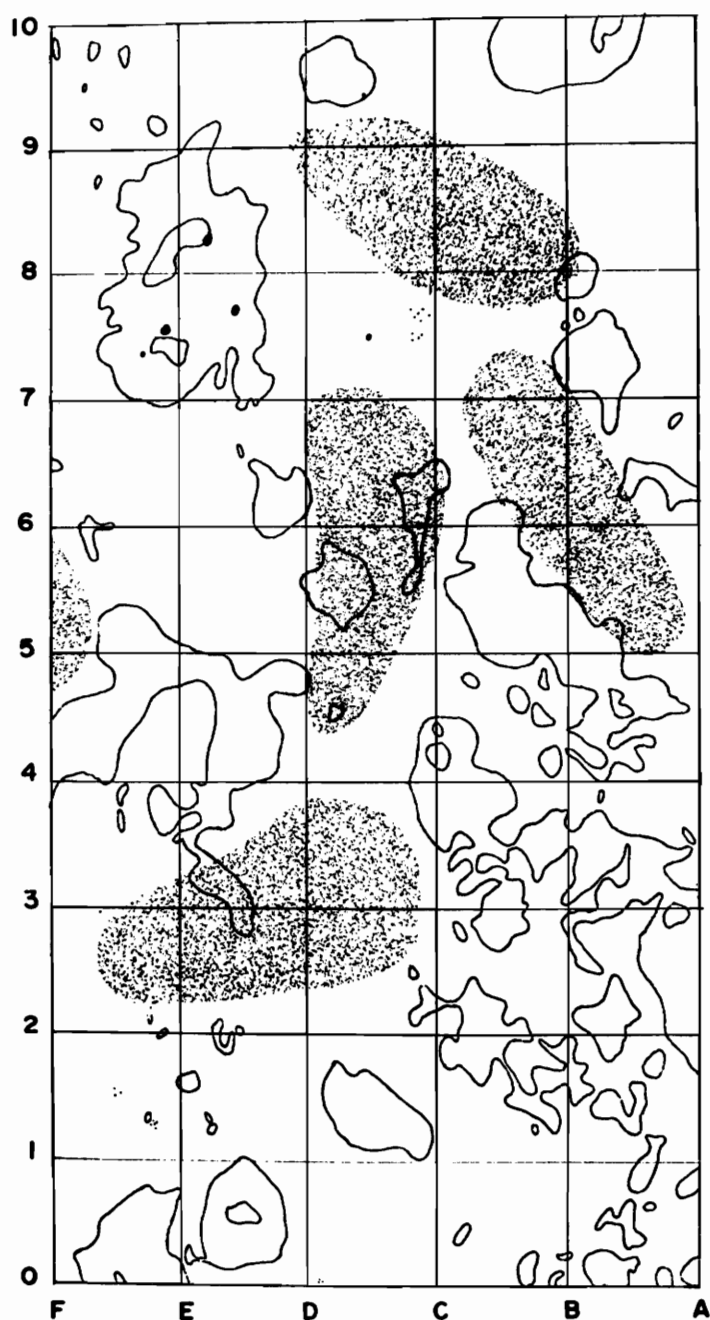


Figure 20. Approximate territories of Baird's Sparrows on the study area in 1967. (stippled).
Brush habitat outlined in black.

9. DISCUSSION

9.1 Breeding Cycle

9.1.1 Chronology

The breeding season of the Savannah Sparrow at Saskatoon spans about one hundred days, from the first of May to early August. The first 20 to 30 days are occupied by pre-nesting activities. In this period their activities are directed toward the establishment of territories and pair-formation.

The five day difference in the first arrival dates of the male Savannah Sparrows in the two seasons was attributable to the abnormally cold temperatures of the last five days of April, 1966 (See Figures 1-3). Nice (1937: 45) has shown that the early migration of Song Sparrows in Ohio is "absolutely dependent on a warm wave the last of February or the first of March ----- severe cold waves stop migration short". The fact that the population of territorial male Savannah Sparrows approached the maximum level at the same time (mid-May) in both years is explainable by the fact that later migrants are much less effected by local, short-term climatic conditions than are the first arrivals (Nice, 1937: 50). The arrival of the first females with only a one day difference in the two years can be similarly explained.

The first females arrived 9 and 13 days after the first males in 1966 and 1967 respectively, before the arrival of the last males. This may be typical of emberizine migration since a similar pattern is found in the Song Sparrow (Nice, 1937: 53). When the first females arrive establishment of territory is well advanced in both the Savannah Sparrow and the Song Sparrow. This is also true of the Snow Bunting (Tinbergen, 1939)

and the McCown's Longspur (Mickey, 1943), where intervals of up to one month occur between arrival of the first males and the first females.

The differential migration of the sexes is related to the establishment of territory by males and the importance of this event in pair-formation and subsequent activities. This will be discussed in a later section.

Full reproductive condition is not attained by either sex until two to three weeks after arrival. During this period the important events of territorial establishment and pair-formation occur. The occurrence of these events prior to the attainment of a breeding state may be an adaptation serving to compress the breeding cycle. Blanchard (1941) found that a migratory race of the White-crowned Sparrow (Zonotrichia leucophrys pugetensis) compressed the active part of their breeding cycle into less than four months, while a non-migratory race of the same species (Z.l. nuttalli) required six to six and one half months to complete the same cycle. This compression was accomplished in part by shortening the time required for territorial establishment and pair-formation. Males of pugetensis arrived on the breeding grounds before testes were completely enlarged.

If full reproductive capacity was prerequisite for territorial establishment and pair-formation, the breeding cycle of the Savannah Sparrow in the Saskatoon area would be delayed by two to three weeks.

The minimum time required for completion of one successful nesting attempt (from nest building to fledging of young) would be 28 days, assuming three days for building and four days for laying. It has been mentioned that the first 20 to 30 days of the breeding season are occupied

by pre-nesting activities. Savannah Sparrows appear to be double-brooded in this locality. In the remaining 70 to 80 days it would be impossible to complete more than two successful nesting attempts unless re-nesting began prior to fledging of the young. This probably does not occur since the parents care for the young for at least 10 days after fledging, and probably longer (Section 4.3.8). It is impossible, therefore, for the birds to increase production of young without lengthening the breeding season, or shortening the period of post-fledging care.

The population of Savannah Sparrows in this study left the breeding area before mid-August, although Savannah Sparrows were recorded in the Saskatoon area for 7 to 9 weeks after the breeding birds had left Kernen's prairie. The last birds recorded were probably migrants from northern populations, although it seems possible that resident birds linger in the area after the completion of breeding activities. The closely related Baird's Sparrow remained on the study area after the Savannahs had left. Singing male Baird's Sparrows were recorded on 11 August, 1966. Many birds of this species were seen carrying food as late as mid-August. Nests of the Baird's Sparrow with half-grown young have been reported as late as 17 and 18 August in Manitoba (Cartwright, Shortt and Harris, 1937). It would appear that the Savannah Sparrows in the Saskatoon area could lengthen their breeding cycle by two or three weeks and produce a third brood during a season. Failure of the species to do so suggests several possibilities. First, food supply on the breeding grounds may not be ample for production of young in mid- to late- August. This seems unlikely because of the opportunistic foraging behavior of the sparrows which allows

them to utilize concentrated areas of food in the vicinity such as wheat fields. Also, the ecologically similar Baird's Sparrow can raise young during this period. Second, the birds may require time to moult and/or build up fat deposits for the pending migration. Wolfson (1945) concluded that the deposition of subcutaneous fat that preceded spring migration in Juncos (Junco oreganus) was an essential "preparation" without which migration was usually not undertaken. Odum (1958) demonstrated that the amount of fat deposited is related to the length of the migration, and that fat content may reach as high as 42 percent of the body weight in some passerines during autumnal migration.

Moulting has also been shown to make demands on the energy requirements of birds. The Chaffinch (Fringilla coelebs) undergoes a 25% increase in metabolic rate while regenerating its flight feathers; and the basal metabolic rate of the Domestic Fowl (Gallus gallus) increases 50% or more over the level during laying, during the autumnal moult (Perek and Sulman, 1945). P.s. savanna undergoes a complete post-nuptial (pre-basic) moult in August (Dwight, 1900). When the local adults moult is not known but it is probably in late August. Three adult females collected on 2 and 3 August, 1967, have extremely worn and faded plumage with no indication of feather replacement.

9.1.2 Pre-breeding behavior

The pre-breeding behavior of the Savannah Sparrow follows a pattern shared by many emberizine finches. The abeyance of song during the prenuptial stage is also found in the Song Sparrow (Nice, 1943), the White-crowned Sparrow (Blanchard, 1941) and the Snow Bunting (Tinbergen, 1939).

This phenomenon is not limited to the Emberizinae. Nice (1943: 172-174) shows that similar behavior is found in such diverse groups as the Charadriiformes and the Ciconiiformes as well as in many Passerine families. Nice explains the almost complete cessation of song during the prenuptial and preliminary periods as definite inhibition by the presence of the female. Resumption of song during incubation is then explained by the removal of this inhibition, since the female is only infrequently in contact with the male.

The male courtship display described in Section 4.3.2 is homologous to the displays of other male Emberizinae (Andrew, 1961). Shared features are the wing vibration, raising of the body feathers and spreading of the tail. The Buzzing Wheent call of males is believed to be sexually motivated. This call was never given during territorial encounters, and chases in which it was used were between birds of a pair in all known cases. Tinbergen (1939: 17) has described by "Swift" call of the Snow Bunting used as part of courtship ritual during sexual flights (p. 21). This call is also given before the arrival of the females and was often accompanied by trembling of the wings, as was the Buzzing Wheent of the Savannah Sparrow. The two calls seem to be homologous in the two species. Tinbergen believes that the "Swift" call of the Snow Bunting may be an outlet for unsatisfied sexual impulse.

Copulatory behavior of the Savannah Sparrow is similar to that of other Passerine birds. The female precopulatory display shows less variation in form in different groups of passerines than any other display except the Head Forward Threat (Andrew, 1961: 344). The Savannah Sparrow

shows the typical pattern of Emberizinae which includes bill raising, wing-quivering, tail raising but not tail vibration.

9.1.3 Breeding behavior

The nests located in this study were similar in construction to those described by other workers. All grass construction of nests has been described by Shields (1935). Linsdale (1938) and Gabrielson and Lincoln (1959) commented on the occasional use of small amounts of horsehair and doghair as lining. Gabrielson and Lincoln (ibid.) also comment on the use of moss in construction of the outer cup of nests of the Savannah Sparrow in Alaska and the lack of a lining of ptarmigan feathers which is almost ubiquitous in the nests of Arctic passerines. The presence of a scrape beneath nests of the Savannah Sparrow was mentioned by Salt (1966). A scrape beneath the nest has been recorded in other ground-nesting emberizines: the Baird's Sparrow (Cartwright, Shortt and Harris, 1937; present study), the Song Sparrow (Salt, 1966) and the Chestnut-collared Longspur (Harris, 1944). The placement of the nest in a natural depression, or in the base of a clump of grass has been noted by Shields (1935) and by Linsdale (1938) for the Savannah Sparrow. Linsdale also comments that many of the nests found were partially or completely roofed over by the thick cover of dead grass; identical to the situation described in the present study.

Egg-laying probably occurs in the early morning at intervals of one day. These two features of laying appear to be typical of emberizine finches (Blanchard, 1941; Mickey, 1943; Nice, 1943; Harris, 1944; Walkinshaw, 1944; Fox, 1961), and indeed are typical of passerine birds (Welty, 1962).

Incubation solely by the female, as found in the present study, is the general rule in the Emberizinae although males assist in incubation in the White-throated Sparrow (Snyder and Lozier, 1930), Chipping Sparrow (Walkinshaw, 1944) and Clay-colored Sparrow (Fox, 1961). Resumption of intense singing by the male is also characteristic of this phase of the nesting cycle.

The incubation period of 12 days determined in this study compares with an incubation period of 12 days for two nests of the Savannah Sparrow at Churchill, Manitoba (Jehl and Hussel, 1966).

The onset of incubation before the clutch is complete and the resultant asynchrony of hatching has been reported for many species of Emberizinae. Weeden (1966) found that female Tree Sparrows gradually develop the activity pattern of incubation during the egg-laying period. The number of visits to the nest was low on the third last day of laying and increased markedly on the second last day when a significant proportion of the daylight hours were spent on the nest. This pattern is probably general in the Emberizinae.

The initiation of incubation with the laying of the penultimate egg has been recorded in the Leconte's Sparrow (Walkinshaw, 1937), Clay-colored Sparrow (Fox, 1961; Salt, 1966), Song Sparrow (Nice, 1937), White-crowned Sparrow (Blanchard, 1941) and McCown's Longspur (Mickey, 1943). Asynchronous hatching (hatching over a period greater than one day) has been recorded in all these species and also in the Baird's Sparrow (Cartwright, Shortt and Harris, 1937), Henslow's Sparrow (Hyde, 1939) and Lapland Longspur (Sutton and Parmelee, 1955; Rowell, 1957).

Asynchronous hatching is known in several groups of birds, including Falconiformes, Strigiformes, Ciconiiformes and Apodiformes. Lack (1954: 41) states that "there is every reason to suppose that the habit of starting incubation before the clutch is complete, and the consequent differences in the size of the young in the early stages, is an adaptation for bringing the family size into closer adjustment with the food supply". In such species the average clutch is somewhat larger than the number of young that the parents can rear in an average year and the extra egg or eggs are a reserve that can be utilized in good years. While asynchronous hatching has not been demonstrated to serve a similar function in the Emberizinae it would seem likely that the great differences in size and motor development that occur during the first day of nestling life would give a distinct advantage to older nestlings during periods of inclement weather or low food supply.

Distraction displays by the incubating female to a potential predator appear to be typical of ground nesting emberizines (Nice, 1943: 284). The wing-raised, tail-lowered display of the Savannah Sparrow is virtually identical to that described for the Song Sparrow (Nice, 1943: 248). This display is very effective in confusing human observers and in diverting attention and may prove as effective against potential mammalian or avian predators.

The wing-raised, tail-lowered distraction display of the Savannah Sparrow has been recorded by Shields (1935) and Linsdale (1938). No mention is made of a "rodent-run" display although Shields states that the female "would run through the grass like a field mouse" after giving a wing flutter-

ing display. Miller (1951) discussed the "rodent-run" of the Green-tailed Towhee (Chlorura chlorura) and noted resemblance of the flushing bird to a chipmunk. He explained this display as a direct modification of a general tendency to run or hop rapidly on the ground when closely pursued. The small mammal run of the Savannah Sparrow is superficially similar to the movements of Meadow Voles (Microtus) through dense grass. It seems possible that this movement would be successful in diverting mammalian predators such as foxes and weasels whose staple diet is small rodents.

The care of the young after hatching is shared by both parents. This is typical of parental care of the Emberizinae (Kendeigh, 1952), although in the polygynous Sharp-tailed Sparrow, the female feeds the young without assistance (Woolfenden, 1956), and the role of the male may be reduced in other species such as the Field Sparrow (Spizella pusilla) and the White-crowned Sparrow (Kendeigh, 1952).

Although two adult alarm calls were distinguished, there is intergradation between the two and they vary mainly in intensity. Smith (1963) distinguishes intensity levels in the alarm calls of the Grasshopper Sparrow, a low intensity "tik", a moderate intensity "chi-ip" or "til-lic" and a high intensity call with the double note given rapidly. Nice distinguishes the "tchunk" alarm call of the Song Sparrow from the "tik" fear call (1943: 255). She also reports that the young respond to the fear call by becoming silent (p.248). The alarm notes of the Brown Towhee (Pipilo fuscus) induce fledglings to freeze up to the age of 43 days (Quaintance, 1941). Young White-crowned Sparrows of fledgling age respond to the "tit" note of their parents by stopping their food cries and crouching (Blanchard,

1941: 29). It seems likely that the "chep" alarm call of the Savannah Sparrow, which was recorded only after hatching, serves as a warning call to the young.

Nest abandonment at a very young age is typical of passerines with open nests (Kendeigh, 1952). Nice (1943: 74) points out that there is a tendency for young to stay in the nest longer when the nest is safely located, such as hole- or basket-nests. It appears that nest abandonment prior to attainment of flight may reduce the probability of predation resulting from an open nest of active, noisy nestlings. The nest period of 9 days determined in this study is similar to that of other ground nesting emberizines (e.g. Cartwright, Shortt and Harris, 1937; Hyde, 1939; Mickey, 1943; Woolfenden, 1956; Smith, 1963; Maher, 1964).

Young Savannah Sparrows are cared for by their parents until at least the age of 19 days, and probably for another week after this. Continued parental care of the young for a considerable period of time after leaving the nest is general in all Fringillidae (Kendeigh, 1952). Nice (1943: 74), has summarized the course of development in passerine birds. The Fringillidae fall into her fifth group; birds which nest in the open, and leave the nest at 8 to 11 days, a week before they are strong on the wing. The majority of passerines become independent of parental care at about 28 days, regardless of nestling periods varying from 8 to 20 days (Kendeigh, 1952).

9.1.4 Success

The 16 percent breeding success as calculated by Mayfield's exposure method is very low. Hypothetically 100 pairs returning in the

spring would produce 144 young from 900 eggs during the breeding season assuming that each pair is double-brooded with an average clutch size of 4.5 and no loss of adults. The results of this study indicate that the first two assumptions are probably correct, the third is probably false, although loss of adults will be reflected in nest-loss figures and thus may be discounted. This figure also omits losses of young after leaving the nest. Nice calculates that returns of adult Song Sparrows from one season to the next (an indication of survival) is about 50 to 60 percent. Other passerine species studied show similar levels of survival (1937: 175-179). An estimated 20 percent of fledged nestling Song Sparrows survived until adulthood, although only an average of 13 percent of banded nestlings returned as breeders (Nice, 1937: 188-189).

Applying these survival figures to the hypothetical population of 100 pairs of Savannah Sparrows at the beginning of season 1, we can derive estimates for the population at the beginning of season 2. Fifty to sixty pairs of adults would survive, plus about 15 pairs of young from the 144 young produced in season 1. Thus the population would not be maintaining itself. Possible explanations are: 1) The survival figure calculated during the present study is lower than the actual survival due to insufficient or biased data. 2) A higher proportion of adult and juvenile Savannah Sparrows survive the winter than do Song Sparrows in Ohio. 3) The seasons of 1966 and 1967 were abnormally poor for reproductive success of the Savannah Sparrow in the Saskatoon area. 4) The population is actually declining. 5) The local population is maintained by immigration from other areas.

The most probable explanation is the first; that the survival figure calculated in this study is exceedingly low, due to inadequate or biased data. To maintain a stable population assuming 50 percent adult survival from season to season, 20 percent survival of juveniles from fledging until first breeding, and 100 percent homing, 500 young would have to survive to fledging. This would mean a 55.5 percent survival compared with 16 percent calculated in this study.

Conventional calculations indicate that 39.4 percent of eggs laid survive until fledging (Table 9). This is also lower than the 55.5 percent survival necessary to maintain the hypothetical population. However, to maintain the population with this low percent fledging, only a 15 percent increase in adult survival (to 65 percent) or an 8 percent increase (to 28 percent) in survival of young from fledging to first breeding would be required.

It is probable that the activities of the observer were responsible for some nest loss. Four of the 10 nests known to have been lost to predators, were predated within a day of finding. Only one of the predated nests survived more than four days after finding. The discrepancy between the survival figures calculated by the two methods (16 percent versus 39.4 percent) largely results from including predated nests for which only a few days observations were available in calculations of exposure. The 39.4 percent survival calculated by conventional means is only slightly lower than the average of 45.9 percent for 35 studies of open nesting altricial birds given by Nice (1957). In another study where both methods of calculating success were used, it was found that nesting

success (hatching success) of 5 species of ducks was 67 percent by the standard method and 51 percent by the Mayfield method. Respective totals of 198 and 215 nests were used for the two methods (Townsend, 1966). It would appear that while the Mayfield method corrects for bias due to incomplete nest histories, it makes the resulting survival figures extremely sensitive to bias from nest loss resulting from the activities of the observer, at least in a small sample. Ground nesting birds are probably more susceptible to this type of predation than are bush- or tree-nesting species such as the Kirtland's Warbler (Dendroica kirtlandii) on which Mayfield's original calculations were made.

In summary, it appears that conventional calculations of success provide the more accurate estimate for this study.

Ground squirrels and mice appear to be the chief predators of nests. Depredations by mice are probably limited to nests with eggs. Stokes (1950) suspected that Deer mice were responsible for destruction of eggs in nests of the American Goldfinch (Spinus tristis). Walkinshaw (1940) places "mice" as a probable enemy of the Grasshopper Sparrow. Lemmings (Dicrostonyx or Lemmus) have been implicated in predation of Lapland Longspur eggs by Sutton and Parmelee (1955). Ground squirrels of the genus Citellus were probably the most important factor in egg loss in the present study. SOWLS (1948) has demonstrated the predation of Citellus franklinii on duck nests and Stanton (1944) states that depredation of upland game bird nests by Citellus beechyi is of "considerable importance". Harris (1944) suspected Citellus tridecemlineatus as a nest predator on the Chestnut-collared Longspur. Because of the general carnivorous tendencies of the genus Citellus (Sealy, 1966), it is highly possible that the losses of nestlings as well as eggs

are partly due to the activities of ground squirrels.

Avian predators are probably not important in nest loss because of nest concealment. They probably are a factor in mortality of fledglings and adults. Burrowing Owls and Marsh Hawks have been demonstrated to be predators of Savannah Sparrows (Longhurst, 1942; Breckenridge, 1935). The Short-eared Owls resident on the study area in 1966 captured fledgling Meadowlarks and undoubtedly preyed on fledgling sparrows as well.

Cowbird parasitism of the Savannah Sparrow was not found in 1966 but occurred in 6 of 17 nests (35.3 percent) in 1967. Cowbird parasitism on nests of other host species on or in the vicinity of the plot was also heavier in 1967 than in 1966 (31.5 versus 12.5 percent). Terrill (1961) records 5 parasitized nests out of 140 nests of the Savannah Sparrow in southern Quebec, and states that this species is rarely affected. The high level of parasitism recorded during the second season of the present study is a result of the noticeably greater numbers of Cowbirds in the area in 1967. The presence of Cowbird young in normal size broods of Savannah Sparrows may have dire results for the host young (Figure 8). Terrill (1961) states that the fledging of even one host young per parasitized nest of the smaller passerines is notable.

9.2 Growth and Development

The growth and development of nestling altricial birds is exceedingly rapid. Behavioral development is dependent on physical development in many cases. Behavioral patterns are also often related to events in the sequence from unhatched egg to independent juvenile bird, and must be considered

adaptations to this sequence. This discussion will attempt to describe as many of these relationships as were noted in the Savannah Sparrow.

The development of the juvenal plumage has been well described for two emberizines, the Rufous-sided Towhee (Barbour, 1950) and the White-crowned Sparrow (Banks, 1959). The plumage development of the Savannah Sparrow as described in the present study is very similar to that of these two species (Table 26). A few minor differences are noted. Banks (1959: 97) commented on the pigmentation of the feather papillae of newly hatched White-crowned Sparrows. In the Savannah Sparrow this pigmentation does not become noticeable until the age of 1-2 days. Banks also noted variations in this feature of the plumage in other nestling passerines.

The relation of feather-development to the development of endothermy is obvious. Maher (1964) has described the development of endothermy in the Lapland Longspur and Snow Bunting. Other studies indicate essentially similar patterns in the Chipping Sparrow and Field Sparrow (Dawson and Evans, 1957) and the Vesper Sparrow (Dawson and Evans, 1960). The beginning of the establishment of endothermy occurs on the third day after hatching. Endothermy is well established by the seventh day, and from the eighth day on the adult pattern is shown (Maher, 1964: 527). A similar pattern is probably to be found in the Savannah Sparrow. Behavioral thermoregulation (shivering and fluffing of the body feathers) was first noted in seven-day young.

Table 26. Ages of various features of plumage development in three species of Emberizinae. Ages in days

Character	Rufous-sided Towhee (Barbour, 1950)	Savannah Sparrow (this study)	White-crowned Sparrow (Banks, 1959)
Papillae of primary remiges protruding	2	2	2
Papillae of all remiges protruding	3	3	3
Papillae of coronal tract protruding	4	4	4
Papillae of all major tracts protruding	4 - 5	4 - 5	5
Ventral tract emerging from sheaths	5 - 6	6	6
Papillae of rectrices protruding	5	5 - 6	6
Primary remiges emerging from sheaths	6	7	7
Coronal tract emerging from sheaths	7	7	8

Growth in altricial birds is extremely rapid. The mensural characters examined in this study show several patterns. The rate of weight gain is rapid, but decreases steadily from hatching to Day 9 when the growth curve essentially levels off at about 70 to 80 percent of adult weight (Figure 9). The decline in weight on Day 10 is due to the small sample of three birds from one nest which were subjected to cool weather with rain.

The logarithmic growth curve shown in Figure 10 differs very slightly from that of other emberizines. Maher (1964) compared logarithmic growth curves for seven species of Emberizinae with data from his own work. All of these curves show a slightly sigmoid shape, resulting from an accelerated rate of weight gain after the first day. The rate of weight gain then either increases slowly, or remains constant until the age of about 5 days when it begins to decrease. From this age, all curves resemble that of the Savannah Sparrow. Growth curves for all species level off at 9 days of age.

The growth curve of the wing (Figure 11) shows an increasing rate of growth until Day 4, a stable rate of growth to Day 7, and finally a decreasing rate until at least Day 15, when the wing has reached approximately 70 percent of adult length. The early changes in growth rates are explainable by the fact that the measurement of wing chord is a combination measurement of the manus plus the longest (third) primary. Until the age of 3 days this measurement represents only the length of the manus. After this age, the measurement includes growth of the third primary, which affects the rate of increase of the measurement. The growth curve for the third primary (Figure 11) shows an initially rapid, but constantly decreasing rate of growth.

The rectices appear on Day 4. The growth curve of the central rectices (Figure 11) is similar to that of the third primary. The apparent decrease in rate of growth on Day 10 and subsequent increase on Day 11 is probably a result of small sample size. There is a possible correlation between the late development of the rectices (in comparison to the remiges) and the fact that these feathers would be extremely susceptible to damage in the overcrowded conditions of the nest shortly before fledging. At fledging (Day 9) the rectices have reached only 12 to 15 percent of adult length while the primaries have reached over 70 percent of adult length.

Both the tarsus and the culmen have rates of growth lower than the flight feathers (Figure 12). The tarsi have a relatively constant growth rate until Day 4, and then a decreasing rate until Day 7 when adult size is reached. The early attainment of adult size of the feet is obviously an adaptation to early nest departure. The growth curve of the culmen has a relatively constant rate of growth to Day 6, and then a decreasing and very low rate of growth to Day 15, when this structure is approximately 80 percent of adult length.

Nice (1943) has divided the development of young Song Sparrows into 5 stages. These are as follows:

- Stage 1: 0-4 days; coordinations mainly concerned with nutrition.
- Stage 2: 5 and 6 days; first appearance of new motor coordinations.
- Stage 3: 7, 8 and 9 days: rapid acquisition of motor coordinations.
- Stage 4: 10-16 days: leaving the nest to attainment of flight.
- Stage 5: 17-28 days: attainment of independent feeding reactions.

Table 27. Ages of appearance of certain behavioral characters in three species of Emberizinae. Ages in days.

Character	Savannah Sparrow (this study)	Song Sparrow (Nice, 1943)	White-crowned Sparrow (Banks, 1959)
Gaping	1	1	1
Begging calls	1	2	3
Standing	6	7	8½
Distress scream	7	7	6
Escape attempts	7	7	8½
Location call	9	9	-
Leaving nest	9	9 - 10	8½
Flying strongly	15	17	-

Behavioral development of the Savannah Sparrow appears to be very similar to that of the Song Sparrow outlined by Nice. Resemblances to the White-crowned Sparrow are also noted (Table 27), although some discrepancies are noted, particularly the first occurrence of the begging call. Banks (1959: 100) mentioned interspecific variations in the appearance of this call in several species of passerines.

A number of correlations between growth, behavioral development and events in the life of the young bird should be noted. The newly hatched Savannah Sparrow is a blind, almost naked, uncoordinated, ectothermic animal. Other than growth, plumage development and motor development, the first major event of nestling life occurs when the eyes open at the age of 3 - 5 days. After the eyes are fully open (Day 5) discrimination in the begging reaction, and attempts to escape the observer begin to appear. Motor coordination has reached the level where the young bird can perch and hop by this age. Understandably, a number of major changes occur at the age of fledging (8 - 11 days). The distress scream appears and becomes well developed by Day 8. By Day 9 fecal sacs have disappeared and the young begin to give the location call. Correlations of growth of tarsi and rectrices with the age of fledging have been noted previously.

Behavioral development after fledging could not be followed in this study but probably resembles that of the Song Sparrow (Nice, 1943: 18-34).

9.3 Territory

Few aspects of avian biology have been the subject of as much controversy and discussion as territoriality. Although many definitions have been applied to the term "territory", that of Noble (1939): "territory is any defended area" is the most satisfactory because of its simplicity and its applicability to many diverse phenomena. The historical development of the concept of territory in birds has been outlined by Nice (1941). The essentials of the territory theory were outlined by Bernard Altum as early as 1868. Most of the controversy since that time has revolved around ascribing a function or functions to territorial behavior and to the discovery of any unifying principles behind the diverse assemblage of territorial phenomena found in birds (for example: Lack and Lack, 1933; Tinbergen, 1936; 1957; Nice, 1941; Hinde, 1956; Carpenter, 1958; Kuroda, 1960).

Nice (1941) has outlined six types of territories found in birds, as follows:

- A. Mating, nesting and feeding ground for young.
- B. Mating and nesting but not feeding ground.
- C. Mating station only.
- D. Restricted to the narrow surroundings of the nest.
 - (1) Colonial species.
 - (2) Solitary species.
- E. Winter territory.
- F. Roosting territory.

An examination of the breeding territories of the Savannah Sparrow produces the following information:

1) Mating occurs on the territory. All courtship behavior observed took place on the territory of the male. The activities of the males are virtually limited to their territory during the period of pair-formation.

2) Nests were generally placed on or at the edge of the territory of the parental male (Table 18).

3) Foraging for the young was carried out to a large extent on neutral areas (grassland or grain fields) at distances as great as 600 feet (6 territory diameters) from the nest site. Similar long foraging flights for this species are mentioned by Marshall (1948). Both males and females were observed foraging on or very near to the territories of other males without expulsion by the territorial male (Section 6.3.2).

In view of these facts, it would appear that the breeding territories of the Savannah Sparrow would fall into the Type B category of Nice.

Most Emberizinae appear to have a Type A territory. These include the Reed Bunting (Emberiza schoeniclus), Snow Bunting, Song, Field, White-crowned, Chipping and many other sparrows (Nice, 1941). The Corn Bunting (Emberiza calandra) is described as having a Type B territory (Nice, 1941) perhaps connected with the polygynous habits of this species. The polygynous male Sharp-tailed Sparrow appears to lack a defended territory while the congeneric and monogamous Seaside Sparrow shows a well-defined Type A territory (Woolfenden, 1956).

Ten possible functions of territory in birds have been outlined by Hinde (1956). These will be examined individually in view of the information available on the Savannah Sparrow and their possible importance will be examined.

1) The familiarity with the area which results from site attachment may assist feeding, escape from predators, etc., and may also increase fighting potentiality. Evidence for these "familiarity" functions of territory is largely circumstantial. Tinbergen (1956) has commented on the importance of knowledge of the terrain in escape from predators by young gulls and Hinde (1956) cites observations by Southern on the role of familiarity of terrain in food finding of the Tawny Owl (Strix aluco). Andrew (1956) does not believe that familiarity assists escape in the Yellowhammer (Emberiza citrinella) and Corn Bunting. In response to a potential predator such as a hawk both species remained still on their perch or dropped into cover; in the second case the cover was nearly always no more than a few feet away, and directly visible. Observations on the Savannah Sparrow during this study indicates similar responses to Marsh Hawks and Short-eared Owls which hunted the study area. It is unlikely that familiarity with the territory is an important factor in either facilitating escape or in locating food in the Savannah Sparrow.

The role of familiarity in increasing fighting potential of males has been demonstrated in many species of birds (Hinde, 1956). Recently established first year male Song Sparrows may be evicted by territory holders of the previous year (Nice, 1941). This function of territorial familiarity may be present in Savannah Sparrows but would be of minor importance.

2) There is strong evidence that territorial behavior can regulate density in favored habitats. There is no direct evidence that territory limits the total population in all habitats. The limitation of breeding

density by territorial behavior was one of the earliest proposed functions and has received support from workers who have witnessed the failure of newly arrived birds to establish themselves (e.g. Tinbergen, 1939, 1956; Lanyon, 1956). Some individuals may be forced to take up territories in sub-optimal habitats. This has been demonstrated by Kluijver and Tinbergen in the Great Tit (Parus major) who believe that the critical density in prime habitats was set by the territorial behavior of the first settlers (Hinde, 1956). In the present study it was noted that the first territories of Savannah Sparrows to be established in the spring were located in brushy habitat which was shown to be preferred to open grassland areas (Section 7.1). Territories which were established in areas with little brushy vegetation were those belonging to males who began to defend territories after the majority of the territories were established (e.g. territory X and the territory of M15 were first defended on 15 May, 1967 when most other territories were firmly established).

Limitation of breeding populations in a given area by territory is also suggested by the presence of non-territorial males. During the present study there appeared to be a surplus of males. Territorial male Savannah Sparrows which disappeared were replaced by other males with little or no shifting of territory boundaries of surrounding males. For example, M14 was last seen on 14 June, 1967. On 30 June, M21 (who had been banded on this territory on 26 June) was defending the same area, and subsequently mated and nested in this area. None of the territories of the surrounding males were effected. In addition, some males were on the study for long periods of time without defending territories. M5 was banded on 10

May, 1967. He was seen again on 6 July, but was not recorded in the intervening time. This bird was definitely a male (the cloacal protruberance was well developed on 10 May) but never established a territory. Large populations of non-territorial males of a number of passerine species have been demonstrated by the removal experiments of Stewart and Aldrich (1951) and Hensley and Cope (1951). In these studies as many as six times the original population of territorial males of some species were removed from a study area during one season.

Thus, it appears that territorial behavior may limit the number of breeding males in available optimum habitat in a number of species of passerine birds, including the Savannah Sparrow. Whether territory can limit the total breeding population in all habitats, as postulated by Wynne-Edwards (1962) is uncertain, and an answer to this question depends on further investigations, on size of territory in relation to quality of the habitat, available resources, and population levels.

3) Territory facilitates the formation and maintenance of the pair-bond. The localization of the activities of a male makes him more likely to obtain a mate since the female can find him again after temporary separations, (Tinbergen, 1939, 1956; Emlen, 1954; Andrew, 1956; Armstrong, 1956; Conder, 1956; Durango, 1956; Gibb, 1956b; Marler, 1956b; Simmons, 1956). The maintenance of the pair-bond is related to the importance of monogamy in successful rearing of the brood. The role of territorial defence by both sexes in promoting monogamy has been stressed by Tinbergen (1939) for the Snow Bunting. Andrew (1956) believes that polygamy is possible in the Corn Bunting only because fighting between females is unimportant.

The self advertisement which accompanies territorial defense is clearly related to pair formation. The abeyance of song at pair formation without a concomittant decrease in aggressiveness has been shown in various *Emberizinae* by Tinbergen (1939); Blanchard (1941); Nice, (1943); and Walkinshaw (1944). The abeyance of singing of Savannah Sparrows noted during the present study would certainly suggest a similar relationship.

4) Territory may reduce interference in various reproductive activities by other members of the species. Armstrong (1947: 278-280) cites many examples of such interference with courtship, copulation and nest-building. This seems to be one of the more general functions of breeding territories in birds and is probably of some importance in the Savannah Sparrow.

5) Defense of the nest site is an important consequence of territorial behavior in many species. This is especially important in species with specialized nesting requirements, such as hole-nesters and cliff-nesters (Haartman, 1956; Tinbergen, 1956). In species with more generalized nesting requirements the initial breeding territories are unrelated to the eventual nest site, but aggressiveness of the male may later become organized around the nest site (Lanyon, 1956; Marler, 1956; Snow, 1956; Young, 1956). This aggressiveness may be directed against members of other species as well as conspecifics (for example, Lack and Lack, 1933).

The relationship of nest-site to territory in the Savannah Sparrow is ambiguous (Section 6.3.1). The unspecialized nature of the nest-site makes it highly unlikely that the nest-site is important in courtship and pair formation as it is in some species (Hinde, 1956: 358). No evidence was obtained in the present study of interspecific defense of either territory or nest-site by the Savannah Sparrow.

6) In a few species territory is primarily concerned with food, but in most the food value of the territory is not significant. The food value of the Type A breeding territory has been one of the most controversial aspects of territory theory. The main arguments against the food "function" of Type A territories have been summarized by Lack (Lack and Lack, 1933; Lack, 1954). This function of territory can be dismissed for the Savannah Sparrow because the bulk of foraging for nestlings appears to be done in neutral grassland and often at some distance from the territory. Also, territorial defense is not directed toward foraging Savannah Sparrows or other species which are possible food competitors. Tinbergen (1939, 1957) has pointed out, however, that in some species, a source of available food close to the nest may be of ultimate importance during the first days of nestling life or during cold weather, when longer foraging trips result in chilling and cessation of begging by the nestlings.

7) In some species the over-dispersion produced by territorial behavior may reduce predation of nests, eggs or incubating females. This idea has received support from many workers (Lack, 1954; Gibb, 1956a, 1956b; Marler, 1956b; Simmons, 1956; Snow, 1956; Swanberg, 1956; and Tinbergen, 1956) although evidence is largely circumstantial. The significance of this function in the Savannah Sparrow is not known, and if predation is decreased by dispersion of nests, this advantage may be secondary.

8) Maintenance of a territory may reduce the despotism of other males. Nice (1941) has suggested that a stable territorial system will reduce the time spent in aggression by individual males. A reduction in overt territorial aggressiveness in the Savannah Sparrow was noted after territorial

establishment (Figure 18) but this also coincided with the termination of pair-formation. Although reduction of despotism may be a result of territorial behavior, the function of territorial aggressiveness is in no way explained (Hinde, 1956).

9) Territorial behavior may reduce disease. This function has been suggested by a number of workers (Nice, 1941; Collias, 1944; Armstrong, 1956; Gibb, 1956a, 1956b; Marler, 1956b) but no evidence has been obtained. This is unlikely to be a significant consequence of such behavior except in some colonial species (Hinde, 1956).

10) Territoriality may prevent inbreeding and promote range extension. These ideas have been suggested by Collias (1944) and Armstrong (1947). Haartman (1956) believes these effects may occur but doubts their importance. Territorial behavior is unlikely to be the factor responsible for the dispersal of young birds (Lack, 1954).

In summary, the functions of territory in the Savannah Sparrow are diverse and some of the possible effects of territorial behavior may be secondary results of such behavior. The defense of an adequate food supply can be ruled out as a possibility and probably the "dispersion" functions in prevention of disease and predation as well. It would appear that the primary function of territorial behavior is concerned with the formation and maintenance of reproductive bonds. The possession of a territory is a prerequisite to the acquisition of a mate and pair-formation is facilitated by the localization of activities in the male and the prevention of interference by other males, both direct consequences of territorial defense. The role of territory in maintenance of the pair-bond which

results in monogamy is less apparent. Whether monogamy is essential for successful reproduction in this species is unknown, and must await further work. Territorial behavior, in conjunction with habitat selection may set a limit on the breeding population of a given area but the importance of this factor in population control is not understood.

The interrelationship of territory size and population in a given area is a complex one involving habitat selection and the proportions of different elements within the vegetational mosaic. The territory size determined in this study (mean area = 0.17 acres) would allow maximum territory density of 5 - 6 males per acre or 500 - 600 per 100 acres. Actually, territories on the study area were limited to brushy vegetation (Figure 16) which composed about 21 percent of the total habitat area (Table 20). Thus the population density should be about one-fifth the possible territory density or 80 - 100 territories per 100 acres. The estimated figure was 68.6 territories per 100 acres (Section 6.2.2). The maximum population which could be carried by similar grassland-brush mosaics of varying proportions would be influenced by the amount of sparse brush and grassland available for foraging. Marshall (1948) has mentioned that Savannah Sparrows do not appear to forage under a vegetation canopy.

Some comparative figures on populations of Savannah Sparrows are available (Table 28). It is apparent that the wide variation in population levels is related to habitat. The lowest population level was found in an area where the habitat offers little brush and where weeds were the tallest vegetation available for song perches (Saunders, 1936). The highest population, that of Mowat and Lawrie (1955) at Nueltin Lake, is an area where

the birds are common only in restricted areas of suitable habitat. In this area the birds are confined to sedge bogs and riverside meadows and utilize bordering thickets of willows and dwarf birch as song perches (Harper, 1952). This situation of ample bushy habitat for territorial activity, plus a central area of sedge bog for foraging area may result in a density approximating that of the maximum territory density calculated in this study. The estimate of Mowat and Lawrie (1955) may be biased by their failure to observe the utilization of the bordering brush. They state "each small muskeg supported a large population, sometimes as high as 6 pairs to the acre".

Table 28. Population densities of Savannah Sparrows in various habitats.

Worker and locality	Habitat	Population (pairs/100 acres)
Saunders, 1936 New York	Moist grassy meadows	16
Saville and Morland, 1951 Ontario	Abandoned pasture with scattered brush	30
Tester and Marshall, 1961 Minnesota	Native long grass prairie	25 - 60
Present study Saskatchewan	Native mixed prairie	69
Mowat and Lawrie, 1955 North West Territories	Small taiga muskegs	600

As was mentioned in discussing territorial function, there is a distinct decline in overt territorial interactions in late May (Table 19, Figure 17). This coincides with the time of completion of pair-formation and the initiation of the first nests. It is not contemporaneous with the stabilization of territorial claims which occurs about mid-May coincident with arrival of the females (Section 6.1). It would appear that territories are stabilized when the females arrive but that territorial defense does not decline until firm pair-bonds are established and nesting is initiated. This points strongly to the importance of territory in the formation of pair-bonds.

The behavioral components of territorial defense of the Savannah Sparrow are equivalent to those of other Emberizinae and other passerines. These have been excellently reviewed by Andrew (1956/57b; 1961) who discusses the derivation and motivation of the components. There is no distinct separation between components used in courtship and those used in reproductive fighting. All the main components appear in both contexts and probably have identical origins in both display functions. This is not surprising if we consider that threat behavior can be interpreted as the simultaneous arousal of tendencies to attack and to retreat, while during courtship displays aggression is often active in addition to the sexual tendency (Tinbergen, 1952). "Tendency" is used here as a descriptive word for "the readiness to show a particular type of behavior, as observed under natural conditions" (Hinde, 1955-56), thus avoiding commitment about controversial and poorly understood internal and external factors of motivation. It does not imply any causation by a unitary "drive".

The Puff-Sing-Wave display has been classified as an aggressive display in this study. Nice, who first described this display in the Song Sparrow states: "It is released in a male in territorial mood by the following situations: another Song Sparrow, not his mate, alights above him, or suddenly flies near him, or when an interloper has taken his territory It is a substitute activity, a formalized threat, a signal that the demonstrator is powerful and tends to attack" (Nice, 1943: 154-155). Andrew (1956/57b, 1961) has questioned this interpretation. He states (1961: 339) that this display "in this monomorphic species seems likely to be a pair-formation response, induced by the bird being unfamiliar rather than because it is a male". Both Nice's observations on the Song Sparrow and observations during the present study support an aggressive function for this display rather than a role in courtship. Nice makes no mention of its use in courtship and Andrew (1956/57b) in his original interpretation of the Puff-Sing-Wave as a possible courtship display to males was puzzled by the fact that neither it or any other display appeared to be used in male courtship to females.

During the present study both the Puff-Sing-Wave and a male courtship display were recorded for the Savannah Sparrow. The courtship display is homologous to those of other Emberizinae as described by Andrew (1956/57b). The elements of puffing and wing movement are shared with the Puff-Sing-Wave but there are two notable differences. Tail spreading was never observed during the Puff-Sing-Wave and the wing movements were different. The wing quivering during the courtship display was bilateral with the wings lifted laterally from the body and quivered. This type of wing-quivering is thought

to be homologous to the wing-vibration of female precopulatory displays and is possibly derived from the juvenile begging display (Andrew, 1961: 334). The Wave, on the other hand, is often unilateral, and the wing is not quivered but is raised vertically over the back and held there for a short duration (see Nice, 1943: 156 for illustration). In the Savannah Sparrow it was noted that the Wave intergraded with Wing-Flicks, which are thought to be intention movements of flight (Andrew, 1956-57a). In this context the Wave would appear to be a high intensity intention movement of flight and would be compatible with an interpretation of threat behavior as an interaction of tendencies of attack and escape.

Similar types of wing movements have been recorded as components of threat displays in a number of fringillids including the Painted Bunting (Passerina ciris) (Thompson, 1965); Chaffinch (Fringilla coelebs) (Marler, 1956a); House Finch (Carpodacus mexicanus), (Thompson, 1960); Common Redpoll (Acanthis flammea) (Dilger, 1960); American Goldfinch (Spinus tristis) (Coutlee, 1967); Green-backed Sparrow (Arremonops conirostris) (Moynihan, 1963) and, significantly, in the Ipswich Sparrow (Hailman, 1958).

It is possible to outline the sequence of events which occur in territorial encounters of the Savannah Sparrow. Figure 21 traces the possible sequence of events from a male alone on his territory, through an encounter, to the situation where the successful male is again alone. The width of the arrows give a subjective estimate of the frequency of different alternatives. These are based on purely qualitative observations and need subsequent quantitative examination.

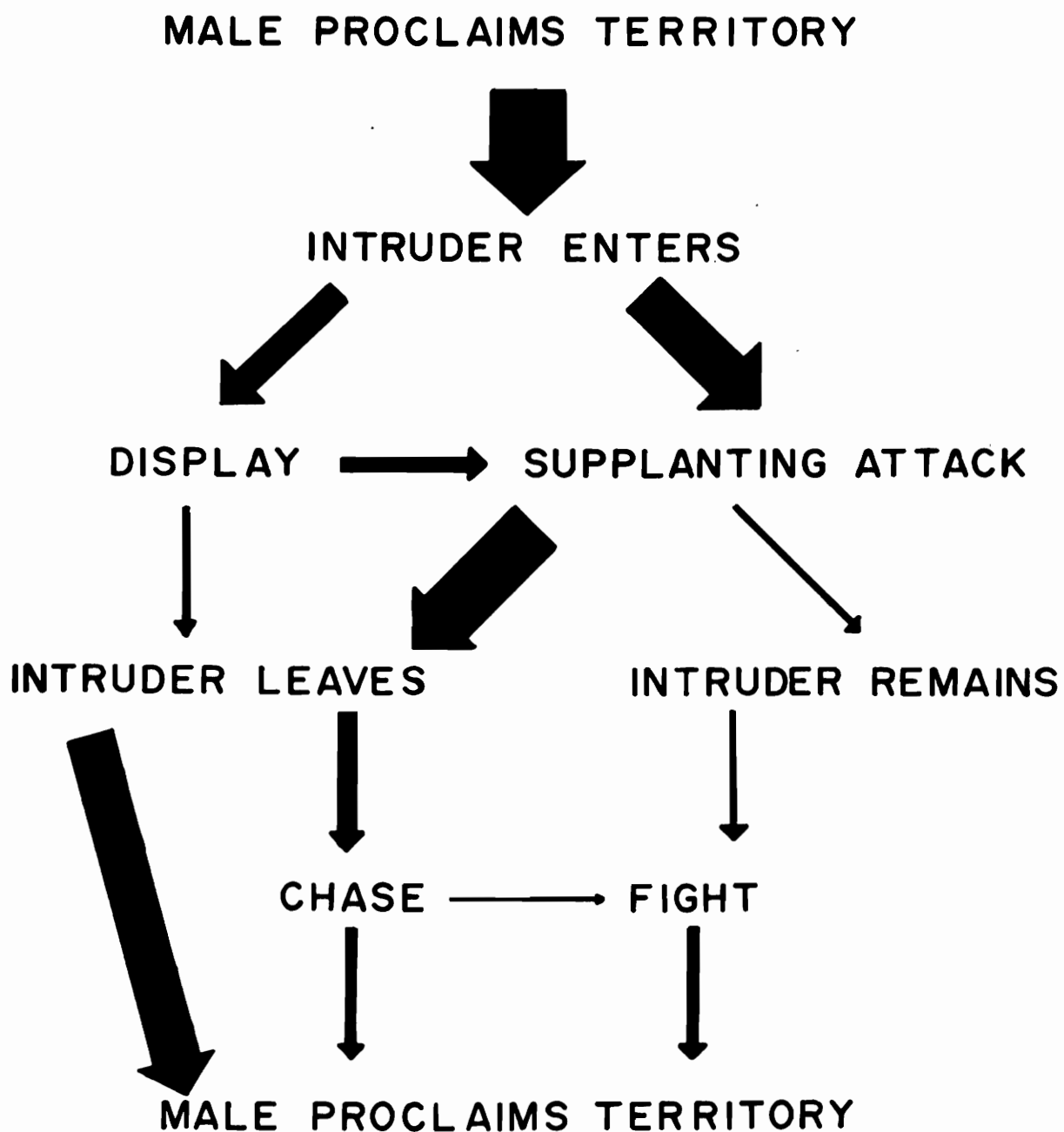


Figure 21. Hypothetical sequence of events in territorial encounters of the Savannah Sparrow. Explanation in text.

9.4 Habitat selection

It is obvious that many factors relevant to the survival of birds, such as food availability and nest-sites effectively restrict the topographic distribution of the species. Such ultimate factors cannot fully explain the mechanism of habitat selection. Territories are often occupied long before the factors affecting reproductive success, e.g. the food supply for the young, are observable. In Greenland, the male Snow Buntings occupy territories in late April when the ground, with the exception of a few projecting rocks, is covered with snow (Tinbergen, 1939). According to presently held views, the birds are guided to their breeding stations by a primarily innate reaction released by certain environmental stimuli, on the principle of summation of heterogenous stimuli. The threshold for the release of the reaction is dependent on the internal motivation of the bird (Hilden, 1965). The proximate factors involved in the release of the settling reaction need not have any biological significance to the species as such. The role of psychological factors in habitat selection has been stressed by Lack (1933, 1937, 1940) and Miller (1942). Lack states "many limits to habitat distribution in birds could be correlated solely with psychological factors, that birds select their habitats by visually prominent features, not necessarily those essential to their existence" (1940: 80). Lack (1944, 1949) and Svardson (1949) have concluded that selection mechanisms are adaptations that have arisen through interspecific competition.

The role of learning in habitat selection has been reviewed by Hilden (1965) and Klopfer and Hailman (1965). The reaction of birds to stimuli

guiding them to the breeding station is inherited, but some facts reveal that the innate pattern of the nesting habitat is reinforced at a later stage by learning. Site tenacity or Ortstreue has been demonstrated to modify habitat selection in cases where the habitat changes. Austin (cited by Hilden (1965)) has shown that old individual Common and Arctic Terns (Sterna hirundo and S. paradisaea) return to their original nesting islands year after year, although spreading shrub vegetation gradually repels all younger birds. Lack (1933) reports similar cases with the Meadow Pipit (Anthus pratensis) and Stone Curlew (Burhinus oedicnemus) lingering as resident species in young pine plantations which replaced the former open countryside.

The role of imprinting in selection of the habitat has been discussed by Klopfer and Hailman (1965). It appears likely that imprinting plays a role in habitat selection but the extent of this role has been clearly defined in only a very limited number of species. Klopfer (1963) raised young Chipping Sparrows in an artificial environment of pine (normal) and oak foliage. He concluded that "these birds, as adults, appear to demonstrate preferences for pine, as opposed to oak, that are relatively independent of their earliest visual experience, although temporary modification in preferences may occur" (1965: 288).

The ultimate factors determining reproductive success are: a) food, b) the requirements imposed by structural and functional characteristics of the species, and c) shelter from enemies and adverse weather (Hilden, 1965). The proximate factors which are considered by Hilden to be characteristic stimuli of the species-specific habitat are stimuli of a) landscape;

b) terrain; c) nest, song, look-out, feeding and drinking sites; and d) other animals. In certain species food also directly influences the choice of territory. In addition, internal motivation contributes to the release of the selection response.

The Savannah Sparrow occupies a seemingly diverse assemblage of habitats, varying from salt marshes to tundra. Many descriptions in the literature are vague and give little impression of the actual physiognomy of the habitat. Table 29 gives a summary of habitat descriptions for different localities in North America. On first examination there appears to be no uniformity in vegetation, but two recurring features may be described. First, all of these habitats are physiognomically similar. All consist of low, dense herbaceous vegetation, be it sedge marsh, prairie grassland, or arctic tundra. Secondly, most appear to offer some type of higher vegetation bordering or scattered throughout the herbaceous matrix.

Three of the authors (Saunders, 1936; Linsdale, 1938; and Tester and Marshall, 1961) have commented on the essential nature of dense herbaceous vegetation cover. Tester and Marshall (ibid.) demonstrated a correlation between Savannah Sparrow population and litter (dead grass) cover. Decrease of litter cover by burning decreased the population of Savannah Sparrows on one plot from four to one pair per acre. Dense ground cover is essential to this species in that it provides nest sites and refuges from climate and predators.

Six of the authors (Shields, 1935; Linsdale, 1938; Harper, 1952; Johnsgard and Rickard, 1957; Gabrielson and Lincoln, 1959; and Todd, 1963) commented on the usage of taller structures (bushes, weeds, rushes, posts)

Table 29. Breeding habitats of the Savannah Sparrow throughout North America

Worker	Locality	Habitat
Shields, 1935	Pennsylvania	Upland fields.
Saunders, 1936	New York	Moist meadows with tall grass or weeds.
Linsdale, 1938	Nevada	Moist pasture lands, alfalfa fields and marshy areas with dense vegetation.
Marshall, 1948	California	Seaside chaparral/grassland mosaic.
Dumas, 1950	Washington	Sedge zone of marshes with grass and rushes (<u>Juncus</u>).
Saville and Morland, 1951	Ontario	Abandoned pasture with scattered bushes.
Harper, 1952	Keewatin, N.W.T.	Sedge bogs and riverside meadows with bordering thickets.
Manning and MacPherson 1952	Northern Quebec	Alder and willow thickets surrounding marshes; patches of alder and dwarf birch on tundra.
Johnsgard and Rickard, 1957	Washington	<u>Festuca</u> grassland with scattered <u>Symphoricarpos</u> .
Gabrielson and Lincoln 1959	Alaska	Tundra or mountain meadows with taller weeds or willows.
Maher, 1959	Alaska	Dwarf shrub-sedge tundra.
Tester and Marshall 1961	Minnesota	Native long grass prairie.
Todd, 1963	Northern Quebec, Labrador	Wet meadows and sedge bogs with intermixture or margin of shrubbery.

in the vegetation mosaic as territorial perches by the males. In the present study the importance of elevated perches was demonstrated (Tables 22 and 23). Only six percent of all song perches were located on the ground or on tufts of grass.

The five categories of proximate factors of habitat selection outlined by Hilden (1965) have been previously mentioned. The features of landscape and terrain enable "rough" selection of the breeding station. By landscape Hilden refers to general features of the area, such as open/closed, flat/undulating, continuous/discrete, and the proportion of water area. By stimuli of the terrain he refers to the physiognomic characteristics of the territory proper among which are included surface formation (structure, slope and soil humidity), quality of the vegetation cover (the covering, density, height and colour of different layers, mode of branching, etc.), and various kinds of man-made structures (Hilden, 1965: 59-60). An examination of the various habitats utilized by the Savannah Sparrow suggests that the appropriate stimuli are 1) open areas, continuous, but not necessarily large; 2) dense ground cover of herbaceous vegetation and litter; and 3) suitable shrubby or weedy vegetation rising above the herbaceous matrix.

The third proximate factor considered by Hilden is the presence of nest-, song-lookout, feeding and drinking sites. The type of terrain that releases the settling reaction of many ground-nesting passerines always provides nest-sites and feeding sites. The birds first choose their territories, and thereafter begin to look for nest sites. This is the case in the Savannah Sparrow. Song perches, on the other hand, may influence

the selection of territory, although this may be included in the more general selection previously mentioned. Lack (1933) has shown that the Tree Pipit (Anthus trivialis) is found in open heath country identical to that frequented by the closely allied Meadow Pipit provided one or more fairly tall trees were present. The presence of these trees was the only difference between the territories of the two species. Surprisingly, the only use of these trees was to provide a landing site after the aerial song of the pipit.

Stimuli provided by other individuals of the same species are important in habitat selection in highly social birds (Klopfer and Hailman, 1965). Even species generally regarded as typically territorial and avoiding company may gather in loose groups and fail to occupy intervening areas which appear to be suitable as breeding terrain. Hilden (1965) lists many examples of this type of phenomenon. The Song Sparrow has been shown to exhibit this type of relationship (Nice, 1937). The role that previously established birds play in territory selection in the Savannah Sparrow is unknown.

An examination of the features of the habitat of the Savannah Sparrow leads to a conclusion that the birds are bound by habitat selection to areas containing shrubby or other vegetation suitable for song perches. The feeding requirements of Savannah Sparrows on the study area were filled largely by grassland areas outside the territories. The nest-sites, although closely associated with shrubby vegetation (Section 7.2) were located in the grass-litter matrix which was also present in areas lacking brush. The grassland similarly provided sufficient cover for escape from enemies and

inclement weather. The only factor which did not appear to be duplicated by the grassland habitat was the provision of elevated perches for use in territorial proclamation. In this respect it is interesting to note the territory of M15 which was located in open grassland but contained one small clump of *Spiraea* and a marker stake which were used as song perches. The provision of artificial perches in an area of open grassland on the study area could effectively test this hypothesis.

9.5 Relations with Baird's Sparrow

At the initiation of this study, it was suspected that the Savannah and Baird's Sparrows displayed interspecific territoriality. This was suggested by prior observations of non-overlap of their territories on Kernan's prairie. Subsequently, these ideas have been modified. While there appears to be little or no overlap of the territories (i.e. defended areas) of the two species (compare Figure 16 and Figure 20), this does not appear to be due to interspecific defense, but rather to the distinct differences in the habitat defended. It has been demonstrated that Savannah Sparrows rarely sing from the ground or grass, while Baird's Sparrows utilized such situations in over 80 percent of the recorded instances, even though elevated perches were provided by shrubs on or bordering the territory. Savannah Sparrows were never recorded to chase Baird's Sparrows, and only one attempted supplanting attack was seen.

Certain observations concerning the Baird's Sparrow in Manitoba appear to be in conflict with results in the present study. Cartwright, Shortt and Harris state (1937: 164) "the nesting territories of Baird's and Savannah Sparrows frequently overlap.....but the relations between them are perfectly amicable". This apparent overlap was not noted in the present study, but this may be explicable if Cartwright and his co-workers did not distinguish between territory (defended) and utilized area of the Savannah Sparrows. In the present study territory did not overlap, but Savannah Sparrows frequently foraged in grassland areas in which Baird's Sparrows had territories.

The second point of conflict is in the utilization of song perches by the Baird's Sparrows. Cartwright and his co-workers stress the utilization of Symphoricarpos and other shrubs as song perches. They state (ibid. p.167): "It is more than likely that these desirable perches were a big factor in determining the shape and layout of (Baird's Sparrow) territories". Cartwright et al. were dealing with a dense population of Baird's Sparrows where the territories of different males adjoined one another. This situation was not present in the study area at Kernan's prairie and may have been a factor in the differences in territorial proclamation. Cartwright and his co-workers also do not give any information on the frequency of utilization of elevated song perches as compared to those on the ground or on grass.

Cartwright et al. do comment on the differences in the brushy vegetation of the territories of the two species. They state (ibid. p.164): "slight changes in the density of the vegetation is sufficient to make it unsuitable for Baird's Sparrow. For instance, it will nest amongst sparse, dwarf wolfberry (Symphoricarpos occidentalis) but if the wolfberry is only slightly more crowded, even if no taller, the Baird's Sparrow will not nest there, but the Savannah Sparrow will".

The differences in territory size of the two species may be indicative of differences in territory function. The territory size of the Baird's Sparrow reported by Cartwright et al. is comparable to those found in the present study, approximately one acre. The Baird's Sparrow may have a Type A territory in which it defends a foraging area. The Type B territory of the Savannah Sparrow does not necessitate such defence and may result

in smaller territory size. A definite answer must await further investigation.

SUMMARY AND CONCLUSIONS

The Savannah Sparrow (Passerculus sandwichensis) was studied at Saskatoon, Saskatchewan (52°08'N, 106°38'W) during the months of April through August, 1966 and 1967.

The environment of the study area is described including such aspects as climate, geology, vegetation and vertebrate fauna. It was possible to delineate four major habitat types on the study area. Information on the breeding cycle, growth and development of nestlings, territoriality, habitat selection and interspecific relationships with the Baird's Sparrow (Ammodramus bairdii) is presented.

The breeding season of the Savannah Sparrow at Saskatoon extends from late April to early August. Males arrived on the breeding grounds about 10 days before the females. The first 20-30 days of the breeding season were occupied by territory establishment and pair formation, with first nests being initiated in late May. Two broods were believed to have been raised, with the second nests initiated in late June. Eggs were laid at intervals of one day and incubation often began before the clutch was complete. Only the female incubated although both adults shared in feeding the young. The incubation period was found to be 12 days, with asynchronous hatching in many nests. Young Savannah Sparrows left the nest at an average age of 9.17 days. Parental care continued until at least the age of 19 days and probably longer. The breeding population left the study area in early August although Savannah Sparrows were recorded in the Saskatoon area for two months longer. Breeding success was 16 percent calculated by the Mayfield exposure method and 39.4 percent calculated by conventional methods. The principal cause of nest mortality was predation by small

mammals. Parasitism by the Brown-headed Cowbird (Molothrus ater) was absent in 1966 but occurred in six of seventeen nests found in 1967.

The growth of nestling Savannah Sparrows is described and plumage development and behavioral development of the young birds are compared to other emberizines.

The pattern of territorial establishment is outlined, and the territorial behavior of the species is discussed. Mean territory size was 0.17 acres. The study area was occupied at a density of 68.6 pairs per 100 acres in 1967. Nests were usually located on or near the territory of the parental male. Foraging was done on neutral grassland, often at some distance from the territory. A marked decline in overt territorial aggressiveness coinciding with pair formation supports the hypothesis that the principle function of the Type B territory of the Savannah Sparrow is the facilitation of pair formation and the maintenance of the pair-bond.

Savannah Sparrows showed a definite selection of portions of the study area containing shrub habitat and territories were not maintained in pure grassland habitat. This selection is probably based on the requirement by the Savannah Sparrow of elevated song perches for territorial proclamation.

The territories of the Savannah Sparrow and Baird's Sparrow on the study area showed little overlap, due to distinct differences in habitat preference rather than to interspecific territoriality. The Baird's Sparrow occupied large, continuous areas of grassland within the vegetation mosaic. Savannah Sparrows frequently foraged on Baird's Sparrow territories.

BIBLIOGRAPHY

- ALDRICH, J.W. 1940. Geographic variation in eastern North American Savannah Sparrows. Ohio J. Sci. 40: 1-8.
- AMERICAN ORNITHOLOGISTS UNION. 1957. Check-list of North American Birds, Fifth Edition. Port City Press, Inc., Baltimore.
- ANDREW, R.J. 1956. Territorial behavior of the Yellowhammer Emberiza citrinella and Corn Bunting E. calandra. Ibis 98: 502-505.
- ANDREW, R.J. 1956/57a. Intention movements of flight in certain passerines, and their use in systematics. Behavior 10: 179-204.
- ANDREW, R.J. 1956/57b. The aggressive and courtship behavior of certain Emberizines. Behavior 10: 255-308.
- ANDREW, R.J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. Ibis 103a: 315-348, 549-597.
- ARMSTRONG, E.A. 1947. Bird display and behavior. Lindsay Drummond, London. Reprint by Dover Publications Ltd., New York, 1965.
- ARMSTRONG, E.A. 1956. Territory in the Wren Troglodytes troglodytes. Ibis 98: 430-437.
- BAINES, G.B.K. 1964. Plant distributions on a Saskatchewan prairie in relation to edaphic and physiographic factors. Unpublished M.Sc. Thesis. Univ. Sask. Saskatoon.
- BANKS, R.C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor 61: 96-109.
- BARBOUR, R.W. 1950. Growth and feather development of Towhee nestlings. Amer. Midl. Natur. 44: 742-749.
- BARBOUR, R.W. 1951. Observations on the breeding habits of the Red-eyed Towhee. Amer. Midl. Natur. 45: 672-678.
- BIRD, R.D. 1961. Ecology of the aspen parkland of Western Canada. Contrib. No. 27, Research Station Can. Dep. of Agr. Winnipeg, Manitoba. Research Branch Can. Dep. of Agr. Ottawa.
- BISHOP, L.B. 1915. Description of a new race of Savannah Sparrow and suggestions on some California birds. Condor 17: 185-189.
- BLANCHARD, B.D. 1941. The White-crowned Sparrows (Zonotrichia leucophrys) of the Pacific seaboard: Environment and annual cycle. Univ. Calif. Publ. Zool. 46: 1-178.

- BRECKENRIDGE, W.J. 1930. Breeding of Nelson's Sparrow (Ammospiza nelsoni) with special reference to Minnesota. Univ. Minn. Mus. Natur. Hist. Occ. Papers 3: 29-38.
- BRECKENRIDGE, W.J. 1935. An ecological study of Minnesota Marsh Hawks. Condor 37: 268-276.
- CADE, T.J. and G.A. BARTHOLOMEW. 1959. Sea-water and salt utilization by Savannah Sparrows. Physiol. Zool. 32: 230-238.
- CAMRAS, S. 1940. A new Savannah Sparrow from Mexico. Field Mus. Natur. Hist. (Publ. 457) Zool. Series 24: 159-160.
- CARPENTER, C.R. 1958. Territoriality: A review of concepts and problems, p. 224-250. In A. Roe and G.G. Simpson (ed.) Behavior and Evolution. Yale University Press, New Haven.
- CARTWRIGHT, B.W., T.M. SHORTT and R.D. HARRIS. 1937. Baird's Sparrow. Trans. Roy. Can. Inst. 21: 153-197.
- CLEMENTS, F.E. and V.E. SHELFORD. 1939. Bioecology. John Wiley and Sons, Inc., New York.
- COLLIAS, N.E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool. 17: 83-123.
- CONDER, P.J. 1956. The territory of the Wheatear Oenanthe oenanthe. Ibis 98: 453-459.
- COUPLAND, R.T. 1961. A reconsideration of grassland classification in the northern Great Plains of North America. J. Ecol. 49: 135-167.
- COUPLAND, R.T. and T.C. BRAYSHAW. 1953. The Fescue grassland in Saskatchewan. Ecology 34: 386-405.
- COUTLEE, E.L. 1967. Agonistic behavior in the American Goldfinch. Wilson Bull. 79: 89-109.
- DAVIS, J. 1958. Singing behavior and the gonad cycle of the Rufous-sided Towhee. Condor 60: 308-336.
- DAWSON, W.R. and F.C. EVANS. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping Sparrows. Physiol. Zool. 30: 315-327.
- DAWSON, W.R. and F.C. EVANS. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor 62: 329-340.

- DICKERMAN, R.W. and K.C. PARKES. 1960. The Savannah Sparrows of Minnesota. *Flicker* 32: 110-113.
- DILGER, W.C. 1960. Agonistic and social behavior of captive Redpolls. *Wilson Bull.* 72: 115-132.
- DILLERY, D.G. 1962. Food habits of Savannah and Grasshopper Sparrows in relation to foods available. Ph.D. Thesis, Ohio State Univ. 1961. *Diss. Abstr.* 22: 4121.
- DILLERY, D.G. 1965. Post-mortem digestion of stomach contents in the Savannah Sparrow. *Auk* 82: 281.
- DUMAS, P.C. 1950. Habitat distribution of breeding birds in south-eastern Washington. *Condor* 52: 232-237.
- DURANGO, S. 1956. Territory in the Red-backed Shrike Lanius collurio. *Ibis*. 98: 476-484.
- DUVALL, A.J. 1943. Breeding Savannah Sparrows of the southwestern United States. *Condor* 45: 237-238.
- DWIGHT, J. Jr. 1895. The Ipswich Sparrow and its summer home. *Mem. Nuttall Ornithol. Club* 2: 1-56
- DWIGHT, J. Jr. 1900. The sequence of plumages and moults in the passerine birds of New York. *Ann. N.Y. Acad. Sci.* 13: 73-360.
- EDMUNDS, F.H. 1962. Recession of Wisconsinian glacier from central Saskatchewan. *Sask. Dept. Mineral Resources Rep.* No. 67.
- EMLEN, J.T. 1954. Territory, nest-building and pair formation in the Cliff Swallow. *Auk*. 71: 16-35.
- FOX, G.A. 1961. A contribution to the life history of the Clay-colored Sparrow. *Auk* 78: 220-224.
- GABRIELSON, I.N. and F.C. LINCOLN. 1959. The Birds of Alaska. Stackpole Co., Harrisburg, Penn.
- GIBB, J. 1956a. Territory in the genus Parus. *Ibis* 98: 420-429.
- GIBB, J. 1956b. Food, feeding habits and territory of the Rock Pipit Anthus spinoletta. *Ibis* 98: 506-530.
- GODFREY, W.E. 1966. The Birds of Canada. *Nat. Mus. Can. Bull.* No. 203.
- GOLLOP, J.B. 1966 (compiler) Bird List, June 1 to October 16, 1966. *Saskatoon Bird Rev.* 1(4): 4-31.

- GOLLOP, J.B. 1967a. (compiler) Bird List, April 17 through June 11, 1967. Saskatoon Bird Rev. 2(4): 8-30.
- GOLLOP, J.B. 1967b. (compiler) Bird List, June 12 through October 9, 1967. Saskatoon Bird Rev. 2(5): 15-37.
- GOLLOP, M.A. and J.B. GOLLOP. 1966. (compilers) Bird List, April 18 to May 31, 1966. Saskatoon Bird Rev. 1(3): 6-25.
- GRINNELL, J. 1910. The Savannah Sparrow of the Great Basin. Univ. Calif. Publ. Zool. 5: 311-316.
- GRINNELL, J. 1939. Proposed shifts of names in Passerculus. Condor 41: 112-119.
- GRINNELL, L.I. 1944. Notes on breeding Lapland Longspurs at Churchill, Manitoba. Auk 61: 554-560.
- HAARTMAN, L. VON 1956. Territory in the Pied Flycatcher Muscicapa hypoleuca. Ibis 98: 460-475.
- HAILMAN, J.P. 1958. Behavior notes on the Ipswich Sparrow. Bird-Banding 29: 241-244.
- HARPER, F. 1952. Birds of the Nueltin Lake expedition, Keewatin, 1947. Amer. Midl. Natur. 49: 1-116.
- HARRIS, R.D. 1944. The Chestnut-collared Longspur in Manitoba. Wilson Bull. 56: 105-115.
- HENSLEY, M.M. and J.B. COPE. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk 68: 483-493.
- HILDEN, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2: 53-75.
- HINDE, R.A. 1955-56. A comparative study of the courtship of certain finches (Fringillidae). Ibis 97: 706-745, 98: 1-23.
- HINDE, R.A. 1956. The biological significance of the territories of birds. Ibis 98: 340-369.
- HUEY, L.M. 1930. Comment on the Marsh Sparrows of southern and lower California, with the description of a new race. Trans. San Diego Soc. Natur. Hist. 6: 203-206.
- HYDE, A.S. 1939. The life history of Henslow's Sparrow. Misc. Publ. Mus. Zool. Univ. Mich. No. 41.
- JEHL, J.R. Jr. and D.J.T. HUSSEL, 1966. Incubation periods of some subarctic birds. Can. Field-Natur. 80: 179-180.

- JOHNSGARD, P.A. and W.H. RICKARD. 1957. The relation of spring bird distribution to a vegetational mosaic in southeastern Washington. *Ecology* 38: 171-174.
- JOHNSON, D.W. 1956. A preliminary study of the subspecies of the Savannah Sparrow at the Savannah River Plant, South Carolina. *Auk* 73: 454-456.
- JOHNSON, R.F. 1956. Population structure in salt marsh Song Sparrows. *Condor* 58: 24-44, 254-272.
- JUDD, S.D. 1901. The relation of sparrows to agriculture. U.S. Dep. Agr. Div. of Biol. Surv., Bull. No. 15.
- KENDEIGH, C.S. 1952. Parental care and its evolution in birds. *Ill. Biol. Monogr.* 22: (1-3).
- KENDREW, W.G. and B.W. CURRIE. 1955. The climate of central Canada. Queen's Printer, Ottawa.
- KLOPFER, P. 1963. Behavioral aspects of habitat selection: the role of early experience. *Wilson Bull.* 75: 15-22.
- KLOPFER, P. and J.P. HAILMAN. 1965. Habitat selection in birds. *Advance. Study Behav.* 1: 279-303.
- KURODA, N. 1960. An essay on bird territoriality. *Misc. Rep. Yamashina's Ins. Ornithol. and Zool.* 2: 133-137.
- LACK, D. 1933. Habitat selection in birds with special reference to the effects of reforestation on the Breckland avifauna. *J. Anim. Ecol.* 2: 239-262.
- LACK, D. 1937. The psychological factor in bird distribution. *Brit. Birds* 31: 130-136.
- LACK, D. 1940. Habitat selection and speciation in birds. *Brit. Birds* 34: 80-84.
- LACK, D. 1944. Ecological aspects of species-formation in passerine birds. *Ibis* 86: 260-286.
- LACK, D. 1949. The significance of ecological isolation, p. 299 to 308, *In*. G.L. Jepsen, E. Mayr and G.G. Simpson (ed.) *Genetics, Paleontology, and Evolution*. Princeton Univ. Press, Princeton.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

- LACK, D. and L. LACK. 1933. Territory reviewed. *Brit. Birds* 27: 179-199.
- LANYON, W.E. 1956. Territory in the Meadowlarks, genus *Sturnella*. *Ibis* 98: 485-489.
- LINSDALE, J.M. 1938. Environmental responses of vertebrates in the Great Basin. *Amer. Midl. Natur.* 19: 1-206.
- LONGHURST, W.M. 1942. The summer food of Burrowing Owls in Costilla County, Colorado. *Condor* 44: 281-282.
- MAHER, W.J. 1959. Habitat distributions of birds breeding along the upper Kaolak River, northern Alaska. *Condor* 61: 351-368.
- MAHER, W.J. 1964. Growth rate and development of endothermy in the Snow Bunting and Lapland Longspur at Barrow, Alaska. *Ecology* 45: 520-528.
- MANNING, T.H. and A.H. MacPHERSON. 1952. Birds of the east James Bay coast between Long Point and Cape Jones. *Can. Field-Natur.* 65: 1-35.
- MARLER, P. 1956a. Behavior of the Chaffinch (*Fringilla coelebs*). *Behavior*, Suppl. No. 5.
- MARLER, P. 1956b. Territory and individual distance in the Chaffinch *Fringilla coelebs*. *Ibis* 98: 496-501.
- MARSHALL, J.T. 1948. Ecologic races of Song Sparrows in the San Francisco Bay region. Part 1: Habitat and abundance. *Condor* 50: 193-215.
- MARTIN, A.C., H.S. ZIM and A.L. NELSON. 1951. *American Wildlife and Plants*. McGraw Hill Book Co., New York. Reprint by Dover Publications Inc., New York, 1961.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261.
- MICKEY, F.W. 1943. Breeding habits of McCown's Longspur. *Auk* 60: 181-209.
- MILLER, A.H. 1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. *Amer. Natur.* 76: 25-35.
- MILLER, A.H. 1951. The "rodent-run" of the Green-tailed Towhee. *Ibis* 93: 307-308.
- MITCHELL, J.H., H.C. MOSS and J.S. CLAYTON. 1947. Soil survey of southern Saskatchewan from township 1 to 48 inclusive. Univ. of Sask., Sask. Soil Surv. Rep. No. 12.

- MOWAT, F.M. and A.H. LAWRIE. 1955. Bird observations from southern Keewatin and the interior of northern Manitoba. Can. Field-Natur. 69: 93-116.
- MOYNIHAN, M. 1963. Display patterns of tropical American "nine-primaried" songbirds. III The Green-backed Sparrow. Auk 80: 116-144.
- NETHERSOLE-THOMPSON, C. and NETHERSOLE-THOMPSON, D. 1943. Nest-site selection by birds. Brit. Birds 37: 70-74, 88-94, 108-113.
- NICE, M.M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc. N.Y. 4: 1-247. Reprint by Dover Publications Inc., New York, 1964.
- NICE, M.M. 1941. The role of territory in bird life. Amer. Midl. Natur. 26: 441-487.
- NICE, M.M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. Trans. Linn. Soc. N.Y. 6: 1-328. Reprint by Dover Publications Inc., New York, 1964.
- NICE, M.M. 1957. Nesting success in altricial birds. Auk 74: 305-321.
- NOBLE, G.K. 1939. The role of dominance in the social life of birds. Auk 56: 263-273.
- NORRIS, R.A. 1960. Density, racial composition, sociality and selective predation in non-breeding populations of Savannah Sparrows. Bird-Banding 31: 173-216.
- NORRIS, R.A. and G.L. HIGHT, Jr. 1957. Subspecific variation in winter populations of Savannah Sparrows: a study in field taxonomy. Condor 59: 40-52.
- OBERHOLSER, H.C. 1919. A revision of the subspecies of Passerculus rostratus (Cassin). Ohio J. Sci. 19: 344-354.
- OBERHOLSER, H.C. 1930. Notes on a collection of birds from Arizona and New Mexico. Sci. Publ. Cleveland Mus. Natur. Hist. 1: 83-124.
- ODUM, E.P. 1958. The fat deposition picture in the White-crowned Sparrow in comparison with that of long-range migrants. Bird-Banding 29: 105-108.
- PALMER, R.S. 1962. (Ed.) Handbook of North American Birds, Vol. I. Yale University Press, New Haven and London.

- PEREK, M. and F. SULMAN. 1945. The basal metabolic rate in molting and laying hens. *Endocrinology* 36: 240-243.
- PETERS, J.L. and L. GRISCOM. 1938. Geographical variation in the Savannah Sparrow. *Bull. Mus. Comp. Zool.* 80: 445-477.
- PETERSON, R.T. 1961. *A Field Guide to Western Birds*, Second edition. Houghton Mifflin Company, Boston.
- POULSON, T.L. and G.A. BARTHOLOMEW. 1962. Salt balance in the Savannah Sparrow. *Physiol. Zool.* 35: 109-119.
- QUAINTANCE, C.W. 1941. Voice in the Brown Towhee. *Condor* 43: 152-155.
- QUAY, T.L. 1957. The Savannah Sparrow (Passerculus sandwichensis Gmelin) in winter in the lower piedmont of North Carolina. *J. Elisha Mitchell Sci. Soc.* 73: 378-388.
- QUAY, T.L. 1958. The foods and feeding habits of the Savannah Sparrow in winter. *J. Elisha Mitchell Sci. Soc.* 74: 1-6.
- ROWELL, C.H.F. The breeding of the Lapland Bunting in Swedish Lapland. *Bird Study* 4: 33-50.
- SALT, W.R. 1954. The structure of the cloacal protruberance of the Vesper Sparrow (Pooecetes gramineus) and certain other passerine birds. *Auk* 71: 64-73.
- SALT, W.R. 1966. A nesting study of Spizella pallida. *Auk* 83: 274-281.
- SAUNDERS, A.A. 1936. Ecology of the birds of Quaker Run Valley, Allegany State Park, New York. *New York State Mus. Handbook* 16: 1-164.
- SAVILLE, Mrs. D.B.O. and T.F. MORLAND. 1951. Breeding census. *Can. Field-Natur.* 65: 81-82.
- SEALY, S.G. 1966. Notes on the carnivorous tendencies of some Sciurids. *Blue Jay* 24: 37-38.
- SHIELDS, T.E. 1935. A study of the Savannah Sparrow in West Virginia. *Wilson Bull.* 47: 35-42.
- SIMMONS, K.E.L. 1956. Territory in the Little Ringed Plover Charadrius dubius. *Ibis* 98: 390-397.
- SMITH, R.L. 1963. Some ecological notes on the Grasshopper Sparrow. *Wilson Bull.* 75: 159-165.
- SNOW, D.W. 1956. Territory in the Blackbird Turdus merula. *Ibis* 98: 438-447.

- SNYDER, L.L. and E.B.S. LOGIER. 1930. A faunal investigation of King Township, York County, Ontario. Trans. Roy. Can. Inst. 17: 167-208.
- SOWLS, L.K. 1948. The Franklin ground squirrel, Citellus franklinii (Sabine) and its relationship to nesting ducks. J. Mammal. 29: 113-137.
- STANTON, F.W. 1944. Douglas Ground Squirrel as a predator on nests of upland game birds in Oregon. J. Wildlife Manage. 8: 153-161.
- STEWART, R.E. and J.W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68: 471-482.
- STOKES, A.W. 1950. Breeding behavior of the Goldfinch. Wilson Bull. 62: 107-127.
- SUTTON, G.M. 1935. The juvenal plumage and post-juvenal molt in several species of Michigan sparrows. Cranbrook Inst. Sci., Bull. No. 3.
- SUTTON, G.M. 1959. The nesting fringillids of the Edwin S. George Reserve, southeastern Michigan. Part IV. Jack-Pine Warbler 37: 127-151.
- SUTTON, G.M. and D.F. PARMELEE. 1955. Summer activities of the Lapland Longspur on Baffin Island. Wilson Bull. 67: 110-127.
- SVARDSON, G. 1949. Competition and habitat selection in birds. Oikos 1: 157-174.
- SWANBERG, P.O. 1956. Territory in the Thick-billed Nutcracker Nucifraga caryocatactes. Ibis 98: 412-419.
- SWARTH, H.S. 1933. The Savannah Sparrows of northwestern North America. Condor 35: 243-245.
- SWARTH, H.S. 1936. Savannah Sparrow migration routes in the Northwest. Condor 38: 30-32.
- TAVERNER, P.A. 1932. A partial study of the Canadian Savanna (sic) Sparrows, with description of Passerculus sandwichensis campestris subsp. nov., the Prairie Savannah Sparrow. Proc. Biol. Soc. Wash. 45: 201-205.
- TERRILL, L.M. 1961. Cowbird hosts in southern Quebec. Can. Field-Natur. 75: 2-11.
- TESTER, J.R. and W.H. MARSHALL. 1961. A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota. Minn. Mus. Natur. Hist. Occ. Papers No. 8.

- THOMPSON, W.L. 1960. Agonistic behavior in the House Finch. Part I. Annual cycle and display patterns. Condor 62: 245-271.
- THOMPSON, W.L. 1965. A comparative study of bird behavior. Jack-Pine Warbler 43: 110-117.
- TINBERGEN, N. 1936. The function of sexual fighting in birds; and the problem of the origin of "territory". Bird-Banding 7: 1-8.
- TINBERGEN, N. 1939. Field observations of east Greenland birds II. The behavior of the Snow Bunting (Plectrophenax nivalis sub-nivalis (Brehm) in spring. Trans. Linn. Soc. N.Y. 5: 1-94.
- TINBERGEN, N. 1952. A note on the origin and evolution of threat displays. Ibis 94: 160-161.
- TINBERGEN, N. 1956. On the functions of territory in gulls. Ibis 98: 401-411.
- TINBERGEN, N. 1957. The functions of territory. Bird Study 4: 14-27.
- TODD, W.E.C. 1963. Birds of the Labrador Peninsula and adjacent areas. Univ. of Toronto Press, Toronto.
- TOMKINS, I.R. 1941. Notes on MacGillivray's Seaside Sparrow. Auk 58: 38-51.
- TOMPA, F.S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. Auk 79: 687-697.
- TOMPA, F.S. 1964. Factors determining the numbers of Song Sparrow, Melospiza melodia (Wilson), on Mandarte Island, B.C., Canada. Acta. Zool. Fenn. 109: 1-73.
- TOWNSEND, G.H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. Can. Field-Natur. 80: 74-88.
- VAN ROSSEM, A.J. 1930. Four new birds from northwestern Mexico. Trans. San Diego Soc. Natur. Hist. 6: 215-226.
- VAN ROSSEM, A.J. 1947. A synopsis of the Savannah Sparrows of northwestern Mexico. Condor 49: 97-108.
- VAN TYNE, J. and A.J. BERGER. 1959. Fundamentals of Ornithology. John Wiley and Sons, Inc., New York.
- WALKINSHAW, L.H. 1937. Leconte's Sparrow breeding in Michigan and South Dakota. Auk. 54: 309-320.

- WALKINSHAW, L.H. 1939. Notes on the nesting of the Clay-colored Sparrow. Wilson Bull. 51: 17-21.
- WALKINSHAW, L.H. 1940. Some Michigan notes on the Grasshopper Sparrow. Jack-Pine Warbler. 18: 50-59.
- WALKINSHAW, L.H. 1944. The Eastern Chipping Sparrow in Michigan. Wilson Bull. 56: 193-205.
- WEEDEN, J.S. 1965. Territorial behavior in the Tree Sparrow. Condor 67: 193-209.
- WEEDEN, J.S. 1966. Diurnal rhythm of attentiveness of incubating female Tree Sparrows (Spizella arborea) at a northern latitude. Auk 83: 368-388.
- WELTY, J.C. 1962. The life of Birds. W.B. Saunders Co., Philadelphia.
- WILLETT, G. 1939. Remarks on Alaskan Savannah Sparrows. Condor 41: 86.
- WOLFSON, A. 1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor 47: 95-127.
- WOLFSON, A. 1954a. Notes on the cloacal protruberance, seminal vesicles and possible copulatory organ in male passerine birds. Bull. Chicago Acad. Sci. 10: 1-23.
- WOLFSON, A. 1954b. Sperm storage at lower-than-body temperature outside the body cavity of some passerine birds. Science 120: 68-71.
- WOOLFENDEN, G.E. 1956. Comparative breeding behavior of Ammodramus caudacuta and A. maritima. Univ. Kan. Publ. Mus. Natur. Hist. 10: 45-75.
- WYNNE-EDWARDS, V.C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Ltd., Edinburgh and London.
- YOUNG, H. 1956. Territorial activities of the American Robin Turdus migratorius. Ibis 98: 448-452.

APPENDIX I

Resident Avian Species Utilizing the Study Area

Common Name	Scientific Name	Status*
Mallard	<u>Anas platyrhynchos</u>	Rp 66,67
Gadwall	<u>Anas strepera</u>	R 66, (Rp 67)
Pintail	<u>Anas acuta</u>	Rp 66, Ra 67
Swainson's Hawk	<u>Buteo swainsonii</u>	Ra66
Marsh Hawk	<u>Circus cyaneus</u>	Ra66, Rp 67
Gray Partridge	<u>Perdix perdix</u>	(Rp 67)
Upland Plover	<u>Bartramia longicauda</u>	Ra66, 67
Willet	<u>Catoptrophorus semipalmatus</u>	Ra 67
Great Horned Owl	<u>Bubo virginianus</u>	(Ra 67)
Burrowing Owl	<u>Speotyto cunicularia</u>	Rp 66, 67
Short-eared Owl	<u>Asio flammeus</u>	Rp 66
Eastern Kingbird	<u>Tyrannus tyrannus</u>	R 66, 67
Horned Lark	<u>Eremophila alpestris</u>	Rp 66, 67
Barn Swallow	<u>Hirundo rustica</u>	Ra 66, 67
Sprague's Pipit	<u>Anthus spragueii</u>	R66, 67
Loggerhead Shrike	<u>Lanius ludovicianus</u>	Ra67
Bobolink	<u>Dolichonyx oryzivorus</u>	R66
Western Meadowlark	<u>Sturnella neglecta</u>	R66, 67
Red-winged Blackbird	<u>Agelaius phoeniceus</u>	Ra 66, 67
Brewer's Blackbird	<u>Euphagus cyanocephalus</u>	R 66, 67
Brown-headed Cowbird	<u>Molothrus ater</u>	R 66, 67
Savannah Sparrow	<u>Passerculus sandwichensis</u>	R 66, 67
Grasshopper Sparrow	<u>Ammodramus savannarum</u>	(Rp 66, 67)
Baird's Sparrow	<u>Ammodramus bairdii</u>	R 66, 67
Vesper Sparrow	<u>Poocetes gramineus</u>	Rp 66, 67
Clay-colored Sparrow	<u>Spizella pallida</u>	R 66, 67

* R = Resident on study plot

Rp= Resident on prairie

Ra= Resident in area

66= 1966

67= 1967

()= probable status

APPENDIX II

Mammalian species trapped or observed on Kernen's prairie

1966, 1967

Masked Shrew	<u>Sorex cinereus</u>
Red Fox	<u>Vulpes fulva</u>
Least Weasel	<u>Mustella rixosa</u>
White-tailed Jack Rabbit	<u>Lepus townsendii</u>
Richardson's Ground Squirrel	<u>Citellus richardsonii</u>
Thirteen-lined Ground Squirrel	<u>Citellus tridecemlineatus</u>
Olive-backed Pocket Mouse	<u>Perognathus fasciatus</u>
Deer Mouse	<u>Peromyscus maniculatus</u>
Meadow Vole	<u>Microtus pennsylvanicus</u>
House Mouse	<u>Mus musculus</u>