11-1967

# Ecology of Henslow's Sparrow

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# ECOLOGY OF HENSLOW'S SPARROW

by

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A Thesis
Submitted to the
Faculty of the School of Graduate
Studies in partial fulfillment
of the
Degree of Master of Arts

Western Michigan University
Kalamazoo, Michigan
November, 1967

## ACKNOWLEDGMENTS

The author wishes to thank Dr. Richard Brewer, thesis advisor and chairman of the graduate committee, for suggestion of the topic and for his advice and guidance throughout the course of this study. He also provided information on the history of the area and unpublished data on bird populations. Sincere thanks are extended to Professor Frank Hinds and Dr. Imy Holt for assistance in the preparation of this report.

To his wife, Joyce, the author extends his appreciation for help with the field work and for typing the manuscript. To Arlo Raim and Jerome Wenger the author is indebted for help given in the field.

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# INTRODUCTION

Understanding of community organization, a central aim in ecology, requires both broad studies such as breeding bird censuses, and intensive studies of population size, intraspecific relations, life history phenomena, etc., of the individual species composing the community. Henslow's Sparrow, Passerherbulus henslowii, is a common resident of some southwestern Michigan grasslands, including one where ecological observations of the first type have been underway since 1961, and thus was suitable for intensive study.

Several aspects of the life history have been described (see Hyde, 1939; Sutton, 1959a and 1959b) but quantitative data are essentially non-existent. The primary objective of this study was to analyze population structure on a brome grass-alfalfa-red clover hayfield where this species was established as a breeding bird. Information was also collected on nesting biology in an attempt to enlarge upon Hyde's (1939) pioneer work. Studies were carried out during the summer of 1966 at Kalamazoo, Michigan; some supplementary observations were made in 1967.

## DESCRIPTION OF THE STUDY AREA

The study area (known as the Colony Farm Tract) is a linear strip of land approximately 43.5 acres in extent. About 33 acres of the area is a brome grass-alfalfa hayfield; the remainder is thicket. The hayfield considered herein contained 30 acres of suitable breeding habitat for Henslow's Sparrows. Located by the Congressional Land Survey System, the area is in the NE ¼ of Sect. 31, T 2 S, R 11 W. It lies within the city limits of Kalamazoo, Kalamazoo County, Michigan. A complete description of the tract has been presented elsewhere (Brewer, R., A. Raim, and J.D. Robins, MS).

The north-south length was about 2600 feet. The width varied from about 300 to 700 feet. The hayfield is gently rolling with a maximum relief of about 20 feet.

Prior to acquisition by Western Michigan University, the field area had been farmed by the Kalamazoo State Hospital. The agricultural portion of the tract, divisible into three different sections, was taken out of cultivation at the following times: north (8 acres) in 1954; middle (5 acres) in 1953; and south (17 acres) in 1958. The first two portions were seeded with alfalfa-brome grass-red clover and the third with brome grass and oats. Through 1959 the area was mowed and the hay removed.

The east border is made up of thicket on the north half

and a well-developed fence row along the southern half. The latter, along with a similar fence row on the narrow south border, separates the Colony Farm Tract from adjacent hayfields that are similar but with more and larger woody plants. On the west, two rows of multiflora rose, Rosa multiflora, separate the study area from land which has been cultivated by the Western Michigan University Agriculture Department in strip-crop rotation since 1961. In 1966 oats, Avena sp., was grown adjacent to the study area. The rose hedge has developed rather poorly, reaching a maximum height of four feet, but with frequent gaps. The north edge, which drops to Parkview Avenue, contains scattered growth of large-tooth aspen, Populus grandidentata; willows, Salix spp.; elms, Ulmus spp.; and several other species.

Brome grass, Bromus inermis, is the predominant herb on the hayfield. In 1963 it was present in all of 29 square meter samples and in 1961 comprised 85 per cent of all stems counted in 16 quadrats (Brewer, R., A. Raim, and J.D. Robins, MS). Alfalfa, Medicago sativa; bluegrasses, Poa compressa and pratensis; and quack grass, Agropyron repens, are also major components of the hayfield. The most common forbs were yellow rocket, Barbarea vulgaris; red clover, Trifolium pratense; and Aster pilosus.

Differences in the amount of vegetation present on the two most distinct portions of the hayfield (northern 13 acres and southern 17 acres) were determined through measurements of leaf

height (ignoring the flowering stalks which had a similar height throughout the area) and light meter readings. The readings of leaf height were taken in August at 51 and 50 regularly spaced points and the light meter readings (also taken in August) were made at 54 and 50 regularly spaced points on the north and south portions respectively. Average height of the foliage was considerably greater on the northern area (75 cm versus 55 cm on the south area). Leaf height varied from 55 to 100 cm on the north portion and from 45 to 65 cm on the south portion. Light meter readings taken six inches above the ground surface showed that the north portion had the denser vegetative cover. Average light penetration was 29 per cent of full sunlight on the north (range 9-73 per cent) and 54 per cent on the south (range 25-79 per cent). Standard deviations for both characters were approximately twice as high on the north portion.

The average standing crop for 12 randomly selected square-meter quadrats taken in August and oven-dried at 110 degrees Centigrade was 3043 grams. Standing crop included all above-ground vegetation, living and dead, within each of the square-meter quadrats.

Variability in the number of woody species on the north and middle portions of the hayfield versus the southern portion was very pronounced. The two northern areas had 48 woody plants scattered among the grasses while on the southern portion there were 551 (Brewer, R., A Raim, and J.D. Robins, MS). White

mulberry, Morus alba; black cherry, Prunus serotina; and staghorn sumac, Rhus typhina, were the most numerous woody species present. The tallest woody plants were over 60 inches tall but the mean height was approximately one-half the maximum (Brewer, R., A. Raim and J.D. Robins, MS).

## METHODS

Prior to the study, the hayfield was marked off into a grid with three-foot-high stakes set at 100-foot intervals. The top four inches of the stakes were systematically painted to allow immediate and precise recognition of any location. During each census of singing Henslow's Sparrows, locations of birds were marked on maps which reproduced the grid as well as the outstanding vegetational features.

Identification of the birds was made with a 7X, 50 binocular and a 40X Bushnell telescope. The latter instrument permitted rapid determination of individually marked birds at distances up to 300 feet. Field work was conducted from April through October. Censuses of singing males were made at various times of the day throughout the year. The majority were made before 9 AM and after 6 PM. Between the first of May and the middle of September census time totaled 182 hours on 65 different days. Approximately half of the census time was accumulated in the morning. By month, the number of days and hours spent in the field mapping singing males was May, 15 days, 31 hours; June, 16 days, 59 hours; July, 14 days, 42 hours; August, 14 days, 37 hours; and September, 6 days, 13 hours.

Observations at nine nests were made from four-foot-tall blinds placed on the ground 5 to 10 feet from the nests. Most observations were made at a distance of five feet. All data

on incubation, brooding, etc. were collected by direct observation. Temperatures were recorded with the thermometers placed in the shade of the blinds at the approximate height of the nests. Time was Eastern Standard Time.

Since records of attentiveness and inattentiveness were not random (they began and ended with the beginning or ending of an attentive or inattentive period) and because unequal numbers of sessions and recesses were collected, percentage attentiveness was calculated by use of Skutch's (1960:8) formula:

$$\text{Percentage attentiveness} = \frac{\text{Mean attentive period}}{\text{Mean attentive period} + \text{Mean inattentive period}} \times 100.$$

Territories were mapped using only the singing locations recorded for the various males. No additional types of territorial defense were observed and human disturbance frequently caused the birds to go out of their territories, often into the bordering thicket. One male, $G_1$, was chased continuously for 45 minutes to determine how far it would go from its territory of 2.38 acres (as previously determined by mapping song posts). The resultant area was 5.88 acres with the greatest linear distance away from its territory being 780 feet. Singing locations were connected by straight lines to form polygons which correspond to the "utilized territory" of Odum and Kuenzler (1955). For some birds the "utilized" and "maximum" territories appeared to be identical. Areas of the polygons were determined by use of a planimeter.

As Hyde (1939:54) pointed out, in southern Michigan the

sexes may be distinguished by the darker dorsal color of the females. A more useful characteristic for distinguishing sexes at close range is the size of the black post-ocular patch. In males this patch is considerably larger. However, use of either of these features was not feasible owing to the quickness of the birds and the concealing nature of the grasses about the nest. Furthermore, both sexes would have to be present for comparison for complete accuracy. At the outset, banding of as many birds as possible was carried out to eliminate confusion of the sexes as well as to individualize the males for territorial determinations. In all, 14 males, 10 females, 18 nestlings and 2 juveniles were marked with numbered aluminum bands of the U.S. Fish and Wildlife Service and colored celluloid leg bands. All except the nestlings were trapped with Japanese mist nests. Several feather dyes were applied but none proved suitable over a long period. One male, S, was not marked because he was identifiable by dull white outer tail feathers resembling those of a Vesper Sparrow, Pooecetes gramineus. Nestlings were banded two or three days before fledging.

For simplification in presentation, males were assigned a letter from A to S excluding letter O. The letters do not indicate chronology. Chronology of territories of individual birds is indicated by the numbered subscript (see Table 1). Nests were numbered in order of their discovery. Nest 1 was located on an ecological research area on the Fort Custer Military Reservation which is located 22 miles east of Kalamazoo, just

Table 1. Territories of Henslow's Sparrows during the 1966 breeding season.

| Male | Size (in acres) | Duration | Duration in days | Number of days recorded | Number of singing points recorded |
|---|---|---|---|---|---|
| $A_1$ | 1.09 | 5/6-6/16 | 42 | 12 | 22 |
| $A_2$ | 0.62 | 6/17-7/9 | 23 | 8 | 12 |
| $B_1$ | 0.61 | 5/6-8/14 | 101 | 30 | 43 |
| $C_1$ | 0.52 | 5/6-5/16 | 11 | 5 | 10 |
| $D_1$ | 0.84 | 5/5-5/31 | 27 | 8 | 14 |
| $D_2$ | 0.32 | 6/1-6/30 | 30 | 6 | 10 |
| $D_3$ | 1.11 | 7/1-7/20 | 20 | 8 | 14 |
| $E_1$ | 0.66 | 5/6-6/2 | 28 | 9 | 20 |
| $E_2$ | 1.06 | 6/5-7/6 | 32 | 9 | 19 |
| $E_3$ | 0.53 | 7/7-7/28 | 22 | 10 | 14 |
| $E_4$ | 1.03 | 7/30-9/1 | 34 | 11 | 22 |
| $F_1$ | 0.66 | 5/6-5/31 | 26 | 10 | 12 |
| $F_2$ | 0.44 | 6/1-6/30 | 30 | 9 | 15 |
| $F_3$ | 0.54 | 7/1-9/2 | 64 | 11 | 19 |
| $G_1$ | 2.38 | 5/16-6/12 | 28 | 13 | 27 |
| $H_1$ | 1.01 | 5/16-5/31 | 16 | 10 | 20 |
| $H_2$ | 0.56 | 6/1-6/30 | 30 | 5 | 15 |
| $H_3$ | 0.29 | 7/1-7/16 | 16 | 5 | 10 |

Table 1. continued

| Male | Size (in acres) | Duration | Duration in days | Number of days recorded | Number of singing points recorded |
|---|---|---|---|---|---|
| $H_4$ | 0.67 | 7/17-8/17 | 32 | 9 | 15 |
| $I_1$ | 0.49 | 5/17-5/31 | 15 | 6 | 11 |
| $I_2$ | 1.54 | 6/1-6/30 | 30 | 8 | 16 |
| $I_3$ | 0.89 | 7/1-7/16 | 16 | 5 | 14 |
| $I_4$ | 0.56 | 7/17-7/30 | 14 | 5 | 11 |
| $J_1$ | 0.49 | 5/21-5/31 | 11 | 6 | 16 |
| $J_2$ | 0.58 | 6/1-6/30 | 30 | 6 | 13 |
| $J_3$ | 0.40 | 7/1-7/16 | 16 | 5 | 12 |
| $J_4$ | 0.39 | 7/17-8/23 | 38 | 7 | 11 |
| $K_1$ | 1.11 | 6/17-7/20 | 23 | 5 | 12 |
| $L_1$ | 2.56 | 6/21-9/16 | 88 | 28 | 49 |
| $M_1$ | 0.41 | 6/8-8/6 | 62 | 15 | 22 |
| $N_1$ | 1.04 | 6/22-8/25 | 65 | 24 | 29 |
| $P_1$ | 1.00 | 6/27-9/12 | 78 | 26 | 32 |
| $Q_1$ | 1.00 | 6/29-9/1 | 65 | 20 | 28 |
| $R_1$ | 0.43 | 7/1-7/16 | 16 | 5 | 16 |
| $R_2$ | 1.27 | 7/17-9/17 | 63 | 8 | 16 |
| $S_1$ | 0.42 | 7/17-9/17 | 13 | 6 | 24 |

across the Kalamazoo River from Augusta, Michigan. The male at the Fort Custer nest was not assigned a letter of identification. The nests on the study area and their respective males were nest 2, male $A_1$; nest 3, male $B_1$; nest 4, male $F_2$; nest 5, male $E_2$; nest 6, male $I_3$; nest 7, male $H_4$; nest 8, male $Q_1$; nest 9, male $J_4$; nest 10, male $F_3$; and nest 11, male $E_4$.

Following Van Tyne and Berger (1959:30) all young birds out of the nest but still dependent on the adults for food were termed fledglings.

# HABITAT AND DISTRIBUTION

## Habitat

The breeding habitat of Henslow's Sparrow seems to be somewhat variable. In the East, breeding habitats include cranberry bogs, fresh water bogs and swamps (Stone, 1908); broomsedge fields and weedy sedge-meadows (Stewart and Robbins, 1958); hillside meadows and swamps partially overgrown with shrubbery (Sage, Bishop and Bliss, 1913); damp, lush meadows (Pearson, Brimley and Brimley, 1942); and "rank grass interspersed with goldenrod in more or less wet fields, but it can also be found on sloping well-drained hayfields or even in hilltop pastures" (Bagg and Eliot, 1937). Further west, hayfields are more commonly reported breeding grounds than wet meadows and swamps, e.g., hayfields of orchard grass, orchard grass-clover, and weedy fields with occasional small bushes (Wiley and Croft, 1964) and hayfields of "high heavy growth usually in dry situations" (Kelley, Middleton and Nickell, 1963). In the tall grass prairie states, typical prairies (Anderson, 1963) and both wet and dry locations in prairies of bluestem, slough grass and porcupine grass (Ennis, 1959) also serve as breeding grounds. Hyde (1939) reviewed a large variety of habitats in which Henslow's Sparrows were known to breed and Table 2 lists habitats which have been surveyed for population analyses.

Table 2. Populations of Henslow's Sparrows.

| Density per 100 acres | Number seen | Acres sampled | Reference, State, habitat. |
|---|---|---|---|
| 1* | - | 65 | Graber and Graber (1963), Ill., timothy, brome and wild grasses, red and sweet clover and alfalfa |
| 3 | 0.5 | 19.4 | Vossler et al., (1965a), W. Va., abandoned field of grasses and weeds with a multiflora rose hedge |
| 4 | 1 | 28.3 | Skaggs (1943), Ohio, a portion of that censused by Knight (1939) below |
| 4 | 1 | 23.4 | Springer (1965), S. Dak., Andropogon, Poa, Stipa, Sorghastrum, legumes, goldenrod |
| 5 | 1 | 20.9 | Vossler et al., (1965b), W. Va., Unmowed abandoned hayfield of orchard grass, alfalfa, panic grasses |
| 5 | 2 | 42 | Moulthrop (1938), Ohio, open field with beginnings of trees |
| 6 | 1 | 16.3 | Baker (1958), Indiana, hayfield of 80% timothy, and 5% each of alfalfa, witchgrass, red and sweet clover |
| 6 | 1 | 16.3 | Baker (1960), see Baker (1958) above |
| 7 | 2 | 30 | Springer and Stewart (1948), Md., switchgrass and broomsedge |
| 9 | 2 | 22 | Moulthrop (1939), open field with tall grass, small trees scattered throughout |
| 9.2 | - | 40 | Graber and Graber (1963), Ill., hayfield of grasses (timothy and other species), yellow and red clover |
| 12 | 2 | 16.3 | Baker (1959), see Baker (1958) above |
| 12* | - | 24 | Graber and Graber (1963), see Graber and Graber (1963 above |

Table 2. continued

| Density per 100 acres | Number seen | Acres sampled | Reference, State, habitat |
|---|---|---|---|
| 15 | 2 | 30 | Stewart and Robbins (1958), Md., abandoned broomsedge |
| 16 | 2 | 12.5 | Stewart and Robbins (1958), Md., weedy unimproved pasture |
| 18 | 3 | 16.3 | Baker (1957), see Baker (1958) above |
| 20 | 5 | 25 | Hamann (1952), Ohio, mixed grasses (mainly timothy) few small trees, bounded by a bushy fence row |
| 20 | 4 | 20 | Hamann (1954), see Hamann (1952) above |
| 28 | 11 | 40 | Knight (1939), Ohio, open fields with numerous weeds |
| 28 | 7 | 25 | Hamann (1953), see Hamann (1952) above |
| 25-38 | 40-60 | 160 | Hennessey (1916) in Hyde (1939), Mich. |
| 44 | 4 | 9 | Hyde (1939), Mich., Cord grass, cinquefoil, few scattered shrubs |
| 54 | 12 | 22 | Moulthrop (1939), see Moulthrop (1939) above |
| 64-85 | 9-12 | 14 | Vickers (1908) Ohio, very heavy upland grass |
| 78 | 7 | 40 | Hyde (1939), see Hyde (1939) above |
| 75-100 | 30-40 | 40 | Hyde (1939), see Hyde (1939) above |
| "2000" | 10 | 0.5 | Anderson (1907), Iowa, small patch of hazel and blackberry briars |

* Data based on strip census

Although the above habitats appear to vary, a certain amount of similiarity exists among them. In most cases the major vegetation is less than four feet high. The vegetative cover is also quite dense or at least dense in certain locations within the overall breeding area. At Kalamazoo, territories were both smaller and more numerous on the north portion which had the highest and densest vegetation. The dense cover appears to be important in providing this secretive, weak-flying bird a safe retreat from danger, in enhancing concealment of the nest and young birds unable to fly, and in serving as an excellent habitat for a large insect population. Wiley and Croft (1964) reported that the habitat requirements of Henslow's Sparrows were "(1) a thick cover of grass, weeds, or clover and (2) tall stalks of weeds or flowers projecting two or three feet above the ground cover" which were needed for singing posts.

The need for singing perches elevated above the ground cover suggested by Wiley and Croft (1964) was not observed at Kalamazoo. The majority of the singing was done in the herbs just below the top of the ground cover. The only perches above the ground cover after June were the invading trees. Trees were nearly absent in the area of greatest density of birds and where trees were numerous they were used as perches only infrequently. During the early part of the breeding season, however, clumps of dead vegetation one or two feet high and projecting above the ground cover were frequently used as perches. In 1967

the vegetation of the study area was nearly level. This appeared to be due to an overwinter storm which deposited about two feet of snow on the area within a three-day period and thereby crushed the standing litter. This destruction of perches appeared to be the only vegetative change in the study area in 1967 and may in part explain a reduction in numbers between the two years. Small and scattered trees are usually present in areas where Henslow's Sparrows breed but this may be simply because of the natural phenomenon that small trees invade most unmowed treeless areas. The almost complete lack of small trees on the portion of the study area at Kalamazoo which had the greatest density of birds and the failure of Henslow's Sparrows to use the grid stakes as perching points suggests that this factor may be unimportant in habitat selection.

The variety of the vegetation seems to be another aspect of the habitat which is important to breeding birds. Favorable breeding habitats such as fields or swamps are not composed mainly of one species, but rather a mixture of grasses, forbs, weeds, and shrubs. Graber and Graber (1963) did not observe this species in extensive areas of croplands of oats, soybeans, wheat, clover, alfalfa, orchard grass, barley, rye, etc. The tendency not to inhabit croplands, however, may be due to the lack of litter as well as the uniform vegetation. In most of the preferred breeding habitats a considerable amount of litter is probably present since the areas are not annually harvested.

The study area in Kalamazoo which consisted of a dense cover of grasses and forbs lies adjacent to hayfields that are equally dense but are mowed every year. Henslow's Sparrows were not found in the latter in 1966 or 1967. Smith (1963) also observed that this species usually avoided hayfields that were regularly cut. He reported that when Henslow's Sparrows did become established in a hayfield, the field was abandoned after the first cutting. Abandonment of croplands (hay and wheat fields) after cutting was also reported by Vickers (1908). Skaggs (1941) observed no breeding Henslow's Sparrows on a "prairie-type field" after spring burning. Two years before, Knight (1939) had observed eleven pairs in the same area.

Henslow's Sparrows probably do not breed in extremely wet or dry areas. This species has not been reported to nest in areas of standing water. Beecher (1942) noted a marked decrease of Henslow's Sparrows after a "relatively slight rise in the water table" in Illinois. Nests are placed on or very near the ground, hence in marshes or wet meadows the nest site may be on a tussock elevated above the damp ground. The dry situations in which Henslow's Sparrows breed may not be as dry as one is led to believe. The hayfield at Kalamazoo is fairly dry and about 50 feet above a nearby marsh, but dew was frequently present until late morning and unless hip boots were worn one became thoroughly wet to the waist soon after entering the field.

## Distribution

Henslow's Sparrows breed in the northeastern quarter of the United States and southern Ontario, Canada. Recent records indicate that the breeding range is increasing. Extensions northward have been reported in Wisconsin to Bayfield County (Soulen, 1966), in Minnesota to Polk County and Duluth (Warner, 1959; Huber, 1961) and in Ontario, Canada (Godfrey, 1966). Expansion southward has been observed in Missouri (Anderson, 1963 and 1964) and in Kentucky to Laurel and Clinton counties (Mengel, 1965). These extensions and the increase in numbers may be due to the increased acreage of suitable habitat following the Soil Bank Act of 1956. Hyde (1939) also reported an increase in distribution and numbers just prior to his study. He believed that the increase was due to clearing of forests and not an increase in observers. For the typical bird, an expansion in range and numbers might be expected soon after an increase in available habitat. However, Henslow's Sparrow is not entirely typical.

The unique pattern of distribution of Henslow's Sparrow has been remarked upon by numerous writers including Hyde, (1939); Woodford and Lunn, (1961); Hall, (1961 and 1965); and others. Invariably the distribution in any particular state is considered "rare and local" or "highly irregular, being common for a few years and then absent for several years". A few

observers have found fairly stable populations but these seem to be exceptions to the rule.

The increase in range and numbers of Henslow's Sparrows has been explained above as being directly related to an increase in suitable habitat. This seems logical, but why are some areas occupied and some not? Why is the distribution in any particular region "local"? One would expect that as a particular population increased in numbers it would spread outward in the immediate area, but this has not been the case. Instead, only additional records of "local" distributions have been reported.

Certainly, the "rare and local" distribution is a phenomenon which is in part true, but the role of observers on the distribution of Henslow's Sparrows may have been underrated. The increased sightings of this secretive bird may be due in part to the increase in observers, the increased proficiency of amateurs (since the advent of field guides) and especially the increased enthusiasm for compiling as large a bird list as possible. This bird is so difficult to find and observe that in most cases one must be in the field before 8 AM or after 6 PM when it is likely to be perched and singing (Table 3) in order to make a positive identification. Hyde's map (1939:23) shows the distribution of this species to be so restricted in five instances that they are recorded only as spots separated from other breeding birds by 100 miles or more. Do these represent

Table 3. Number of songs per hour at four periods during the breeding season.

| | 10-11 May | | | 26-27 May | | | 18 July | | | 15-16 August | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Individual birds | | | Individual birds | | | Individual birds | | | Individual birds | | |
| Hour | D | E | F | E | H | J | I | J | S | H | J | R |
| 12 | 0 | 7 | 4 | - | - | - | - | - | - | - | - | - |
| 1 AM | 2 | 3 | 3 | - | - | - | - | - | - | - | - | - |
| 2 | 2 | 3 | 3 | - | - | - | - | - | - | - | - | - |
| 3 | 0 | 4 | 2 | 2 | 4 | 0 | 1 | 1 | 4 | - | - | - |
| 4 | 0 | 205 | 96 | 269 | 332 | 334 | 0 | 190 | 421 | - | - | - |
| 5 | 63 | 696 | 554 | 498 | 363 | 691 | 10 | 434 | 667 | 206 | 577 | 138 |
| 6 | 0 | 362 | 108 | 63 | 0 | 58 | 0 | 3 | 761 | 81 | 443 | 0 |
| 7 | 0 | 118 | 110 | 78 | 12 | 24 | 0 | 0 | 755 | 82 | 33 | 0 |
| 8 | 0 | 170 | 2 | 111 | 102 | 12 | 0 | 5 | 537 | 0 | 168 | 0 |
| 9 | 0 | 0 | 33 | 244 | 197 | 0 | 9 | 13 | 423 | 0 | 0 | 0 |
| 10 | 0 | 0 | 124 | 132 | 71 | 0 | 2 | 15 | 26 | 0 | 38 | 0 |
| 11 | 0 | 0 | 3 | 2 | 13 | 0 | 33 | 24 | 64 | 0 | 151 | 0 |
| 12 | 0 | 0 | 0 | 21 | 56 | 0 | 4 | 14 | 84 | 0 | 0 | 0 |
| 1 PM | 0 | 0 | 0 | - | - | - | 0 | 62 | 26 | 2 | 0 | 0 |
| 2 | 0 | 0 | 2 | - | - | - | 0 | 272 | 6 | 20 | 0 | 0 |
| 3 | 0 | 0 | 2 | - | - | - | 0 | 92 | 79 | 1 | 0 | 0 |
| 4 | 0 | 0 | 3 | 0 | 169 | 0 | 0 | 197 | 120 | 46 | 0 | 0 |
| 5 | 0 | 0 | 3 | 0 | 385 | 172 | 0 | 357 | 54 | 2 | 1 | 0 |
| 6 | 0 | 0 | 2 | 117 | 225 | 141 | 109 | 136 | 425 | 0 | 0 | 0 |
| 7 | 0 | 139 | 85 | 0 | 168 | 44 | 45 | 264 | 295 | 292 | 268 | 26 |
| 8 | 0 | 237 | 178 | 7 | 114 | 69 | 287 | 20 | 215 | 14 | 0 | 59 |
| 9 | 0 | 5 | 1 | 102 | 3 | 1 | - | - | - | - | - | - |
| 10 | 0 | 9 | 2 | 457 | 0 | 0 | - | - | - | - | - | - |
| 11 | 0 | 2 | 2 | - | - | - | - | - | - | - | - | - |
| Total | 67 | 1960 | 1322 | 2103 | 2214 | 1546 | 500 | 2099 | 4962 | 746 | 1679 | 223 |
| Sunrise | 5:25 AM | | | 5:10 AM | | | 5:20 AM | | | 5:48 AM | | |
| Sunset | 7:50 PM | | | 8:08 PM | | | 8:14 PM | | | 7:41 PM | | |

the true picture or do they merely represent records by individuals who have not ventured far from home? Hyde possibly serves as an example of how the numbers of observers may play an important role in the distribution of this species. He felt that one of the areas of greatest abundance was within 150 miles and centered about his study area in southern Michigan. It seems that this opinion could have arisen as a result of increased endeavor and awareness of the immediate area by Hyde and his colleages.

As a further example of the role observers play one needs only to review recent issues of the state bird journals. For example, in Minnesota (The Loon) Henslow's Sparrows are reported almost every year from Winona County and irregularly from several others; in Wisconsin breeding birds are regularly reported from Dane and Chippewa counties (Passenger Pigeon) and occasionally from others; in Missouri (Bluebird) they have been reported regularly only from the Tucker and Taberville prairies in recent years. In almost all of the above cases and frequently in other local journals, reports of this species come from a few individuals who are evidently familiar with the bird and make a special effort to find it.

A problem equally as difficult to explain as the "rare and local" distribution is the irregularity of occurrence reported for many areas. Once a bird is established in an area, why do population levels fluctuate from "entirely absent" to "relatively common" or vice versa within a few years? Because these

birds breed in such varied habitats as swamps, wet meadows, abandoned fields, and prairies small changes in the climate or habitat probably do not significantly influence distribution. Between 1961 and 1966 the number of Henslow's Sparrows present on the Colony Farm Tract varied from 12 to 17.5 singing males (Richard Brewer, personal communication). A drought occurred between 1960 and 1964 and yet the population remained quite stable. However, in 1967 only eight singing males were present. As was reported above, in 1967 there were almost no perches available early in the year due to leveling of the standing litter by snowfall. In this case the destruction of perches may be the reason for the reduced population. However, this phenomenon cannot explain similar fluctuations in areas of limited snowfall and it does not explain why no marked individuals (44 birds were marked in 1966) were among the breeding birds observed on the tract or in the immediate area in 1967. It seems unlikely that all the marked birds would have died. Another alternative is that individuals do not return to the same breeding ground every year. If this were true it would help to explain why population levels fluctuate but it would raise an even more perplexing question as to the development of this habit.

Smith (1963) observed similar phenomena for the closely related Grasshopper Sparrow, Ammodramus savannarum, which is also a grassland bird. He reported that this species likewise

fails to occupy all the areas of suitable habitats in a particular region and the populations fluctuate considerably from year to year.

At present the causes for the spotty and fluctuating distribution are unknown.

## ARRIVAL AND DEPARTURE

In 1966 the first Henslow's Sparrow was observed on 22 April singing 100 yards southwest of the study area. Two days later two males were singing on the Colony Farm Tract. The first arrival in 1963 was 26 April (Richard Brewer, personal communication). In 1967 three males arrived on 30 April.

The average date of arrival for 23 years between 1932-1960 at Battle Creek, Michigan (at approximately the same latitude as Kalamazoo but 21 miles east) was 27 April (Walkinshaw, 1941 and 1961). The range was from 16 April to 17 May.

The last date a Henslow's Sparrow was seen in 1966 was on 16 October, but the last identification of a resident bird was made on 17 September. The average date Henslow's Sparrows were last seen in southern Michigan by Walkinshaw (1941 and 1961) for eight years was 17 September (range 3 September to 9 October). Hyde (1939) observed several birds as late as 24 October, but like Walkinshaw he had no way of knowing whether the birds he observed were southern Michigan residents or migrants from further north.

The average length of time spent on the summer nesting grounds is difficult to evaluate because the birds remain in the grass and are virtually impossible to flush after breeding activities have ceased. Three resident males (B, E, and F) were first seen on 6 May and were recorded singing over periods of

101, 119 and 120 days respectively (Table 1). Additional time would be required for postnuptial molt before leaving their summer residence. However, this period may be rather short. The dense cover and seemingly high insect population could permit extensive and therefore rapid molt. Kumlien and Hollister (1903) reported that "during the latter part of August and September the adults especially are in a condition of such extreme molt as to be almost unable to fly, there being many days when not an individual can boast of even a single tail feather". Several birds without tail feathers were observed during this same period in southern Michigan. The fact that fall migration occurs over a two-month span (Hyde, 1939:22) implies that migration is gradual and that a large build up of fat may not be necessary. TV tower fatalities were collected in Leon County, Florida, by Stoddard and Norris (1967:97) between 7 October and 10 December. Both extensive molt and limited fat deposition would allow rapid departure after the final brood becomes independent.

## THE ROLE OF SONG IN THE ESTABLISHMENT AND MAINTENANCE OF TERRITORIES

Sutton (1959b:148) stated that territorial defense included frequent chasing by the males. During extensive observations at Kalamazoo no similar incidents were observed. Territorial disputes between adjacent males were limited to formal song-fests. "Singing" and "song" are here used to refer to the vocalization given by the male represented as "flee-sic" (Faxon, 1889:44) or "tsi-lick" (Peterson, 1947:231). Soon after one male began singing, one or more of its neighbors also started to sing. They frequently remained at the same location for a half hour or more although occasional movements were made from place to place within their respective territories. There was no tendency for adjacent males to come to their nearest borders for a duel. In cases where one male moved near the border of its territory and that of a nearby male, the latter usually continued singing at the same location, even if on the opposite side of its territory. With these observations as a basis territories are here considered to be any area defended by song.

The average distance between simultaneously singing males on adjacent territories for 107 cases was 216 feet. The range was from 52 to 423 feet. There was only one case in which two birds sang while closer than 74 feet and only two cases in which birds were over 400 feet apart. Wiley and Croft (1964)

reported that the distance between seven singing males was between 200 to 300 feet.

On 10-11 May a continuous 24-hour song count of all the songs of three birds on the north portion were recorded for each minute (Table 3). The history of the birds was as follows: Male D arrived and was in song on 5 May and the remaining two birds (E and F) arrived the following day. The territory of male E was approximately half-way between the other two. No other males were singing nearby except for a male whose territory came to within 145 feet of D's territory.

A considerable variation existed among the three birds. Male D sang only 67 songs all day, most of which came within the hour after 5 AM. Male E sang the greatest number of songs (1960) and concentrated his singing mainly between 4:45 and 8:30 AM, and between 7:45 and 8:20 PM. This appeared to be the typical pattern of song throughout the area. Although F sang more during the midday hours, his singing was also largely concentrated in the early morning and evening. Almost no singing was observed between 9 PM and 4 AM.

Later, on 26 and 27 May a similar song count was conducted. Songs were not recorded for the early afternoon, but typically very few songs were uttered during this period. At this time male E had been present for 20 days but left the territory eight or nine days later. Male H had arrived on 16 May and male J on 21 May. Two singing males were located north and east of

E, and three males were located north, east and south of both H and J. This song count represents that period when many of the males were in the earliest stages of the breeding cycle; i.e., pair formation, copulation and nest building. Males E and H which had been present longer sang approximately one-fourth more songs than J which was located between them.

A song count of overnight singing was not carried out because it had been observed that singing during that period was rare. On this evening continual song by all three males ended by 8:38 PM. Male E, however, began singing at a rate of eight to nine songs per minute at 9:45 and continued beyond 11 PM at which time the song count was terminated. This was the only time a bird was heard singing regularly after nightfall all summer which was surprising since several observers have heard this bird singing throughout the night (Hyde, 1939; Roger T. Peterson, personal communication; and others).

On 18 July a third song count was taken using three males in adjacent territories. Male S arrived on 17 July, the day before the census was begun, and left the area on 29 July. On the evening of 8 July, male I had lost a nest of five young. He was last observed singing on 30 July. Male J's mate began incubating on approximately 23 July. Males I and J, were bordered by three males each.

Most of the activity was centered about S. He established himself among five birds on portions of three previous territories. Male S sang more than twice as many songs as had been

previously recorded and sang during all hours from 3 AM to 9 PM. Male J and his mate were approximately in the copulation and nest-building stage. Male J sang 2099 songs, a figure similar to that of birds at the same stage earlier in the year. This bird also sang during the midday hours, probably in response to the efforts of S. Except during the evening hours, male I sang very little. Inasmuch as he had recently lost a brood of nestlings and probably did not renest, his limited involvement in territorial singing is, perhaps, understandable.

In the latter part of the breeding season (15-16 August) a fourth song count was made. Male H had fledged three young on 25 July and was last observed singing on 17 August. Male J fledged one young on 12 August and was last observed singing on 23 August. Male R was the last bird to continue proclaiming a territory. He was last observed singing on 17 September. H and J were partially surrounded by three singing males, and R was located adjacent to two other males. Male J may have been attempting to begin another clutch; his total number of songs (1679) approached that heard earlier in the year. The same phenomenon may have been true of male H. Late clutches were observed by Sutton (1959b) to leave the nest one month beyond this date. Although no nest was found the number of songs by R suggests that he may have been caring for young.

No other extensive song counts were made, but on 26 August between 6 PM and 9 PM only 32 songs were uttered by three males

on the north area.

The maximum singing rate for one minute decreased from 18 on the first song count in early May to 16.5 in late May and mid-July, to 14 in mid-August.

While observing feeding of the nestlings at nests 5 and 7, observation of singing by the males was also attempted. All activities could not be determined and therefore the following data should be regarded as estimations. During the day songs were limited to intervals of only two or three minutes; these song periods immediately followed feeding of the nestlings by the males. The males flew from the nest to a perch and began singing after 55 per cent of the feeding trips between 10 AM and 6 PM. During the early morning and evening hours the males frequently engaged in periods of singing not associated with feeding at intervals of one to ten minutes. However, singing did occur after 40 and 33 per cent of the feeding trips before 10 AM and after 6 PM respectively.

In summary, territorial defense appeared to be limited entirely to singing, with the males remaining some distance apart in their respective territories. This was due in part to the presence of buffer zones between the territories (see discussion of Territories). Maximum singing rate was not at its highest among first arrivals but reached its peak about the time of laying of the first clutches. At this time more males were present than before. During the nestling period when the males were feeding young, territorial defense was continued, but only

to a limited extent. From the time of laying of the first clutches on, the singing rate of the population as a whole decreased. However, because of second nestings and re-nestings following loss of nests, considerable variability existed because different birds were at different stages of the nesting cycle. Territorial singing appeared to be continued after breeding was completed but not during the molting period.

## POPULATION ECOLOGY

### Territories

During the course of the breeding season, shifting of territories, "departure" of singing males, and establishment of males new to the area were common occurrences. Thirty-six different territories, existing for various periods, were present over the summer (Table 1), but only 18 males were involved. Ten birds had only one territory which appeared to remain stable during their stay on the area (three were present less than 30 days), two birds had two territories, two birds had three territories, and four birds had four territories.

An illustration of territorial change during the course of the breeding season on the northern portion of the study area (8 acres of suitable habitat between lines 1 and 4) is presented in Figs. 1-3. Size and duration of the territories are listed in Table 1. During the first half of May only one male, $F_1$, was present. At various times during the latter half of May three more males, $H_1$, $I_1$, and $J_1$, arrived and established territories. Throughout June no new birds arrived, but the territories present shifted in both size and location. Another shift in territories took place in the first half of July. This may have been due to the arrival of $R_1$ on 1 July. On 17 July a sixth male, $S_1$, initiated singing in the midst of five established birds. This male remained for only 13 days, singing

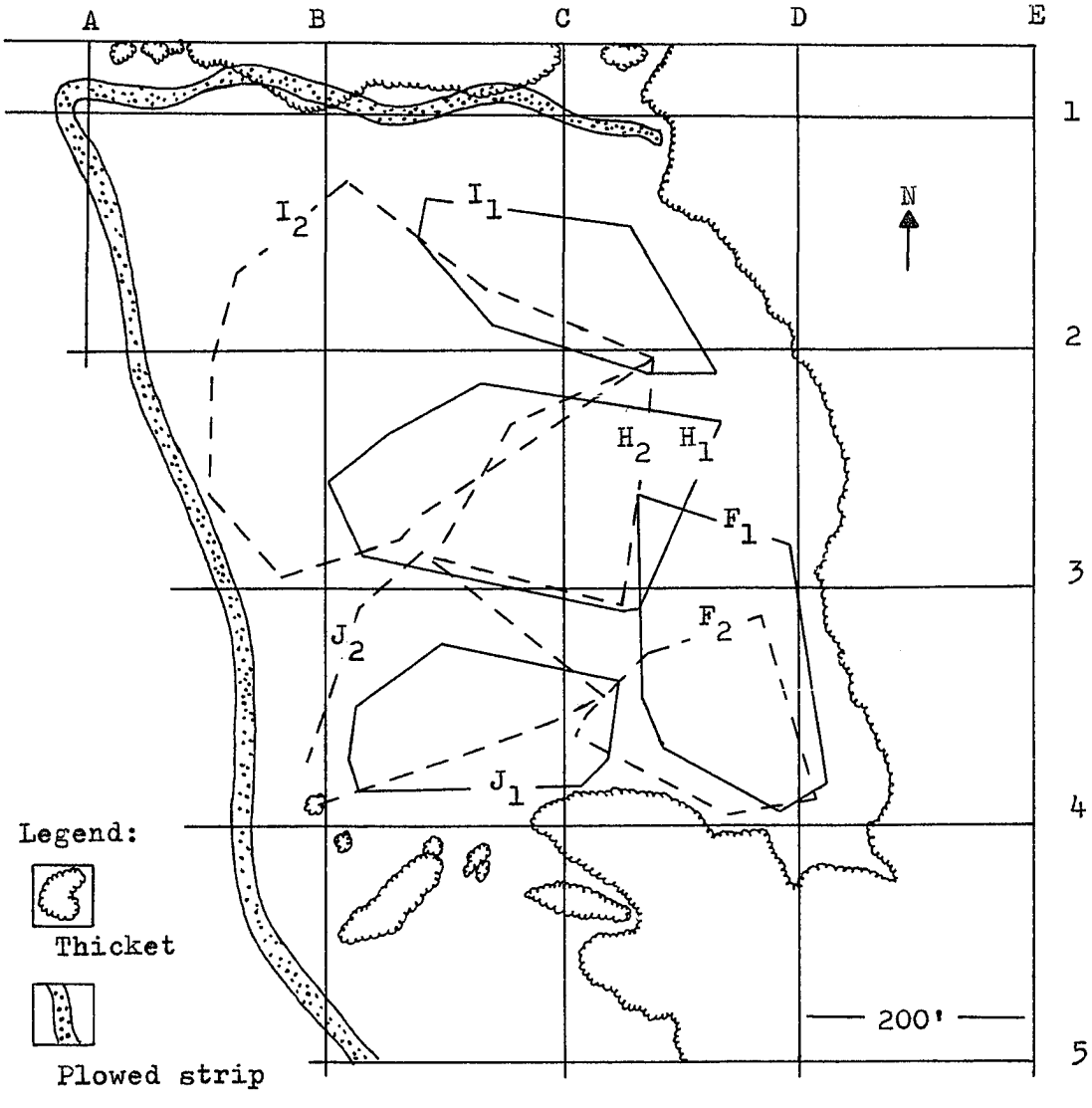


Figure 1. Henslow's Sparrow territories on the northernmost eight acres of the Colony Farm Tract during May and June. The solid line represents territories present in May and the dashed line represents territories present in June.

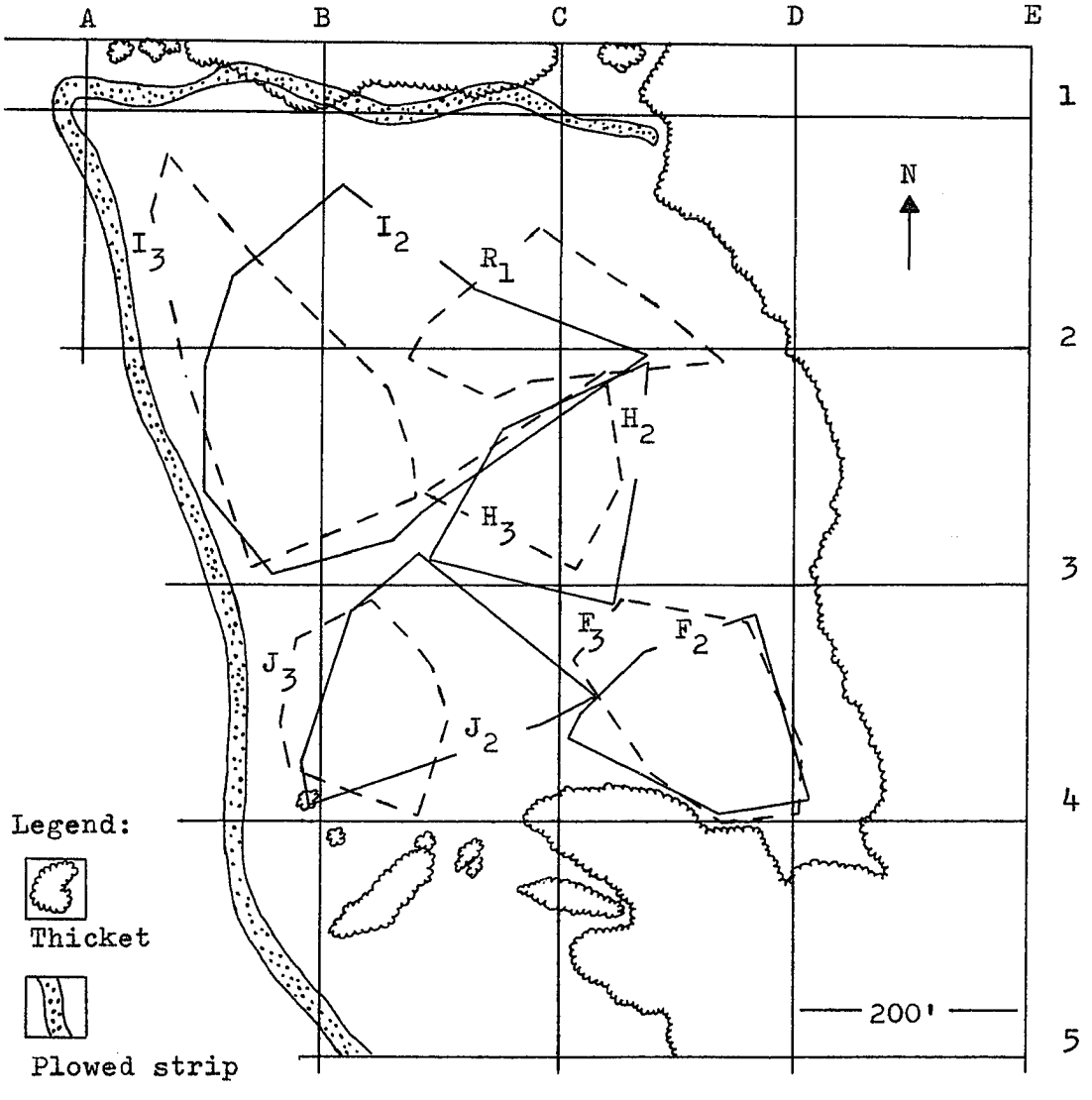


Figure 2. Henslow's Sparrow territories on the northernmost eight acres of the Colony Farm Tract during June and July. The solid line represents June territories and the dashed line represents territories present during the first half of July.

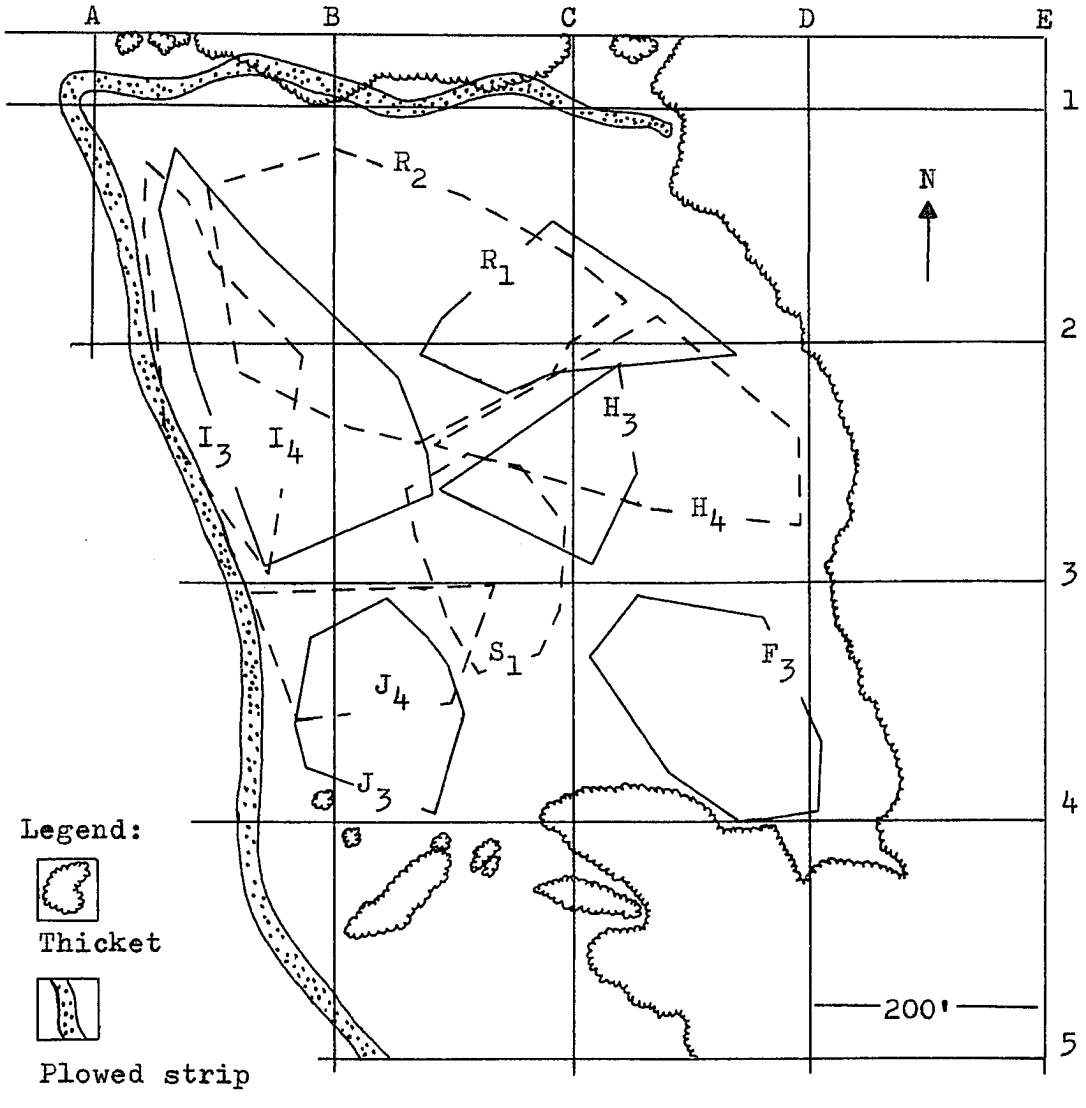


Figure 3. Henslow's Sparrow territories on the northernmost eight acres of the Colony Farm Tract during July. The solid line represents territories prior to the arrival of male S on 17 July and the dashed line represents territories after 17 July.

continually while most of the other birds sang very little. Probably as a result of the presence of $S_1$, another shift of territories occurred in the latter half of July (all except $F_3$). Thereafter the only changes were in the successive disappearances of $I_4$ (at the end of July), $H_4$ (in mid-August), $J_4$ (in the latter part of August), $F_3$ (in early September) and finally $R_2$ (in mid-September).

The greatest shift of territories on the study area was exhibited by male E. After setting up his first territory he moved south 625 feet; later he moved 65 feet further south, and finally northeast 605 feet. Duration of these territories was 28-30 days, 32-34 days, 22-23 days and 34-35 days. Young were known to be successfully fledged in the second and fourth territories.

Occasional overlap was evident after plotting the territories on maps. Most instances of overlap, however, were probably due to daily or weekly shifting of territories within the time span selected for mapping and, therefore, do not represent actual overlap. The only cases of consistent overlap were those involving males $G_1$ and $L_1$. These two birds had territories about three times larger than average; they overlapped the territories of $E_2$ and $N_1$ respectively. For the most part, territories were distinct units separated from others on all sides by buffer zones where neither male sang. Throughout the summer the average distance between adjacent territorial boundaries was 81 feet. Distance between adjacent territories was

inversely related to the number of territories present, ranging from 47 feet in July when the population was the highest, to 431 feet in September when the population was the lowest (Table 4).

Territory size for all territories throughout the year and over the entire study area averaged 0.82 acres. However, on the northern part of the tract (13 acres of suitable habitat) territory size averaged 0.70 acres for 24.8 territories. On the southern part (17 acres of suitable habitat) the 11.2 territories present had an average size of 1.09 acres. Two territories covered parts of both the north and south portions of the study area. Unlike the Song Sparrow, Melospiza melodia, whose territories are large at the beginning of the year and "decrease under preseure of-competition" (Nice, 1941) the average size of Henslow's Sparrow territories was smallest at the beginning of the year and gradually increased through the summer (Table 4). This pattern, however, was not universal for all individuals.

During the first half of July, 15 territories were present over the entire 30 acres and had an average size of 0.84 acres (0.98 acres for 7.3 territories on the southern portion and 0.70 acres for 7.7 territories on the northern portion).

The presence of buffer zones of unoccupied area between most of the territories, the lack of territorial defense other than by song, and the extensive amount of the habitat which was not occupied (almost 60 per cent) suggests that for the

Table 4. Henslow's Sparrow territories on the Colony Farm Tract. (Present 8 or more days during the half-month intervals).

| | May | | June | | July | | August | | September |
|---|---|---|---|---|---|---|---|---|---|
| | 1-15 | 16-30 | 1-16 | 17-30 | 1-16 | 17-30 | 1-15 | 16-30 | 1-17 |
| Number of territories | 6 | 9 | 10 | 12 | 15 | 13 | 10 | 8 | 3 |
| Density per 100 acres | 20.0 | 30.0 | 33.3 | 40.0 | 50.0 | 43.3 | 33.3 | 26.7 | 10.0 |
| Mean territory size in acres | 0.73 | 0.91 | 0.90 | 0.89 | 0.84 | 0.85 | 1.01 | 1.10 | 1.61 |
| Average distance between adjacent territories (in feet) | 221 | 69 | 83 | 77 | 47 | 55 | 75 | 82 | 431 |

Kalamazoo population, territorial behavior probably did not regulate density.

That territories or utilized areas of breeding birds vary in size with the stage of the breeding cycle has been shown for several species (Weeden, 1965; Stefanski, 1967; and others). This does not represent change from one area to another, but it represents fluctuation in size about a focal point -- the nest. Other observers cited by Weeden (1965) have observed no change in territory size and boundaries throughout the breeding season. Nice (1937) reported that male Song Sparrows generally remained on the same territory but that shifting of territories was not uncommon.

The Henslow's Sparrow population at Kalamazoo contained males which remained on a stable territory all season, males that changed territories but remained in the same general area, and males that shifted territories over considerable distances.

Knowledge of which species shift territories and which do not is of no little importance to population studies. Preferably population studies should be carried out on communities in which all birds are individually marked, but with few exceptions this would be an impossible task. With marked birds the observer could determine whether or not an individual has been counted in another territory earlier in the year, whether or not a particular territory has been inhabited by more than one male, the extent of individual territories, etc. Some species nest only once, but birds re-nesting after loss of the first

clutch and multiple-nesting species may be counted more than once if they shift territories.

Male E provides an excellent example of the way in which data from unmarked birds could be misinterpreted. He defended four different territories which might have been interpreted as four different singing males had he not been marked. However, two territories were adjacent to each other and could have been interpreted as one bird on an atypically large territory. The first area he occupied was later occupied by male Q and the last area he established had been occupied earlier by male D. In the final analysis male E may have been recorded only once but on a larger territory than was occupied, and males Q and D would have been recorded as being present over longer periods than was actually true. All of the misconceptions added together would give the impression that the population was more stable than it actually was.

Breeding-bird censuses could easily be improved to collect more valuable data. To eliminate the impossible task of marking all the birds in a particular community and still obtain an accurate estimate of the population the observer should carry out thorough surveys over short periods throughout the breeding season. This would enable him to determine the population at any given period as well as separate spring-nesting from fall-nesting birds. For many areas the shorter census intervals would show that the population size and number of species would vary significantly from the clumped season-long total (see

Table 4 for variability in Henslow's Sparrows).

## Population Levels

Only six territories were defended on the entire area during the first half of May. This number increased gradually to a maximum of 15 territories during the first half of July and then gradually decreased to three territories in the first half of September (Table 4). Thereafter no territories were discernible although birds were present in the area until 16 October. The total number of breeding pairs per 100 acres during the first half of May, June, July, August and September was 20, 33.3, 50, 33.3 and 10. During the first half of July density of breeding birds per 100 acres was 59.3 on the north area and 42.9 on the south area.

Richard Brewer (personal communication) estimated singing males for 1961 through 1965 using the Williams (1936) spot-map method. Over this five-year span he found the grassland to have a population of 15.5, 17, 17.5, 16.2 and 12 singing males. Using the latter method in 1967 the maximum population was determined to be eight males.

The large decrease in numbers in 1967 from a rather stable population may be a temporary decline or it may be the first step in the abandonment of this field as a breeding area for Henslow's Sparrows. Sutton (1959b) observed another Michigan population over a 14-year period in which abundance of Henslow's Sparrows changed from common during the first part to

absent during the latter part. Moulthrop (1939) reported a change from 54 to 22 to 0 breeding birds per 100 acres on a 22-acre open field of tall grass and small shrubs in Ohio over three consecutive years.

The mean number of breeding birds per 100 acres from records in the literature (Table 2) was 23 (range 1 to 75 or 100). Anderson (1907) reported an observation by Berry of 10 breeding pairs on a half-acre patch of hazel and blackberry briars in Iowa. Use of a similar habitat is unknown in the literature; this, taken with the high density and his discovery of 10 nests makes the report questionable. The majority of the studies (18) reported figures lower than the mean indicating that the mean does not represent the normally-encountered density. During the height of the breeding season at Kalamazoo (50 singing males per 100 acres) territories were present on only 41.4 and 42.1 per cent of the available habitat on the north and south portions of the Colony Farm Tract. Seemingly, the area could support a population more than double that observed in 1966. Inasmuch as the average size of Henslow's Sparrow territories was less than one acre on the Colony Farm Tract, the density of 75 to 100 birds per 100 acres observed by Hyde (1939) may be near the maximum density to be expected for this species.

## Utilized Area and Territoriality During the Nestling Period

Locations to which adults flew to forage during the nestling stage were observed from blinds placed near the nests. Because information on food of the nestlings was also recorded it was not always possible to follow a bird leaving to forage if its mate fed immediately afterwards. Nevertheless 429 of 484 trips by males and 750 of 902 trips by females were accurately determined. Because the birds usually twittered to and from foraging areas, the direction from the nest was ascertained for many cases even though the bird was not seen.

The average distance away from the nest that males and females flew to forage was 33.7 yards and 27.2 yards respectively (Fig. 4). The difference between the means is significant at the 0.001 level using Student's *t* test. A much greater variability was evident for the males than females (standard deviations were 4.9 and 2.3 respectively). Forty per cent of the trips by females were 25 or 30 yards away from the nest and 36 per cent of the trips by males were 40 or 45 yards away from the nest. Only 6.8 per cent and 14.4 per cent of the trips by the males and females were made to locations less than 20 yards from the nests.

During incubation 42 feeding trips by the females at nests 3 and 5 were observed on seven days. Only four trips were made to locations less than 25 yards from the nests; none were

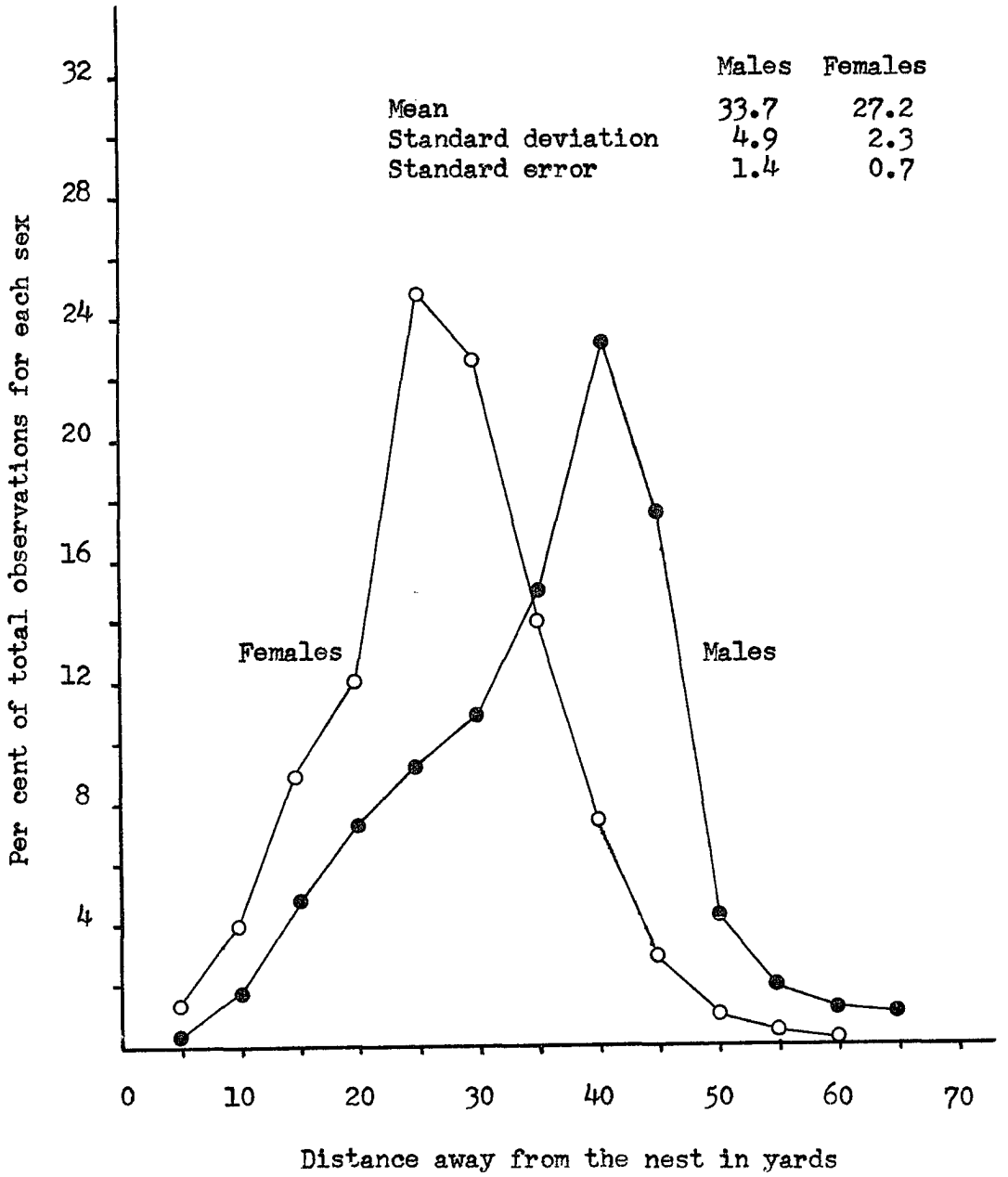


Figure 4. Distances males and females foraged away from the nest. Total observations were males 429 and females 750 at six different nests.

within 20 yards.

The direction from the nest to which each adult flew to forage was also recorded for each nest (Table 5). Directions presented in Table 5 represent obvious concentrations of the raw data. The percentages not presented in the table were small and scattered among the remaining directions. At nest 3 where only the female fed the nestlings, no pattern was evident. At the remaining nests, however, a definite pattern was evident for each bird of the pair, indicating a strong preference for particular foraging areas. In addition, there was no appreciable overlap in the major feeding areas of the two adults except at nest 6. At several nests foraging in one or more directions was limited due to a "natural barrier". Nests 5 and 6 were about 100 feet east of the field of oats which was not utilized as a foraging area; thus few foraging trips were made west of the nests. At nest 7 the nest was near the west edge of the territory which was bordered rather closely by additional territories from the southeast to northwest. A space of only 100 feet separated nest 8 from a thicket located to the northeast. Henslow's Sparrows were observed to go near or into the thickets only when being pursued.

To determine the degree of utilization of the male's singing territory as a food source, the number of times each bird foraged in and out of the territory was counted (Table 6). The percentage of times the adults foraged outside the singing territory varied from 12.2 to 78.5 for the males and from 12.6 to

Table 5. Directions from the nest in which males and females foraged during the nestling period. Only the female fed the nestlings at nest 3.

| Nest and adult | Per cent of foraging trips | Directions from the nest | Number of observations | Number of observation days |
|---|---|---|---|---|
| Nest 3 | | | | |
| Female | 35 | N to ENE | | |
| | 29 | E to SSE | 295 | 7 |
| | 14 | S to WSW | | |
| | 22 | W to NNW | | |
| Nest 5 | | | | |
| Male | 91 | N to NE | 67 | |
| Female | 74 | SE to S | 159 | 7 |
| Nest 6 | | | | |
| Male | 75 | NE to E | 59 | |
| Female | 76 | N to E | 108 | 3 |
| Nest 7 | | | | |
| Male | 75 | NE to ENE | 180 | |
| Female | 78 | ENE to E | 110 | 5 |
| Nest 8 | | | | |
| Male | 89 | SW to N | 95 | |
| Female | 78 | SE to SW | 132 | 4 |
| Nest 9 | | | | |
| Male | 64 | E to SW | 83 | |
| Female | 76 | SW to N | 98 | 6 |

Table 6. Amount of time spent foraging in and out of the territory of the singing male.

| Nest and adult | Number of times foraged out of singing territory | Number of times foraged in singing territory | Total number of times recorded | Percentage of times foraged outside of singing territory |
|---|---|---|---|---|
| Nest 3 | | | | |
| Male | Did not feed young | | | |
| Female | 211 | 59 | 270 | 78.1 |
| Nest 5 | | | | |
| Male | 20 | 39 | 59 | 33.9 |
| Female | 28 | 110 | 138 | 20.3 |
| Nest 6 | | | | |
| Male | 6 | 43 | 49 | 12.2 |
| Female | 12 | 83 | 95 | 12.6 |
| Nest 7 | | | | |
| Male | 107 | 64 | 171 | 62.6 |
| Female | 14 | 52 | 66 | 21.2 |
| Nest 8 | | | | |
| Male | 28 | 57 | 85 | 32.9 |
| Female | 89 | 20 | 109 | 81.7 |
| Nest 9 | | | | |
| Male | 51 | 14 | 65 | 78.5 |
| Female | 59 | 13 | 72 | 81.9 |
| Total | | | | |
| Males | 212 | 217 | 429 | 49.4 |
| Females | 413 | 337 | 750 | 55.1 |
| Combined | 625 | 554 | 1179 | 53.0 |

81.9 for the females. The percentage of times foraging occurred outside the singing territory was slightly greater for females (55.1 versus 49.4 per cent).

A second index used to determine the degree of utilization of the singing territory as a food source for the nestlings was the overlap of utilized areas and singing territories (Table 7). The utilized area was the largest area produced by drawing lines between the points to which the adults flew to forage during the nestling period. It was not known whether or not adjacent pairs used the same foraging area. In the case of females, 42 per cent of the utilized area overlapped the territory of the singing male (range 18-61.5), while the overlap for the males was 50.5 per cent (range 31.5-82.1). The females were able to forage closer to the nest (Fig. 4) and yet have a smaller overlap of utilized area and singing territory because most of the nests were located near the periphery of the singing territory.

At nest 3 there was only a small portion of overlap of utilized area with singing territory (18 per cent) and a high percentage of feeding trips were made to points outside the singing territory (78.1 per cent). This is probably due in part to the fact that the male did not feed the nestlings and his territory did not include the nest.

At nest 9 both adults had a high percentage of times foraged outside the singing territory and a high percentage overlap. This apparent anomaly appears to result from the fact that

Table 7. Comparison of singing territories and utilized areas during the nestling period at six nests.

| Nest | Territory size of singing male (Acres) | Utilized area of male (Acres) | Utilized area of female (Acres) | Utilized area of male in territory of singing male (Per cent) | Utilized area of female in territory of singing male (Per cent) |
|---|---|---|---|---|---|
| 3 | 0.61 | - | 0.59 | - | 18.0 |
| 5 | 1.06 | 0.63 | 0.72 | 51.9 | 61.3 |
| 6 | 0.89 | 0.32 | 0.55 | 31.5 | 46.1 |
| 7 | 0.67 | 0.59 | 0.34 | 52.2 | 32.8 |
| 8 | 1.00 | 0.55 | 0.79 | 35.0 | 32.0 |
| 9 | 0.39 | 0.84 | 0.51 | 82.1 | 61.5 |
| Mean | 0.77 | 0.59 | 0.58 | 50.5 | 42.0 |

this male had the smallest singing territory of the group (0.39 acres).

The tendency for females to forage closer to the nest may have survival value in that it would reduce the expenditure of energy by the female, allow her to spend more time brooding and reduce her exposure to predators. The males do not brood the young and therefore they would be more expendable than females. It appears that a female may be able to raise the young by herself (see Multiple Nesting and Nesting Success).

The utilization of different foraging areas by the males and females (Table 5) could eliminate competition between the adults and familiarize each bird with one particular area which would decrease the time required for foraging. At nest 3 where the male did not feed the young the female showed no directional preference. This suggests that where the male and female both feed, they are aware of each other's foraging habits and adjust accordingly. Differential niche utilization by males and females has been reported for several additional species (see Selander, 1966).

The tendency for males to forage within their singing territories more than females is probably related to a better knowledge of the territorial boundaries. However, both adults foraged outside the singing territory as much as or more than inside. Birds from the largest territories remained within them more than did birds with smaller territories. Adults from the smallest territory (nest 9) left it the most often. If

territories were smaller due to a greater abundance of food the adults would be expected to do the majority of their foraging in the territory. With one exception the utilized areas of the male and female were smaller than the singing territory. If the singing territory contained enough food the smaller utilized areas would be expected to fit within the former's boundaries. It is possible that the territories did contain enough food but for some reason the adults left the territory to forage. The extensive area unoccupied by singing males (almost 60 per cent of the available habitat) may have been responsible, in part, for the extension of foraging areas out of the singing territories.

Territories were smaller on the north portion where the vegetation was densest and probably contained a greater food supply. However, foraging outside of the territorial boundaries in the north area (nests 6, 7, 8 and 9) was greater than at the only typical nest (nest 5) on the south area. Stenger (1958) observed that an inverse relationship existed between territory size and the abundance of the food supply for Ovenbirds, Seirus aurocapillus. She suggested that territory size may be directly adjusted to the amount of food present. The same inverse relationship probably existed for Henslow's Sparrows but other data indicated that territories, regardless of size, did not provide the majority of the food for the nestlings. Thus the inverse relationship, although interesting, is not in itself proof that territories are regulated by the food

supply. Since about half of the food for nestlings probably came from the territory, the territory does have considerable food value.

## Relations With Other Animals

### Breeding associates

The grassland portion of the Colony Farm Tract had an estimated 37.4 breeding males in 1966 (Richard Brewer, personal communication). The seven species present and their numbers were: Henslow's Sparrow, 15; Red-winged Blackbird, Agelaius phoeniceus, 7.2; Short-billed Marsh Wren, Cistotherus platensis, 6; Eastern Meadowlark, Sturnella magna, 4.5; Bobolink, Dolichonyx oryzivorus, 4.0; Savannah Sparrow, Passerculus sandwichensis, 0.5; and Grasshopper Sparrow, Ammodrammus savannarum, 0.2. The wren and the Grasshopper Sparrow were not present prior to 1966 and the latter was absent in 1967. Henslow's Sparrows comprised 40 per cent of the total number of males present. Inasmuch as the Red-winged Blackbird, Eastern Meadowlark and Bobolink are polygynous (Verner and Willson, 1966) they would have, in comparison with Henslow's Sparrows, larger populations and more nests than is indicated by the number of males.

Behavioral interactions with four of the community associates were observed. The most frequent interactions were with male Bobolinks and Red-winged Blackbirds. Both occasionally

chased singing Henslow's Sparrows and adults flying to and from the nest during the nestling stage. Such incidents appeared to occur only when a blackbird or Bobolink by chance happened to fly over a singing male or cross the path of a flying Henslow's Sparrow. Attacks were limited to dips in the flight pattern to within a few feet of the grass into which the Henslow's Sparrows immediately retreated. This was followed by an immediate resumption of flight by the blackbird or Bobolink.

On several occasions when Short-billed Marsh Wrens began singing, a neighboring Henslow's Sparrow male was observed to fly to a location near the wren and also begin singing. On one morning a pair of Henslow's Sparrows were observed attacking a Short-billed Marsh Wren (see Behavior of Parents After Loss of Young). During the first half of June, when Short-billed Marsh Wrens first arrived on the area, inter-specific territoriality appeared to exist between Henslow's Sparrows and the wrens. All points of observation of the two wrens present were outside the Henslow's Sparrow territories (Table 8). Later in the season, as the population of wrens increased to six males, there was no clear-cut exclusion of them from the Henslow's Sparrow territories. These two species have similar habitat requirements and are common breeding associates (Walkinshaw, 1935 and Bent, 1948). A further study of possible competition between these species would be valuable.

The Grasshopper Sparrow on the study area was pursued several times by male B, when the former flew across the latter's

Table 8. $Chi^2$ test of the relationship of singing points of Short-billed Marsh Wrens to Henslow's Sparrow territories.

| Date | Observed | Expected | $Chi^2$ |
|---|---|---|---|
| June 1-16 | | | |
| Area outside Henslow's Sparrow territories (8.31 acres) | 11 | 7.9 | |
| Area inside Henslow's Sparrow territories (3.30 acres) | 0 | 3.1 | - |
| June 17-30 | | | |
| Area outside Henslow's Sparrow territories (10.70 acres) | 15 | 14.7 | |
| Area inside Henslow's Sparrow territories (5.78 acres) | 8 | 8.3 | 0.016 |
| July 1-16 | | | |
| Area outside Henslow's Sparrow territories (9.13 acres) | 9 | 8.3 | |
| Area inside Henslow's Sparrow territories (7.35 acres) | 6 | 6.7 | 0.132 |
| July 17-31 | | | |
| Area outside Henslow's Sparrow territories (5.05 acres) | 12 | 7.6 | |
| Area inside Henslow's Sparrow territories (4.20 acres) | 2 | 6.4 | 5.572 |
| August 1-15 | | | |
| Area outside Henslow's Sparrow territories (6.03 acres) | 7 | 6.5 | |
| Area inside Henslow's Sparrow territories (3.22 acres) | 3 | 3.5 | - |

territory. At Fort Custer where the territories of two individuals of these two species overlapped, a Grasshopper Sparrow was frequently seen chasing a male Henslow's Sparrow. On these occasions soon after the Henslow's Sparrow flew up the grasshopper Sparrow would fly up and chase the former until it dropped into the vegetation. When the Grasshopper Sparrow perched on a blind placed five feet from the Henslow's Sparrow nest, the brooding female remained quiet and the male did not bring food.

Cowbird parasitism

Because of the limited number of Henslow's Sparrow nests that have been found, the incidence of parasitism by the Brown-headed Cowbird, Molothrus ater, is difficult to evaluate. Friedmann (1963) found little to indicate that Henslow's Sparrows are regularly parasitized by cowbirds.

In the present study parasitism was discovered only at the Fort Custer nest. The nest contained two eggs of the cowbird and two of the Henslow's Sparrow. All hatched, but on the sixth day of the nestling period the two Henslow's Sparrow nestlings were found dead two and three feet northeast of the nest. Both appeared to have died shortly before discovery. One of the two cowbird nestlings still in the nest was also dead. It weighed 15.4 grams and appeared to be the same size as the live one; it also appeared not to have been dead long. The two sparrows weighed 5.3 and 6.5 grams. Their size compared with others

of the same age weighed by Hyde (9 gm; 1939) is probably the result of a greater proportion of the food being given to the cowbirds. The second cowbird was missing from the nest two days later; it probably did not fledge successfully.

Predators

Although Hyde (1939:51) considered the Marsh Hawk, Circus cyaneus, and possibly also the Sharp-shinned Hawk, Accipiter striatus, to be important predators of Henslow's Sparrows, almost no raptorial birds were noted in the area during this study. Because of the continuous cover of the vegetation the most important enemies were probably those living wholly or partially within the concealing grasses.

All of the following animals which were observed on the study area have been reported to eat eggs or immature birds: blue racer, Coluber constrictor; eastern hognose snake, Heterodon platyrhinos; opossum, Didelphis marsupialis; raccoon, Procyon lotor; and red fox, Vulpes fulva (Wright and Wright, 1957; Jackson, 1961).

Periodic trapping for small mammals has indicated that few are present (Richard Brewer, personal communication). Evidently the thirteen-lined ground squirrel, Citellus tridecemlineatus, is the most abundant mammal. Seeds and insects have been reported as the main food of this species but they do eat meat occasionally (Jackson, 1961). This was the only species actually observed preying upon Henslow's Sparrows. Upon arrival at

2:50 PM on the day of fledging (25 July) at nest 7 the nest contained only one bird. Three young birds that had recently left the nest were not heard until the male arrived five minutes later with food. Two young less than 10 feet from the nest called repeatedly until the male fed one and departed. At 2:59 screeching at the nest directed my attention to it. A ground squirrel was observed to pick up the bird still in the nest and carry it off through the grass. During the next 45 minutes the male brought food to the nest once and the female twice. On each occasion the adults remained at the nest for approximately 15 seconds before taking the food to one of the nearby young.

Because of their diurnal mode of life and their abundance on the area, ground squirrels may be important predators of the ground-nesting birds. In daylight when the birds are active the ground squirrels may discover nests more readily than would nocturnal predators since the latter would be searching when activity at the nests was almost nil.

# NESTING BIOLOGY

## Nest Site

As has been noted repeatedly in the literature, Henslow's Sparrow nests are difficult to locate. On numerous occasions a 100-foot rope was dragged through the field in an attempt to flush females off the nests. However, no nests were found using this technique. All nests were located more or less accidently while taking singing censuses. In each case the hen flushed off the nest when approach was within one or two feet of her concealed position. After the hen left, diligent searching was still required before the nest was located.

Although the study area appeared to have a continuous cover, clumps of grasses were discernible upon parting the vegetation. All of the nests located were at the base of these clumps. Only one of the 10 nests discovered on the study area was similar to the roofed nests described as typical by Hyde (1939). It was located in a place where the immediate vegetation was low and thin and was completely covered above by dead grasses. The Fort Custer nest which was found on a sparsely covered old field dominated by weedy perennials also had a "roof". This nest was placed on the ground adjacent to a two-foot high knapweed, Centaurea calcitrapa, which partially covered the nest. Additional cover was provided by litter from previous years and by the as-yet low green vegetation.

The remaining nests on the study area were usually resting upon the previous year's litter. They were one to several inches above the ground surface and not fastened to the standing vegetation as Hyde (1939:36) reported, but merely placed among the stems. Sutton (1959b) also observed the latter phenomenon.

## Nest

Nests were constructed of the ubiquitous grasses. Large broad brome grass leaves comprised an outer layer of the nest and the interior was lined with small, fine bluegrass stems. No green vegetation was present in the nests. The greatest diameter during incubation was approximately halfway between the top and bottom of the nest giving the nest a vase-shaped appearance. During the nestling period, however, the constricted opening at the top expanded to become the widest portion. The grasses comprising the nests were loosely woven together and, thus, as the nestlings grew the nest also expanded.

Mean outside diameter at the lip, inside diameter at the lip, overall depth and inside depth for 10 nests measured during various stages of incubation were 2.5, 1.6, 2.4 and 2.0 inches. Similar measurements in inches for three nests after four young had fledged were 3.5, 2.3, 2.8 and 2.0. Two nests removed intact from the field weighed 5.8 and 6.0 grams (air-dry).

## Clutch Size and Laying

Six nests contained five eggs, three contained four eggs or young, one nest contained only two young birds and one nest contained two eggs of the Henslow's Sparrow and two of the Brown-headed Cowbird.

Four or five eggs has been reported as a complete clutch by Harlow (1918), Hyde (1939), Sutton (1959a) and others. The Kalamazoo nesting records and those in the literature indicate no trend toward smaller clutch size as the season progresses.

The laying season probably extends from May to the first of September in southern Michigan. The earliest nest discovered was found on 28 May. It was in the second or third day of the incubation period. On 6 and 7 June hatching took place at two other nests. Assuming the incubation period to be 10 or 11 days (as Hyde, 1939, reported), the date of completion of the clutch for all three of these nests is approximately 27 May, or about one month after the first arrivals reached the breeding ground. Hyde (1939) estimated that 20-30 May is the period when first clutches are normally completed in southern Michigan.

Late August or early September appears to be the usual time of fledging of the latest broods. On 25 August a recently fledged bird (six fecal sacs were found next to the bird) was discovered and banded. A nestmate was heard nearby but its location was not determined. In addition, two young about three

or four days old disappeared from nest 10 on 19 August. Sutton (1959b) estimated the latest time of fledging for two nests in southern Michigan as 1 and 15 September.

## Multiple Nesting and Nesting Success

Male E defended four territories, successfully fledging young in the second and fourth. Based on this observation and the length of time birds were present (late May to early September) it seems possible that some birds could raise three broods in one season. Two, however, is probably normal.

In 11 nests (one from 1967) 40 eggs and six young were present when discovered. Seventeen or 37 per cent of the eggs and young fledged successfully. Six or 55 per cent of the nests fledged one or more young. Only at nest 3 was fledging 100 per cent successful. Oddly enough, this was the only nest at which the male did not participate in the care of the young. No trend of greater or lesser success was apparent as the season progressed. However, in each of two early August nests two of the four eggs failed to hatch. Three of the eggs were infertile and the embryo in the fourth died early in the period of incubation. The young are not able to fly when they leave the nest, thus losses are probably also high during this period.

## Incubation

During 59.4 hours of observation at two nests over the latter half of the incubation period, only the females

incubated. At no time were males observed near the nests. Roosting on the nest by the females was well established halfway through the incubation period. During that period two females were observed on the nest before dawn five times and after nightfall seven times. No nests were observed during the first half of the incubation period.

Percentage attentiveness at nests 3 and 5 was 72.6 and 66.5 per cent during the period prior to the hatching of the first egg (Table 9). Mean length of attentive periods at the two nests was very similar (44.59 and 42.67 minutes). Variability in length of attentive periods was also similar (standard deviations were 14.10 and 17.28).

Between hatching of the first and fifth eggs attentiveness was 72.9 and 57.4 per cent (Table 10). At nest 3 the mean attentive period decreased from 44.59 minutes before hatching to 11.56 minutes during the hatching period (Tables 9 and 10). A nearly identical drop occurred at nest 5. The length of the inattentive period decreased from 16.83 to 4.30 minutes at nest 3 and from 21.52 to 8.69 minutes at nest 5. All of the above changes in mean values of attentiveness before and during the hatching period are significantly different at the 0.001 level using Student's *t* test.

The smaller percentage attentiveness at nest 5 during the periods before and during hatching is due to the duration of the inattentive periods. In both cases the female at nest 5 spent longer periods away from the nest. The difference between

Table 9. Attentiveness at two nests of the Henslow's Sparrow during the period of incubation preceding hatching of the first egg.

| Item | Nest 3 | Nest 5 | Combined |
|---|---|---|---|
| Hours observed | 31.3 | 23.9 | 55.2 |
| Percentage attentiveness | 72.6 | 66.5 | 70.0 |
| Attentive periods | | | |
| Number | 30 | 22 | 52 |
| Range in minutes | 20.5-79 | 18.75-72 | 18.75-79 |
| Mean | 44.59 | 42.67 | 43.78 |
| Standard deviation | 14.10 | 17.38 | 16.73 |
| Standard error | 2.62 | 3.79 | 2.34 |
| Inattentive periods | | | |
| Number | 32 | 23 | 55 |
| Range in minutes | 5.75-52.75 | 9.75-35.5 | 5.75-52.75 |
| Mean | 16.83 | 21.52 | 18.79 |
| Standard deviation | 10.58 | 6.99 | 9.54 |
| Standard error | 1.90 | 1.49 | 1.29 |

Table 10. Attentiveness at two nests of the Henslow's Sparrow between hatching of the first and last eggs.

| Item | Nest 3 | Nest 5 | Combined |
|---|---|---|---|
| Hours observed | 1.1 | 3.1 | 4.2 |
| Percentage attentiveness | 72.9 | 57.4 | 62.1 |
| Attentive periods | | | |
| Number | 4 | 9 | 13 |
| Range in minutes | 6.25-25 | 2-29 | 2-29 |
| Mean | 11.56 | 11.72 | 11.67 |
| Standard deviation | 7.78 | 8.42 | 8.22 |
| Standard error | 4.49 | 2.98 | 2.37 |
| Inattentive periods | | | |
| Number | 5 | 9 | 14 |
| Range in minutes | 2-7 | 5.75-13.75 | 2-13.75 |
| Mean | 4.30 | 8.69 | 7.13 |
| Standard deviation | 1.63 | 2.36 | 2.99 |
| Standard error | 0.82 | 0.83 | 0.83 |

the mean inattentive periods at nests 3 and 5 during incubation did not, however, reach significance at the 0.05 level; during hatching the difference was significant at the 0.01 level. The standard deviation about the mean inattentive period was greater at nest 5 during both incubation and hatching.

Indications were that attentiveness and temperature were inversely related. The mean temperatures in degrees Fahrenheit during incubation and hatching were 68.5 and 60 for nest 3 (percentage attentiveness was 72.6 and 72.9 per cent) and 80.7 and 79.6 for nest 5 (percentage attentiveness was 66.5 and 57.4 per cent). Figures comparing attendance with temperature on a day-to-day basis indicated no definite pattern. The number of days when a direct relationship with temperature existed was equal to the number of days when attendance and temperature were inversely related.

A comparison of incubating attendance between the forenoon and afternoon (Table 11) indicated that temperature and attendance were inversely related and that the time of day did not influence attentiveness. At nest 3 percentage attentiveness decreased 17.3 per cent in the afternoon while the average temperature increased 6.4 degrees Fahrenheit. At nest 5 temperature and attentiveness remained virtually constant from morning to afternoon.

Table 11. Incubation at two nests of the Henslow's Sparrow before and after noon during the final six days of the incubation period. Time is recorded in hours and temperature in degrees Fahrenheit.

| Item | Forenoon | Afternoon |
|---|---|---|
| Nest 3 | | |
| Percentage attentiveness | 81.4 | 64.1 |
| Number of attentive periods | 10 | 20 |
| Mean attentive period | 49.5 | 42.2 |
| Mean inattentive period | 11.3 | 23.6 |
| Total observation time | 9.6 | 21.1 |
| Mean temperature | 65.4 | 71.8 |
| Nest 5 | | |
| Percentage attentiveness | 66.9 | 67.1 |
| Number of attentive periods | 6 | 16 |
| Mean attentive period | 53.5 | 38.6 |
| Mean inattentive period | 26.5 | 18.9 |
| Total observation time | 8.9 | 15.0 |
| Mean temperature | 80.7 | 81.4 |
| Combined | | |
| Percentage attentiveness | 72.4 | 65.3 |
| Number of attentive periods | 16 | 36 |
| Mean attentive period | 51.0 | 40.6 |
| Mean inattentive period | 19.4 | 21.5 |
| Total observation time | 18.5 | 36.1 |
| Mean temperature | 71.1 | 76.0 |

## Brooding

Hyde (1939:39) reported that both parents brooded at one nest containing three young and one egg. Throughout almost 130 hours of observation of individually marked adults at six nests during the nestling period, the males never brooded. Frequently, however, the males remained standing on the edge of the nest or close by for several minutes after feeding. If the nest could not be directly observed, which appeared to be the case during Hyde's observations, this phenomenon could be mistakenly interpreted as "brooding".

The brooding female usually flew from the nest when the male approached, leaving the latter to feed the young. Occasionally part of the food brought by the male was passed to the female. When this happened the female fed the nestlings first. Because the males did not brood or remain at the nest very long after feeding, both adults occasionally arrived to feed at the same time. Here again, the hen fed first and waited until after the male had left to initiate brooding.

Brooding attendance generally decreased as the nestlings aged (Table 12). On five occasions at four different nests when the attendance increased above that of the previous day the mean temperature decreased (Table 12), indicating again that attendance is inversely related to temperature. The decreasing attentiveness with age was inversely related to an increase in

Table 12. Brooding attendance at six nests of the Henslow's Sparrow. Day one of the nestling period corresponds to the day on which hatching of the last egg occurred. Attentive and inattentive periods are given in minutes.

| Nest and dates | Day of nestling period | Percentage attentiveness | Mean attentive period | Mean inattentive period | Mean temperature (Fahrenheit) | Observation period (hours) |
|---|---|---|---|---|---|---|
| Nest 1 | | | | | | |
| 6/6 | 1** | 53.8 | 14.7 | 12.6 | 66.1 | 6.1 |
| 6/7 | 2* | 58.5 | 17.2 | 12.2 | 58.0 | 5.9 |
| Nest 3 | | | | | | |
| 6/14 | 1 | 65.9 | 11.0 | 5.7 | 66.2 | 9.9 |
| 6/15 | 2* | 48.3 | 5.7 | 6.1 | 60.6 | 6.1 |
| 6/16 | 3** | 43.1 | 8.8 | 11.6 | 62.5 | 2.6 |
| 6/17 | 4* | 35.2 | 11.8 | 21.7 | 57.3 | 6.1 |
| Nest 5 | | | | | | |
| 6/28 | 1** | 51.2 | 8.4 | 8.0 | 75.3 | 1.9 |
| 6/29 | 2* | 54.0 | 12.7 | 10.8 | 67.8 | 4.9 |
| 6/30 | 3 | 31.4 | 8.6 | 18.8 | 77.9 | 10.4 |
| Nest 6 | | | | | | |
| 7/6 | 1** | 33.1 | 5.2 | 10.5 | 83.7 | 3.8 |
| 7/7 | 2** | 24.5 | 7.0 | 21.6 | 80.4 | 6.3 |

Table 12. continued

| Nest and dates | Day of nestling period | Percentage attentiveness | Mean attentive period | Mean inattentive period | Mean temperature (Fahrenheit) | Observation period (hours) |
|---|---|---|---|---|---|---|
| Nest 8 | | | | | | |
| 8/1 | 6 | 34.1 | 9.3 | 18.0 | 72.7 | 12.1 |
| 8/2 | 7 | 23.2 | 6.1 | 20.2 | 79.2 | 9.7 |
| 8/3 | 8 | 29.6 | 9.7 | 23.1 | 59.3 | 4.2 |
| 8/4 | 9* | 18.1 | 5.4 | 24.5 | 61.3 | 5.9 |
| Nest 9 | | | | | | |
| 8/7 | 4 | 36.8 | 11.4 | 19.6 | 79.9 | 8.3 |
| 8/9 | 6* | 51.1 | 16.8 | 16.1 | 67.4 | 7.1 |
| 8/10 | 7* | 56.1 | 16.9 | 13.2 | 64.2 | 5.2 |
| 8/11 | 8 | 49.5 | 14.6 | 14.9 | 64.4 | 8.6 |
| 8/12 | 9* | 44.8 | 15.0 | 18.5 | 59.7 | 4.5 |

* Represents data collected in the morning only
** Represents data collected in the afternoon only

the length of the inattentive period with age. Possibly more time was spent foraging to collect a larger amount of food as the nestlings increased in size.

The number of days of the nestling period on which the young were brooded varied from nest to nest. Daytime brooding was terminated by the third day at nest 6, by the fifth day at nest 3 and by the fourth or fifth day at nest 5. Overnight brooding was last recorded on the sixth day at nest 5 but continued through the nestling period at nest 3.

At nests 8 and 9 daytime brooding was observed throughout the latter half of the nestling period, even on the day when the young fledged (Table 12). This difference in behavior from the earlier nests may have been caused by the presence of two unhatched eggs in each nest throughout the nestling stage. These were the only nests in which eggs were present during the nestling period. These observations indicate that attentiveness during the hatching period is more dependent on the presence of eggs than on the presence of young.

A comparison of forenoon and afternoon brooding behavior was possible for seven days at four different nests (Table 13). In all cases, an inverse relationship existed between percentage attentiveness and temperature. Temperature increased each afternoon while attentiveness decreased. In the afternoon of each day the length of the mean attentive period decreased and with one exception, the length of the mean inattentive period increased.

Table 13. Brooding attendance at four nests of the Henslow's Sparrow in the forenoon and afternoon.

| Nest and dates | Percentage attentiveness AM | PM | Mean attentive period (minutes) AM | PM | Mean inattentive period (minutes) AM | PM | Mean temperature (Fahrenheit) AM | PM | Observation period (hours) |
|---|---|---|---|---|---|---|---|---|---|
| Nest 3 | | | | | | | | | |
| 6/14 | 75.0 | 57.1 | 13.5 | 8.9 | 4.5 | 6.7 | 62.1 | 67.5 | 9.9 |
| Nest 5 | | | | | | | | | |
| 6/30 | 30.6 | 32.9 | 9.6 | 6.9 | 21.8 | 14.1 | 71.7 | 88.0 | 10.4 |
| Nest 8 | | | | | | | | | |
| 8/1 | 60.1 | 21.2 | 11.0 | 7.5 | 7.3 | 27.9 | 64.9 | 76.7 | 12.1 |
| 8/2 | 41.6 | 19.5 | 10.4 | 5.2 | 14.6 | 21.5 | 72.5 | 80.0 | 9.7 |
| 8/3 | 48.5 | 14.9 | 12.9 | 5.7 | 13.7 | 32.6 | 56.7 | 65.0 | 4.2 |
| Nest 9 | | | | | | | | | |
| 8/7 | 39.5 | 35.1 | 11.9 | 11.1 | 18.2 | 20.5 | 78.0 | 80.1 | 8.3 |
| 8/11 | 49.8 | 48.0 | 14.7 | 14.4 | 14.8 | 15.6 | 62.9 | 66.3 | 8.6 |
| Combined | 49.3 | 32.7 | 12.0 | 8.5 | 13.6 | 19.8 | 67.0 | 74.8 | 63.2 |

Despite the inverse relationship between temperature and attentiveness it is not clear whether temperature or time of day was more important in causing the decline of attentiveness in the afternoon.

## Hatching

Hatching was observed at nests 3, 5 and 6. Each nest contained five eggs. The time between hatching of the first and fifth egg was quite variable. Hatching at nest 3, on 13 and 14 June, took less than 13 hours, 36.5 minutes but more than 11 hours, 0.5 minutes. Less than 3 hours, 44 minutes but more than 3 hours, 19 minutes was required to complete hatching of the eggs in nest 5 on 28 June. The longest period required for hatching may have extended over a period of four calendar days (less than 64 hours, 45 minutes, but more than 46 hours, 30 minutes at nest 6). One clutch of four observed by Hyde (1939) required less than 28 hours, 40 minutes, but more than 23 hours, 50 minutes to complete hatching.

Seven eggs, five from nest 5, hatched in the afternoon (12 noon to nightfall). Three eggs hatched in the forenoon (dawn to 12 noon), and one egg hatched overnight. Hatching time in Hyde's (1939) study is evident for only one nest. Of four eggs, two hatched in each the forenoon and afternoon.

In hatching, the eggs were cut latitudinally. The larger end of the egg which made up about two-thirds of the shell was pushed up by the young, exposing it to the world. Since the

lower portion of the shell was rather small, little movement was necessary for the chick to escape its confines. In some cases the hen may have pulled the remaining portion of the shell from beneath the newly hatched chick.

All eggshells were probably eaten. None were found near the nests. Six young hatched in the author's presence and all of the six eggshells were eaten by the female. The hen cut around the edge of the broken shell much as one would peel an orange hemisphere with a knife, eating the "peeled" portion as she went. Unhatched eggs were left in the nest.

Males were not observed at or near the nest during the hatching period.

Complete eggshells taken from a recently hatched chick, an infertile egg, and an egg in which the embryo had died, had a mean weight of 0.11 grams when oven dried at 105 degrees Centigrade. For a clutch of five eggs this would correspond to 0.55 grams or 4.1 per cent of a female's total body weight, 13.13 grams (Hyde, 1939). Laying of eggs probably taxes the mineral resources of the female, especially in multiple nesting species. Eggshells may provide an immediate and large source of minerals necessary for egg production in subsequent nests with a minimum of expended energy on the part of the female. Eating of eggshells from the final clutch could hasten preparations prior to fall migration.

## First Feeding of the Young

Initiation of feeding of the young occurred soon after hatching. The first egg to hatch at nest 5 hatched between 2:30 and 2:55 PM on 28 June. The female flew off to forage at 3:09. At 3:10 the chick begged when the observer parted the grass around the nest. At 3:17 the female fed "caterpillars" to the new arrival. However, this may not have been the first feeding.

The remaining young hatched at 3:25, 3:54, 4:46.5 and 6:14 PM. Nine foraging trips and feeding periods were counted between 2:55 and the hatching of the fifth egg.

At 6:13 the female flew north twittering. The remaining egg could be seen moving so the nest was approached to observe the chick hatch. After the chick completed the process of hatching both pieces of the shell were removed. When the hen returned at 6:27 with two or three leafhoppers, all five chicks begged for food.

There was no indication that the female "missed" the eggshell that had been removed.

## Food of the Nestlings

Food of the nestlings was determined by direct observation of feedings from blinds five feet from the nests followed by a comparison with food items in a reference collection. Thus, only a general idea of the food fed to the nestlings was

obtained. Larval forms of Lepidopterans and scarab beetles were given to the young on 44 per cent of the feeding trips (Table 14). Other important orders and the percentage of the total were Orthoptera (17 per cent), Homoptera (5.4 per cent), and Hemiptera (5.4 per cent). Leafhoppers (Cicadellidae) and assasin bugs (Reduviidae) were both small and probably formed a large part of the "small unidentified" food. All of the brome grass florets were fed by the female at nest 3 to nestlings one and two days old. During 17 hours of observation on 14 and 15 June, 82 feeding trips were made by the female at nest 3. On 40 trips brome grass florets were fed. On 31 trips the food was within her bill and thus unidentifiable, but some of the unknowns may have also been grass florets. Larvae were fed on eight other trips and adult insects on three trips. Five days later, on 20 June, the brome grass in the field began blooming. Small insects and larvae were the major food items fed to nestlings less than three days old. Thereafter there appeared to be little discrimination in the selection of size of the food by the adults. Although Orthopterans were fed throughout the nestling period, most were fed during the three days prior to fledging. Typically, the hind legs of grasshoppers and crickets and the forelegs of mantids were missing when these items were given to the young birds. Large insects such as grasshoppers and crickets were usually brought to the nest one at a time. Smaller items including larvae, leafhoppers, grass florets, etc. were normally brought several at a time and fed to more

Table 14. Food of Henslow's Sparrow nestlings at six nests.

| Classification | Number of times each item was fed |
|---|---|
| Insecta | |
| Lepidoptera | |
| Unidentified adults | 33 |
| Unidentified larvae* | 36 |
| Noctuidae* | 28 |
| Pyralidae* | 577 |
| Orthoptera | |
| Gryllidae | 80 |
| Mantidae | 61 |
| Locustidae | 96 |
| Tettigoniidae | 41 |
| Homoptera | |
| Cicadellidae | 88 |
| Hemiptera | |
| Reduviidae | 89 |
| Coleoptera | |
| Scarabeidae* | 78 |
| Elateridae | 3 |
| Lampetridae | 2 |
| Hymenoptera, Neuroptera and Odonata | 9 |
| Arachnida | |
| Araneae | 15 |
| Phalangida | 1 |
| Brome grass florets | 40 |
| Unidentified small "insects" | 351 |
| Unidentified abdomens | 15 |
| Total | 1643 |

* Larvae

than one nestling.

Feeding rates were analyzed for four nests containing four or five young, for one nest of five young (nest 3) at which only the female fed, and for two nests which contained two young and two eggs through the nestling period (Table 15). Average feeding rate per nestling increased with age except for the two-young broods where a decrease in feeding rate occurred on the ninth and last day. The average for the two-young broods for the last day was based on data collected between 5 AM and noon. Nestlings at nests with only two young appeared to receive more food than counterparts in nests of four or five young during the latter half of the nestling period (except for day nine).

The female was the only adult which cared for the young at nest 3. Nevertheless the feeding rate at that nest was approximately the same as that of broods of a similar size where the males also fed the young.

During the latter half of the nestling period, males made about half of the feeding trips. Variability of feeding by males in the early portion of the nestling period was due to the variation in the initiation of feeding. At nest 6 the male began feeding young on the first day, but at nests 5, 1 and 9 the males did not begin feeding young until the second, third and fourth days respectively. At the two nests which contained eggs which did not hatch, there was no indication of increased feeding on the part of the males despite the maintenance of

Table 15. Feeding rates of Henslow's Sparrow nestlings at seven nests. Percentage of feedings by the males are in parentheses. Only the female fed the young at nest 3. Day one of the nestling period was the day on which hatching of the last egg occurred.

| Day of the nestling period | Hours observed | | | Feedings per nestling per hour | | |
|---|---|---|---|---|---|---|
| | Four nests of four or five young | Nest 3 (five young) | Two nests of two young | Four nests of four or five young | Nest 3 (five young) | Two nests of two young |
| 1 | 8.9 | 10.1 | - | 0.99 (23) | 0.91 | - |
| 2 | 17.7 | 6.1 | - | 1.35 (40) | 1.25 | - |
| 3 | 22.2 | 2.3 | 7.0 | 1.34 (37) | 1.91 | 1.29 (0) |
| 4 | - | 6.2 | 2.3 | - | 1.52 | 1.74 (13) |
| 5 | 1.1 | 3.3 | - | 2.27 (60) | 1.39 | - |
| 6 | 13.2 | - | 17.8 | 1.60 (47) | - | 3.05 (50) |
| 7 | 15.6 | 9.1 | 14.3 | 2.00 (33) | 1.82 | 3.39 (46) |
| 8 | 17.4 | 4.2 | 17.1 | 2.22 (61) | 3.33 | 3.40 (54) |
| 9 | 10.3 | - | 12.7 | 3.27 (48) | - | 2.63 (54) |

incubation through the nestling period by the females.

## Nest Sanitation

At all nests where both parents fed, both disposed of the fecal sacs of the young. After each feeding an adult would remain standing on the rim of the nest and, if a nestling raised its posterior and started to defecate the adult would take the fecal sac and either eat it or carry it away. If no fecal sac was forthcoming the adult would remain for 30 seconds to one minute before flying off, or in the case of females, begin brooding. In almost all cases only one fecal sac was removed at a time. On those occasions when two fecal sacs were produced after a feeding, the parent ate the first one and carried the second away. A high percentage of fecal sacs were eaten during the first days of the nestling period. Thereafter, the percentage of those carried away from the nest gradually increased (Table 16).

Fouling of the nests was not observed. At nest 7 where the young left the nest between noon and 3 PM (25 July), fecal sacs were produced and carried away by both adults until 5:30 PM. At 6:24 PM one of the young birds was no longer producing fecal sacs. However, at nest 11 one young bird was discovered out of the nest on 25 August standing near six fecal sacs.

The rate of production of fecal sacs generally increased with age of the nestlings (Table 16) and was directly related to feeding rates (Table 15). At the two nests with only two

Table 16. Fecal sac production at seven nests of the Henslow's Sparrow. Total hours are the same as those for feeding rates (Table 15). Day one of the nestling period was the day on which hatching of the last egg occurred.

| Day of the nestling period | Five nests of four or five young | | | Two nests of two young | | |
|---|---|---|---|---|---|---|
| | Total sacs produced | Per cent of sacs eaten | Sacs per nestling per hour | Total sacs produced | Per cent of sacs eaten | Sacs per nestling per hour |
| 1 | 13 | 100 | 0.14 | - | - | - |
| 2 | 16 | 56 | 0.14 | - | - | - |
| 3 | 42 | 67 | 0.66 | 9 | 44 | 0.65 |
| 4 | 5 | 20 | 1.24 | 3 | 33 | 0.65 |
| 5 | 5 | 20 | 0.25 | - | - | - |
| 6 | 25 | 8 | 0.47 | 35 | 6 | 0.99 |
| 7 | 66 | 3 | 0.69 | 38 | 0 | 1.33 |
| 8 | 63 | 0 | 0.72 | 41 | 2 | 1.20 |
| 9 | 32 | 0 | 0.75 | 21 | 14 | 0.83 |

young, fecal sacs were produced at a faster rate than at nests of four and five young. The drop in the rate of fecal sac production on day nine at the two-young nests corresponded to a decrease in the feeding rate.

## Behavior of Parents After Loss of Young

On the evening of the third day the female at nest 6 began overnight roosting at 8:34 PM, 14 minutes past sunset. Observations were discontinued at 8:45 with the female still on the nest. The next morning the blind was entered at 4:30 AM, 43 minutes before sunrise. The female remained on the nest until 4:53 AM. At that time she stood on the rim and probed into the nest for about 30 seconds. Soon the male arrived with food and the female flew off to forage. The male remained at the nest for three minutes apparently searching for the young which had disappeared overnight. At 4:58 the female returned with food but soon ate it and began "brooding". After four minutes of sitting she stood on the rim of the nest and began probing in the bottom of the nest. Between 5 and 6 AM the female alternately "brooded" and probed into the nest five times and made two foraging trips. Several minutes after each arrival with food she finally ate it. The male brought food to the nest only once during that hour.

At 6:18 AM a Short-billed Marsh Wren flew to a point about five yards northwest of the nest. Immediately the sparrows from nest 6 chased it. One of the Henslow's Sparrows hovered over

the marsh wren for about 30 seconds before dropping into the grass. Within the next six minutes the marsh wren flew up from the grass three times and on each occasion both of the Henslow's Sparrows chased it. One of the sparrows made physical contact with the wren on two occasions before the latter retreated into the vegetation. The wren was not observed again after 6:24 AM.

Between 6:30 and 7 AM the male sang continually at a rate of 12 to 14 songs per minute.

## Daily Cycle

The daily duration of song of the males was calculated from Table 3 beginning with their first regular singing in the morning and ending with their last regular singing in the evening. Duration of daily song was 15 hours, 30 minutes on 10-11 May; 16 hours, 3 minutes on 26-27 May; 15 hours, 54 minutes on 18 July; and 14 hours, 47 minutes on 15-16 August. In each case the duration of song was directly related to and varied six minutes or less from being one hour longer than the period from sunrise to sunset. The time of initiation of song was latest on those days with the highest percentage of cloud cover (Table 17). Time of ending of song was fairly constant in relation to sunset through the year. The earliest ending of song occurred on 18 July when there was a continuous cloud cover.

Incubating and brooding females showed no significant difference in the beginning and ending of overnight roosting on

Table 17. Initiation and ending of regular song.

| | 10-11 May | 26-27 May | 18 July | 15-16 August |
|---|---|---|---|---|
| Initiation of song (minutes before sunrise) | 42 | 39 | 54 | 28 |
| Temperature (degrees Fahrenheit) | 16 | 64 | 66 | 66 |
| Cloud cover (per cent) | 0 | 85 | 10 | 90 |
| Ending of song (minutes after sunset) | 26 | 25 | 13 | 25 |
| Temperature (degrees Fahrenheit) | 36 | 50 | 67 | 63 |
| Cloud cover (per cent) | 75 | 20 | 100 | 0 |

the nest. On 15 of 22 occasions females left the nest prior to sunrise, but unusually late departures on three rainy days moved the average to five minutes past sunrise. On only four of 26 occasions did females begin overnight roosting on the nest prior to sunset. Average time of initiation of overnight roosting was 12 minutes past sunset.

Late morning and early evening roosting by females was directly related to higher temperatures and a high percentage of cloud cover (Table 18). The small difference in temperature and the large difference in cloud cover percentages suggests that the latter was more important in regulating the beginning and ending of a female's day as was true for the males.

Table 18. Ending and beginning of overnight roosting on the nest by nine females. Numbers in parentheses are total observations.

| | Morning | | Evening | |
|---|---|---|---|---|
| | Temperature in degrees Fahrenheit | Per cent cloud cover | Temperature in degrees Fahrenheit | Per cent cloud cover |
| Before sunrise or sunset | 53.4 (15) | 28.3 | 64.7 (4) | 80.0 |
| After sunrise or sunset | 58.0 (7) | 60.7 | 61.6 (22) | 29.2 |

## SUMMARY

Studies during the 1966 breeding season have yielded information on the ecology of Henslow's Sparrow, a rare and little known bird. This species breeds in the northeastern quarter of the United States and southern Ontario, Canada, and appears to be extending its breeding range north and south. The breeding habitat is varied, ranging from swamps and marshes to hayfields and tall grass prairies. A dense vegetative cover seems to be an important requisite in the habitat of this species. The presence of litter also appears to be important in habitat selection inasmuch as fields that are regularly mowed are usually not inhabited by Henslow's Sparrows.

The first Henslow's Sparrows arrive in southern Michigan in late April and final departure of residents occurs during the latter half of September. Some birds, which may be migrants from further north, are present in southern Michigan through October.

Territories were established and maintained exclusively by song. Many territories (any area defended by song) were surrounded by areas where neither male sang. The average distance between singing males was 216 feet and the average distance between adjacent territories was 81 feet. During the height of the breeding season 60 per cent of the suitable habitat remained unoccupied.

The Henslow's Sparrow population at Kalamazoo was somewhat unstable. About half of the males present shifted territories one or more times during the course of the breeding season. The number of males defending territories ranged from six during the first half of May (20 per 100 acres), to 15 during the first half of July (50 per 100 acres), to three during the first half of September (10 per 100 acres). The mean density from 26 records in the literature was 23 singing males per 100 acres.

The average size of all territories was 0.82 acres. During the height of the breeding season (1-16 July) territory size averaged 0.84 acres. Territories were smaller on the north portion of the study area which also had the tallest and densest vegetation. Although territories were smaller on the area where the vegetation was the most dense (and probably had the highest insect population), the adults from larger territories tended to forage within their territory more than adults with smaller territories. This suggests that an inverse relationship between food supply and territory size does not neccessarily mean that territory size may be adjusted according to the food supply.

During the nestling period males and females tended to forage in different areas. Additionally, males flew further away from the nest than did females, and both foraged in the immediate area of the nest only to a limited extent. Although the defended territory did provide food during the nestling period it appeared that half of the food fed to nestlings was

captured outside of the male's singing territory.

Henslow's Sparrows appeared to be subordinate in status to Red-winged Blackbirds, Bobolinks and Grasshopper Sparrows, but not to the Short-billed Marsh Wren.

Parasitism by the Brown-headed Cowbird was very limited. The amount of predation was unknown but believed to be limited mainly to mammals and snakes.

Nests were built of dead grasses, and were placed in the center of clumps of vegetation. Clutch size was four or five eggs. No seasonable variation in clutch size was apparent. Thirty-seven per cent of the eggs and young discovered were successfully fledged.

Incubation was performed exclusively by the female. Of the two nests studied, attentiveness was greater at the chronologically later one during which the average temperature was lower. Percentage attentiveness averaged 70 per cent for both nests. Attentive periods averaged about 44 minutes and inattentive periods averaged about 19 minutes at both nests. During the hatching interval percentage attentiveness and the mean length of the attentive and inattentive periods decreased. Temperature and attentiveness appeared to be inversely related.

Only the females brooded the young. At all nests attentiveness during the brooding period decreased as the nestlings aged. Brooding was terminated by the fifth day at all nests except those in which unhatched eggs were present. At two nests where two of the four eggs did not hatch, brooding was

continued until the young left the nest. As was true during the incubation period, brooding attendance and temperature were inversely related.

Food of the nestlings was primarily insects. Larval forms of Lepidopterans and scarab beetles were fed the greatest number of times. The only vegetative matter fed to the nestlings was brome grass florets which were given to one and two-day old nestlings at nest 3.

Average feeding rate per nestling increased with age except for two nests of two young where a decrease occurred on the day of fledging. At one nest of five young where only the female fed, the nestlings received approximately the same amount of food as nestlings in broods of four or five young where both parents fed. At two nests of two young the nestlings received more food than did counterparts in nests with larger broods. Initiation of feeding by the males varied from day one to day four. Males made about 50 per cent of the feeding trips during the second half of the nestling period.

All fecal sacs were removed. During the first days of the nestling period most of the fecal sacs were eaten but as the nestlings aged, the number of fecal sacs carried away increased. Fecal sac production corresponded directly to feeding rate.

Daily duration of song by the males was directly related to, but one hour longer than, the period from sunrise to sunset. In general, incubating and brooding females first left the nest several minutes prior to sunrise and began overnight

brooding several minutes after sunset. Cloud cover appeared to be important in influencing the beginning and ending of the active day for both males and females.

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