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Territory and Mating System in the Bobolink, *Dolichonyx Oryzivorus*

Arlo J. Raim

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TERRITORY AND MATING SYSTEM
IN THE BOBOLINK,
DOLICHONYX ORYZIVORUS

by

Arlo J. Raim

A Thesis
Submitted to the
Faculty of The Graduate College
in partial fulfillment
of the
Degree of Master of Arts

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Arlo J. Raim

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INTRODUCTION

Mating and territorial systems in the New World avian family Icteridae are extremely diverse. Polygamy is frequent (Verner and Willson, 1966) but monogamy (Ficken, 1963) and promiscuity (Selander and Giller, 1961) also occur. Territories may be Type A (i.e., those encompassing mating, nesting, and feeding; Nice, 1941) or Type B (in which some or all food is gathered outside the territory), with considerable variation in the size of the territory and the proportion of the diet it supplies (Lanyon, 1956, 1957; Willson, 1966; Orians, 1961). Females of several species are known to defend territories (see Nero, 1956: 144-145). In a few species the males are said to be non-territorial (Chapman, 1928; McIlhenny, 1937).

In studies on the organization of grassland communities in southwestern Michigan (unpublished data), population sizes of Bobolinks, Dolichonyx oryzivorus, proved difficult to determine using the standard Williams spot-map method (Williams, 1936). This method uses cumulative data from periodic censuses to delimit approximate territories. The method, consequently, relies on the existence and reasonable stability of territories, conditions that are often met (Cox, 1960; Davis, 1965; Dixon, 1956; Evans, 1969; Gould, 1961; Kendeigh, 1945; Mayfield, 1960). Census data for the Bobolink, however, proved difficult to interpret.

Specifically, territories were not recognizable from census data (R. Brewer, unpublished data) because males flew about in seemingly helter-skelter fashion over the grassland in which they were evidently

resident and off it. Brewer observed groups of males flying about, showing no obvious antagonism; these groups included birds resident on the area under study but also included, at times, birds seemingly visitors from some distance. Further, numbers of males seemed to vary throughout the breeding season. Numbers of the relatively inconspicuous females also were difficult to determine.

Little published information was available on the territory and mating system in the Bobolink. Buttrick (1909) and Kendeigh (1941b) had suggested that the birds were polygynous but on rather meager evidence. Kendeigh (1941b) had further suggested that the birds either did not establish territories or else maintained them only early in the breeding cycle. It was decided to undertake a study with the basically descriptive aim of determining the territory and mating system in the species. This could be accomplished only in the context of a study of the breeding cycle of the species.

DESCRIPTION OF STUDY AREA

The study area was a strip of grassland and thicket owned by the Department of Biology of Western Michigan University. The area is located within the southwest city limits of Kalamazoo, Kalamazoo County, Michigan in the NE 1/4 of Sec. 31, T 2 S, R 11 W. A complete description is presented by Brewer, Raim, and Robins (1969).

The tract is 2600 feet long and varies from about 250 to 800 feet wide. The total acreage of the study area, estimated by the use of a planimeter, is about 41.1 acres of which about 32.9 acres consisted of grassland (Figure 1).

The gently rolling grassland varied between 920 and 940 feet above sea level. The north boundary was a steep bank dropping to a heavily traveled road. A thicketed slope (20 per cent) descended to a marsh east of the tract from line 4 northward (Figure 1). A ravine ran west to east between lines 4 and 5. A closed drainage centered at D/10.

The west edge of the tract consisted of a discontinuous double row of multiflora rose, Rosa multiflora, planted in 1961. The height was variable with the maximum about four feet. The south and east borders of the south half of the tract consisted of a fence border with black cherry, Prunus serotina; pignut hickory, Carya ovalis; sassafras, Sassafras albidum; and red oak, Quercus borealis. The main species over 1 inch dbh in the thickets were black cherry, black locust, Robinia pseudoacacia; hickory, Carya sp.; and elm, Ulmus sp. The most numerous species below 1 inch dbh was black cherry.

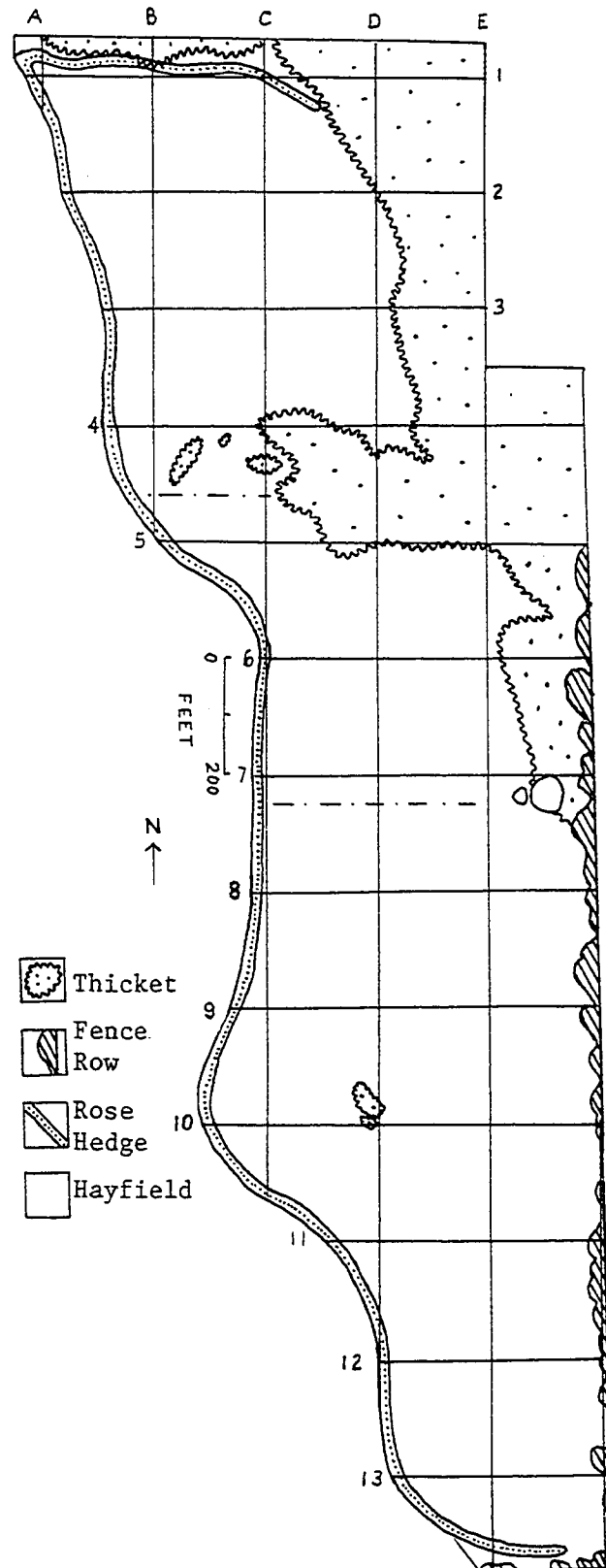


Figure 1. Map of the Colony Farm Tract, Spring 1967.

The grassland was dominated by smooth brome grass, Bromus inermis, which appeared with 100 per cent frequency in 29 square meter quadrats in 1963. Other common species were alfalfa, Medicago sativa (48 per cent); bluegrass, Poa compressa and P. pratensis (37 per cent); and quack grass, Agropyron repens (37 per cent). The most frequent forbs were Aster pilosus (18 per cent); yellow rocket, Barbarea vulgaris (15 per cent); and red clover, Trofolium pratense (15 per cent). Stem counts for the northern area in 1961 averaged 657 per square meter of which 558 were Bromus (Brewer et al., 1969).

The general height of the brome grass foliage was 45-100 cm., being lowest on the southern third with a mean of 55 cm. Middle and northern mean heights were 78 and 73 cm., respectively. Light penetration to 15 cm. above the ground indicated plant cover was most dense in the middle (19 per cent) and least dense in the south (54 per cent) with the north area intermediate (Brewer et al., 1969).

The average weight of the standing crop on the grassland for 12 randomly selected square meter quadrats taken in August of 1966 was 3043 grams. This included all above ground vegetation, both living and dead.

Most of the few (84) woody plants in the north half of the area were in the ravine area (B-C/4-5) with practically none in the flat areas. Woody plants were more numerous in the south (551) with white mulberry, black cherry, and staghorn sumac most abundant. Common elderberry was most numerous in the closed drainage.

To the northeast of the grassland were thicket and marsh. To the east of the south end (7 on south) and bordering the south was old

field habitat with considerably more woody growth than the study area. To the west of the hedge, the land was cultivated in strip crop rotation. The land immediately west of the north-south grid line A was dense alfalfa hay with yellow rocket quite numerous during the time of the study.

METHODS

The general approach employed was intensive observation on a mapped area of a population in which birds were color-marked for individual recognition. A considerable amount of time was spent attempting to apply biotelemetric techniques for the same basic purposes, especially for locating the destination of birds taking long-distance flights and for detecting the presence of birds concealed in the grass. Various technical problems prevented the gathering of any useful data by this approach and biotelemetry will not be dealt with further here.

When the study began in 1966 the Colony Farm Tract was divided by north-south, east-west grid lines 200 feet apart (Figure 1). Wooden stakes projecting 2 1/2 - 3 feet above the ground were located at each grid intersection. In early 1966 an additional grid line was added between each of the original lines making grid lines 100 feet apart with stakes at each intersection. To distinguish the various grid lines, the top two to three inches and second two to three inches of each stake were painted fluorescent colors to indicate respectively which major north-south, east-west lines crossed at each of the 200 foot intersections. Stakes not on a major grid line were painted white.

Bobolinks were captured using Japanese mist nets during 1966 and 1967. Wind blew the nets much of the time increasing their visibility and decreasing their catching ability. The usual technique for catching males was to observe their general flight paths and place the 30 x 7 feet

and 42 x 7 feet nets perpendicularly across the paths. Bobolinks appeared to become aware of the presence and location of the nets while they were being put up and avoided them. Netting was, therefore, attempted when Bobolinks were most active the first two hours in the morning (1966 and 1967) and when illumination was poorest early and late in the day (1966).

Efficiency was highest in 1967 owing to the availability of assistance in the field. Individual Bobolinks were observed to determine the area of activity and perch locations. Nets were then quickly moved to the area and the bird chased into the net. This proved successful most of the time.

After capture, all Bobolinks were banded with aluminum Fish and Wildlife Service bands, color banded, and color marked. Celluloid color bands of the colors orange, green, pink, yellow, blue and white were used alone or in combination. Male Bobolinks were marked on the end of the tail and on the rump and shoulder patches. The first Bobolinks were marked with feather dye which proved to fade rapidly. Fluorescent Hi-Vis red, green, orange, and yellow spray paint was subsequently used and lasted two or more months. The tail feathers were marked by spreading the tail as much as possible and spraying lightly. While the paint dried a thin object was run between the feathers to insure that none stuck together. If the color was not dark enough, the process was repeated. For marking the rump and shoulder patches, a piece of paper or sack with a small hole positioned over the area to be marked was used to protect the head or other feathers from stray paint. On one occasion the tail feathers of a male were

accidentally pulled out in marking. The male remained on the area defending his territory.

Female Bobolinks generally proved harder to catch than males and were generally caught later in the season when an actual nest site was known. Only the tail was marked on females so two colors were sometimes used.

Fifteen Bobolinks (7 male, 8 female) were banded in 1966 and 26 (15 male, 7 female, 4 young) in 1967. It was thought that banding in the nest might cause the young to leave too early so no attempt was made to band the young until they had left the nest. The young then proved very difficult to catch.

Except for 1966, daily visits of 1-2 hours were made during the few days prior to Bobolink arrival. In May, June and early July during 1966 and 1967 the tract was usually visited and censused during maximum territory activity from before sunrise except when netting until shortly before noon or later and again in the afternoon and evening unless weather proved too unfavorable (rain or fog). During later months and during 1968 generally only one visit was made, this usually being in early morning. In 1966, 1967 and 1968 censuses were made on 26, 31, and 29 days during May; on 22, 27, and 28 days during June; on 18, 26, and 8 days during July; and on 7, 19, and 4 days during August. During 1966 and 1967 censuses were also made on 3 and 8 days in September and 4 and 2 days in October.

Censuses were made by walking over the area and mapping the locations, movements, and actions of all the Bobolinks observed as far as was possible. A 7 x 35 binocular was used to identify marked birds up

to 600 feet or greater distances. The birds' movements were recorded on maps showing the grid lines and main vegetational features. The map scale was 1 1/4 inch per 200 feet. In 1966 a portable tape recorder was used to record observations of Bobolink behavior. During 1968 the activities and singing times of a different male was tape recorded each day at the same relative time (in relation to sunrise) for 15 minutes. With the exception of the few days in which one individual or area was watched all or much of the day, the whole area was always covered. During 1966 and 1967 a circular circuit of the area was made, reversing direction periodically to give all parts of the tract early-morning coverage. In 1968 when each territory was watched and mapped for 15 minutes each day, the order was rotated from day to day to make sure each territory would be censused an equal amount during the various time intervals. Each census lasted from one and one-half hours to over six hours with the shorter censuses usually being after netting in the morning when the Bobolinks were still quite active. The afternoon and evening censuses were usually shorter but sometimes lasted more than six hours.

On some occasions a 12-foot tower was used in censusing. More often the tower was used to watch long-distance flights and observe other activities such as the behavior of adults bringing food to young. The tower was usually located in the C/5 area of the tract (Figure 1). A magnesium 6-foot step ladder was also used on many occasions to provide an elevated site for observing individual Bobolinks.

The areas of similar habitat next to the tract on the south, east, and west of the southern part of the tract were also censused though

not always as regularly as the tract itself. Grassland areas up to a mile away were occasionally visited to find or look for marked males which had left the area.

The tall grass on the tract (waist high in northern half of tract in early June) made it difficult to observe mating and territorial activities taking place below the top third of the grass. Wary birds could move through the vegetation without being observed, and observations of nesting behavior were greatly impeded.

A rope was dragged across the tract on several occasions to find nests in June but only one nest was found using this method. The thickness of the brome grass made finding nests very difficult. The movement of female Bobolinks great distances through grass made it difficult to detect nests before hatching of young. Even then lengthy observations were often required to find the nests of wary adults. A blind was set up and feeding of the young was observed at two nests in 1966 and two nests in 1967. Much data were marred by the possibility of having disturbed the adults. The young of the late nest 9-67 were photographed and measured daily until they left the nest. The movements and behavior of the parents and young were then observed on succeeding days.

The data from censuses were compiled on individual maps summarizing the activities of each male Bobolink. These maps indicated the daily status of each Bobolink or territory. Territories were determined by mapping the song perches and fights between males. Such data from the part of any one day often did not coincide with the total area defended when watched all day. Weekly compilation of daily maps were therefore made. When weekly patterns indicated large overlap of

territories because of appearance, disappearance and shifts of males, shorter time periods were adopted to give a better view of the short-term change. The outer-most territorial observations from each week were connected by lines as done by Evans (1969) to form a polygon. The size of these polygons were determined by use of Bruning Areograph charts placed on maps of the tract on which 1 1/4 inches equaled 200 feet. The figures obtained were checked by use of a planimeter. Territories, and the males occupying them, were numbered in order of their apparent appearance each year (e.g., 6-67 was the sixth male observed showing territorial behavior on the tract in 1967).

RESULTS AND DISCUSSION

Arrival of Bobolinks

In 1966 and 1967 a male Bobolink was first observed on or adjacent to the tract on May 2 (no visits were made to the tract on the three days prior to May 2) and May 1, respectively. Three males were observed May 1, 1968. The first singing males were observed on May 2, 3, and 5 in 1966, 1967, and 1968, respectively, and singing males were commonly observed by May 4, 5, and 10, respectively. These male arrival dates are similar to the average April 30 date given by Martin (1967) for southern Wisconsin and May 1 given by Kingsbury (1933) for central New York.

The first female Bobolinks were observed May 2, 5, and 11 in 1966, 1967, and 1968, respectively, being first observed in numbers May 9, 11, and 14, respectively. The recorded difference in arrival times between male and female Bobolinks was 0-10 days. This compares with reported differences of nine days (Kingsbury, 1933), as much as a week (Bent, 1958) and seven days (Martin, 1967).

Non-singing males that did not remain in any particular area were arbitrarily considered transients as were two males marked early in 1966 and 1967 that were never observed again. Since territorial males feeding outside their territories and resident males not yet settled on a territory (Martin, 1967) might behave in a similar fashion, determinations were limited to early morning observations when territorial behavior was greatest.

The time of appearance of such apparent transient males varied. In 1966 no transient males were observed passing through the tract until May 4-6 after territorial males arrived (some transients could possibly have passed through during the three days prior to May 2 when no visits were made). In 1967 the males observed on May 1, 2, 5, 6, 7, and 8 were thought to be transients while in 1968 male Bobolinks observed May 1, 5, 7, 9, and 10 appeared to be transient males. There did not appear to be any great number of transient males passing through during the three years. Nero (1956) similarly found some resident Red-winged Blackbird males among the first arrivals.

Female Bobolinks did not sing and appeared to travel over a large area before pairing making it difficult to determine if the females were transient. Kingsbury (1933) thought transient females arrived six days or more before resident females.

Territorial Establishment

In 1966 eight territories on the tract were established in a period of about a week (Figure 2). There was then a definite break before further territories were established about ten days later. In the following two years no definite break occurred, new territories being added every few days into early June. Several males appeared on the area scattered from May 18 through June 2 in 1966, May 19 through June 7 in 1967 and as late as June 9 in 1968. Martin (1967) found a much shorter period of arrival with all sixteen of his Bobolink territories being filled between May 7 and May 15. Wiens (1969), however, observed a slow build-up through May and early June similar

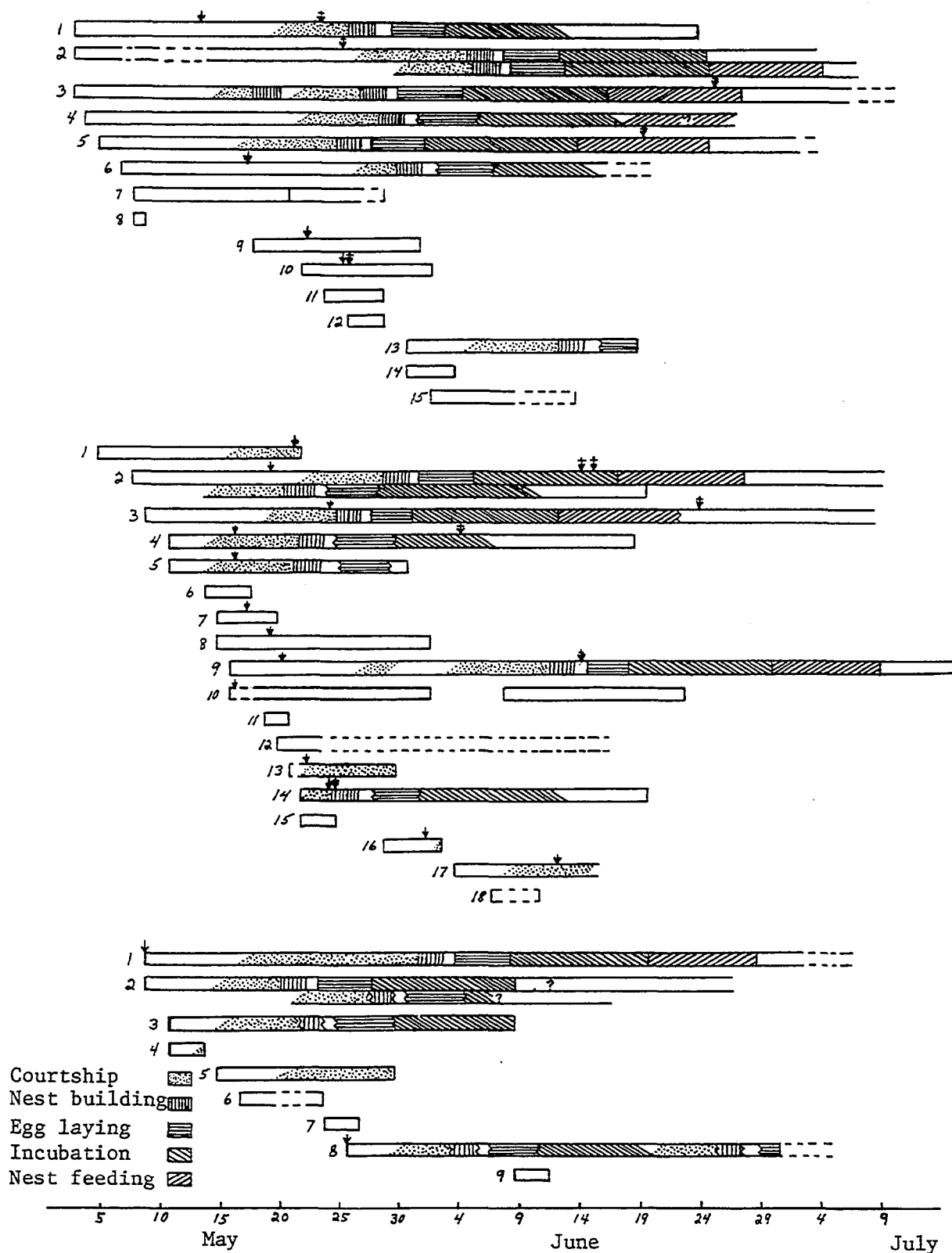


Figure 2. Territory longevity and progression of breeding cycle. (---) dashed lines indicate presence of a male in territory was in question. (---) zig-zag lines indicate time is approximate. Arrows indicate when the male (♂) or the female (♀) was marked.

to that in the present study in an area only a few kilometers from Martin's study area.

The territory establishment patterns noted could correspond either with the arrivals of the various resident males in the region or be the result of late territory establishment on the tract by males which had been in the region for a period of time. In the latter case they may have had a territory set up elsewhere which was abandoned in favor of one on the tract or may have spent more time scouting around before settling on the tract.

The first territories each year were established within six days of the first-noted arrivals. Such birds probably had not set up a territory elsewhere though this cannot be ruled out. This was probably also the case for territories 6 through 10 in 1967 (Figure 2), all started within two days of each other. Such an influx of males probably resulted from a wave of migrants arriving around May 13 or, less likely, from mass abandonment in some close-by area. No dense population of Bobolinks was known in the area, nor disruptive agricultural activities of that time which would have caused the abandonment of such a number of new territorial males. The earliness in the season, being only 9-11 days after the first territory establishment, also suggests that male Bobolinks may have been still arriving. Less certain are the later males (Figure 2) which could have been late in arriving, slow to establish territories, or birds which abandoned or had been evicted from territories elsewhere in the vicinity.

Territorial Defense

Defense of the territory was by the male Bobolink. The females did not exhibit any recognition of territory boundaries and took no part in defense of the territory or of the immediate vicinity of their nests from other Bobolinks.

Territorial defense of the male consisted mainly of song spread displays (Nero, 1956) and song flights with occasional chases and infrequent aerial fights. Part of the song spread display consisted of the primary song which contained a few whistle-like notes followed by a rolling sequence of bubbly notes. Songs varied from .01 to .14 minutes in length during the last two weeks of May, but generally were between .04 and .07 minutes (67 per cent of 171 songs picked randomly out of several thousand measured). Some males tended toward slightly longer or shorter songs than others. The interval between songs generally ranged between .14 and .20 minutes.

The display started with the male lowering his head while partially spreading his wings, lowering and spreading his tail feathers, and raising the feathers on his nape, back, and rump. The male sang his primary song as he raised his head. The interval between displays generally ranged between .14 and .20 minutes. This display was usually performed from an elevated perch position on either a stake, shrub, forb, hedge, or any object strong enough to support a perched male in an elevated position. The extent of feather spreading and raising was greatest during greatest territorial conflict. At its fullest extent the display gave greatest expression to the dorsal color pattern.

As mentioned by Martin (1967), such high intensity display usually preceded other aggressive activities. When territorial friction appeared relatively low, feathers were raised only slightly, the wings and tail only spread a small amount. The song spread display besides being used in territorial defense also appeared to function in advertisement to prospective mates. Similar song spread displays are evidently given by the Brewer's Blackbird (Williams, 1952), the Red-winged Blackbird (Nero, 1956), and the Common Grackle (Ficken, 1963).

Song flight territorial defense was also extensively used. The male made circular flights to the edge of the territory or beyond while singing once or several times usually for .08 to .20 minutes at a time. Occasionally the song continued after landing. The male sometimes flew more than 40 feet high fluttering or gliding on upward deflected wings back to the area from which he came or to another part of the territory. During early territory establishment, song was given each time the male flew within his territory.

Chase flights were initiated when a male flew into another male's territory in circle flight, passed over another male's territory, or gave song flight or song spread display in another male's territory. The territorial male then would fly, singing periodically, after the intruding male which usually flew out of the territory. The territorial male generally circled and returned to his territory. If the neighboring male was not evident in this territory or was in another part of his territory, these chase flights would sometimes extend a considerable distance over the neighboring territory.

Chase flights were of greatest intensity and frequency during territory establishment when the number of neighboring and intruding males was the greatest. Martin (1967) also noted that chase flights during territory establishment generally were much longer than later in the season. Chase flights of females also caused many territorial chase flights because of the tendency of males to all join in chasing a passing female. Such chases tended to disintegrate with several males out of their territories when the female landed. This often led to one or more males being chased back to their home territory or, at least, out of the one they were in.

Occasionally a territorial male would dive at an invading male which was perched on a shrub or stake in the diving male's territory. The invading male usually retreated from the territory. In cases in which an intruding male did not flee until closely approached by the resident male, a vigorous chase usually took place. Even in such vigorous chases contact was rarely observed.

A "trick" sound was sometimes heard during vigorous chase flights. The significance of the call was unknown. It was not certain which of the males involved gave the call, though Martin (1967) thought the note (which he rendered as a "tcheck") was given by the pursued male.

Follow flights were when one male would follow another male at a speed slower than during chase flights and without any attempt to catch the followed male. Often in follow flights the pursued male circled back into the territory from which he was previously displaced. This resulted in a series of displacement flights in which the intruding male was repeatedly followed from the territory or in which the two

males landed in a bush or in the grass. One (usually the territorial male) or both males might sing or sit quietly. Sometimes the more aggressive male hopped toward the other male which moved away with short hops. A chase or follow song flight would usually take place eventually terminating with each male returning to his territory or with the above behavior being repeated.

Occasionally vigorous fighting would result with both males flying vertically while making contact with feet and bill. Contact might be broken at any time in the vertical rise. Sometimes the combatants fluttered to the ground where they continued to fight while at other times they would make repeated vertical fight flights. After fighting, the less aggressive forms of territorial defense were generally renewed. Often two males would perch close to each other singing and preening in the grass or in a shrub without any apparent territorial antagonism only to resume the above types of territorial behavior. Such on-and-off conflict could last for hours.

Often several males were observed in a bush with one male giving extensive song display while other territorial or wandering males preened and made "chip" notes occasionally. Such behavior was also observed in the grass with one territorial male giving extensive display above other males which apparently were feeding and preening. The defense by the territorial male was not usually of great intensity and sometimes was not apparent. Members of such groups gave no evidence of any aggressiveness toward the territory holder or others in the group.

Singing and displays started from 9 to 40 minutes before sunrise, averaging about 18 minutes before sunrise (on nine occasions in May and June). Singing was heard earliest on clear days. The last song in the evening took place from about sunset to 25 minutes after sunset, averaging about seven minutes after sunset (20 days). The earliest song cessation occurred on cloudy evenings.

The displays used by the Bobolink are similar in some respects to those found in many other Icteridae (Nero, 1956; Orians, 1961). The main song spread display and song flight display mainly seemed to function in advertising to other males that a certain male controlled a certain territory. The presence of the display seems innate, with the level of the display dependent on environmental factors (Nero, 1956). Song spread display and song flight display take place in the apparent absence of other territorial males, though their intensity seems to be determined by the point in the breeding cycle and the appearance of new or intruding males. This high intensity of territorial defense during establishment is also noted in many other species (Cox, 1960; Drury, 1961; Gibb, 1956b; Kendeigh, 1945; Krebs, 1971; Schwartz and Zimmerman, 1971; Simmons, 1956; Verner, 1965; Welsh, 1971). An increased intensity of song spread display was noted by Nero (1963) when Red-winged and Yellowheaded Blackbirds were closely confronted by other highly territorial and aggressive males. This increase in intensity noticed in the Red-winged Blackbird song spread display (Nero, 1956) is considered similar to that in the Bobolink but may be more extreme. A similar display also seen in the Brown-headed Cowbird (Laskey, 1950), the Brewer's Blackbird (Williams, 1952), and the Common

Grackle (Ficken, 1963) seems to serve as a threat and secondarily to attract mates. Displays given by other species also often perform these dual functions (Hinde, 1956; Mayfield, 1960; Nice, 1941; Ken-deigh, 1941a).

The perched song spread and the song flight displays are ritualized in form but vary in intensity. The aerial fights, which only seem to be observed when a transgressing male persists in a defender's territory, appear provoked by the lack of success in the ritualized displays. The vigor of aerial fights (though difficult to quantify) seems dependent on the intensity of territorial defense and offense. Aerial fights are also recorded by Williams (1952) in the Brewer's Blackbird. In the Bobolink the occasion for aerial fights is a territorial dispute while in the Brewer's Blackbirds it is a dispute over a female.

During windy and rainy weather territorial activities and singing seemed to be curtailed with flights being less frequent.

Interspecific Interactions

Territory overlap (R. Brewer, unpublished data) indicated little if any interspecific territoriality involving Bobolinks; however, both dominance by Bobolinks of other species and dominance of Bobolinks were noted (Figure 3). Aggression toward Bobolinks was from Red-winged Blackbirds except in one case. In most interactions (47) male Bobolinks were chased by male Red-winged Blackbirds. On only two occasions were male Bobolinks noted to be chased by female Red-winged Blackbirds. Only one instance of each was noted of a male and female

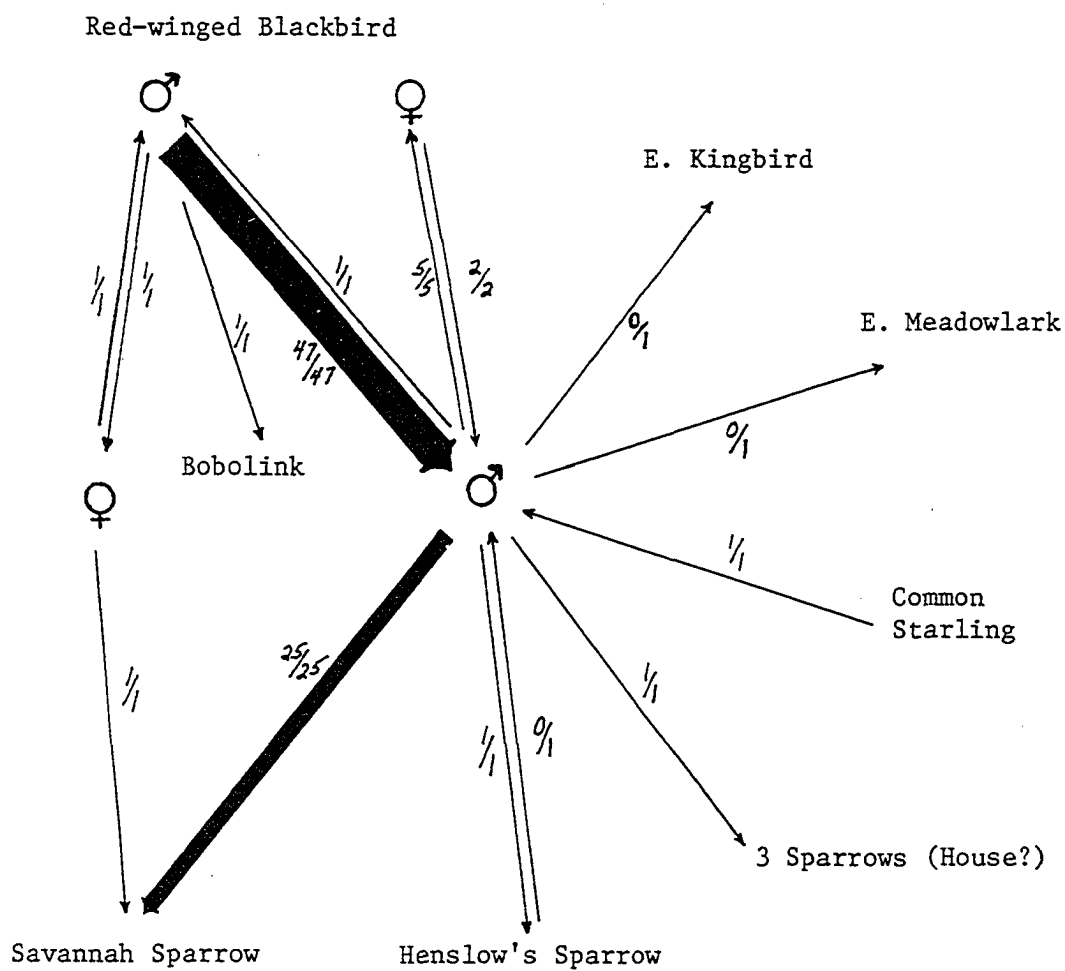


Figure 3. Frequency and direction of interspecific aggression.

Bobolink together being chased by a male Red-winged Blackbird, of a female Bobolink being chased by a male Red-winged Blackbird, and of a male Bobolink being chased by a Starling.

Bobolinks made aggressive acts toward several smaller species and under special circumstances toward larger species. A male Bobolink was successful in chasing a male Red-winged Blackbird which was close to recently fledged young Bobolinks and to a nest with young. Four and possibly five times a male Bobolink chased a female Red-winged Blackbird. The only time a female Bobolink chased a male Red-winged Blackbird was when the Red-winged Blackbird was close to the female's nest of young Bobolinks.

Savannah Sparrows were the main species chased by the Bobolinks with Henslow's Sparrows and House Sparrows occasionally being chased. A male Bobolink dived from the air at both an Eastern Meadowlark and an Eastern Kingbird but with no apparent effect.

Martin (1967) observed the Bobolink to show dominance over the same species mentioned above and a Traill's Flycatcher, a female Brown-headed Cowbird, and a Song Sparrow while on a few occasions being dominant over a female Red-winged Blackbird and once over a male. Savannah Sparrows were the most frequent recipients of male Bobolink aggression.

Females were generally not involved. Martin (1967) found Red-winged Blackbird males were most dominant to male Bobolinks. He observed no effect during single encounters with an Eastern Meadowlark, female Red-winged Blackbird, and Common Grackle.

A similar pattern was observed by Wiens (1969), except that Red-winged Blackbirds were not present so Bobolinks were the dominant nesting passerine with the Savannah Sparrow the most frequent recipient of male Bobolink aggression.

Courtship and Pairing

The first females to arrive did not appear to gain much attention from the males present. These first females may have been transients. Courtship activities were first observed when females were present in numbers several days after the beginning of male territorial behavior.

The earliest evidence of male interest in females involved chase flights. In these the male flew after any female which he came across in his or adjoining territories. The route of the chase seemed determined by the female. Sometimes the females appeared to stimulate chase flights by perching near males and giving a "zoo" note. The chases would usually end when the female landed, but were sometimes terminated by the male flying back to his territory. Sometimes a male would dive at a perched female precipitating a chase flight. The male then pursued the female around the area, often passing over several territories. Other males often joined in on the chase flights so that early in the breeding season four or more males often were observed chasing one female. Similar cases were also noted by Kingsbury (1933). Termination of group chase flights often resulted in territorial chases because males often ended up over other males' territories. The males sing more during group chases of a female than during single

chase flights. Martin (1967) felt this may be due to territorial antagonism between males.

Male chase flights of females have been observed in a number of species (Drury, 1961; Elliott, 1969; Gibb, 1956a; Von Hartman, 1956; Zimmerman, 1963). Among the icterids, sexual chasing has been observed in the Brewer's Blackbird (Williams, 1952), Brown-headed Cowbird (Friedmann, 1929), Yellow-headed Blackbird (Willson, 1966), and Red-winged Blackbird (Nero, 1956). Nero (1956) suggested this group flocking of males after a pursued female may be similar to group flocking around a predator. Curiosity may also be involved in group chase flights, as Michener and Michener (1935) suggested, it is for certain events which caused Mockingbirds to leave their territories.

Chase flights were observed occasionally throughout the breeding season though decreasing in number and duration as the season progressed. Martin (1967) suggested that the chases were longest just after pair formation and functioned in mutual stimulation of members of the local population.

While perched, males often gave a courtship display which was similar to the territorial display. This display involved the male singing while spreading wings and tail, lowering tail, bowing, and elevating back, rump, and nape feathers. The raising of feathers made the male appear much larger in body size. This display was usually performed facing the female or facing so the male's back was directed toward the female.

Also prominent in courtship were male circle flights. Circle flights usually were less than 100 feet in diameter and sometimes as

small as 10-20 feet in diameter. The male would generally land from within a few inches to a few feet of the female. In landing the male would dangle its legs and glide down, generally giving a weezing sound twice just before landing. Though this "weeze" or "rasping buzz" was given most frequently during courtship, it was heard through fledging in response to the female's presence. These circle flights occurred as frequently as two per minute, being carried on over varying periods of time. The male also upon landing often spread his wings in pre-copulatory behavior (Martin, 1967), frequently being answered by a "zoo" sound. Females were heard to emit this sound while the male was courting, chasing other females, and before copulation. Its function appeared to be the attraction of the male to which it was directed.

Observations of behavior and calls were used in determining when pair formation had occurred. Pair formation was considered to have taken place when a female returned to or stayed within a male's territory at the end of a chase. After pairing, the male and female were often seen flying together without any obvious chasing. Two calls also appeared to be heard only around paired Bobolinks. While perched, a "chu" call was given in a long series or singly by a male when his (?) female was present. When both the male and female were feeding close together on the ground (often on neutral ground west of the tract), a "tu tu tuwak" call was sometimes given by the male though its significance was unknown.

Territorial Stability and Population Size

The establishment and breakdown of territories varied from year to year (Figure 1). During the first week (beginning May 1), five territories were set up in 1966, but only one in 1967, and none in 1968. The second week showed a decrease in new territories in 1966 with only two new territories, while there were five new territories in 1967 and four in 1968 (one male returned from 1967). Three territories shifted and two disappeared. In Martin's (1967) study all males (16) arrived in about one week, between May 7 and May 15.

During the third week, 1, 5, and 2 territories were added in 1966, 1967, and 1968 with some shifting and two abandonments. The fourth week added 3 and 2 territories in 1966 and 1968, respectively. All proved to be of short duration with the exception of a returning male in 1968. During this week in 1967 one male replaced another.

In the fifth week several males disappeared (2 in 1966, 4 in 1967, 1 in 1968) with some of their areas being taken over by other males. A male in both 1966 and 1967 tried to take over a territory without apparent success.

There was little change during the sixth week. One male disappeared in 1966, one arrived in 1968 while in 1967 two arrived (one pressuring an established male and one previous tract male (10-67) returned after a six day absence to set up a new territory.

The seventh week four males left their territories. Three males left the eighth week and eight males with young abandoned their territorial activities. The last two males disappeared the ninth week.

The stability of territories varied. A few showed long-term stability of boundaries. Other territories were spatially stable but lasted only a short time. Territories which shifted either did so by changing shape or shifting the center of their activities.

Only three territories each year in 1967 and 1968 exhibited long-term stability. This contrasts with the situation reported by Martin (1967) in which most of his territories (15 of 16) were stable. Thirteen territories which lasted less than two weeks also showed little shifting. Intermediate between the above extremes were six territories of two to three weeks duration which showed little shifting after the initial days of establishment.

Factors enhancing stability probably include environmental features. Territory boundaries often fell along ravines, steep banks, rows of trees, and sharp changes in vegetation. Such natural boundaries did not seem to require defense against neighboring males except when the whole territory was threatened.

All ranges of territory shifts were observed. The largest territory shifts (the abandonment of one territory for a new location) were the most difficult to detect. A shift of this magnitude could be determined for certain only for two males (10-67, and 16-67). Male 7-67 was defending a territory on the south end of the tract when caught and marked (Figure 3). Male 10-67, when first banded and marked, did not exhibit territorial behavior but was observed feeding in bordering fields up to at least one-half mile west of the tract. Two days later 10-67 was observed showing territorial behavior on a small area bordering territory 7-67. During the succeeding two days 10-67

controlled more and 7-67 less of 7-67's original territory until 7-67 disappeared. Male 7-67 was subsequently found a quarter mile north showing no signs of territoriality. Male 10-67 remained on territory until June 1 though exhibiting a decreased level of activity and exhibiting territorial behavior over a smaller area. Male 10-67 was then not observed for the following five days, but on June 7 he was again observed holding a territory adjacent to where he was first banded but separated by several hundred feet from his first territory (Figure 4b). Male 10-67 remained on his second territory through June 22.

Another example of territory shifting is male 16-67. This male disappeared from the north area of the study tract (Figure 4b) and subsequently was found exhibiting territorial behavior at a site more than one quarter mile west of the tract. These observations suggest late arrivals on territories may have been around without setting up a territory prior to this time or may have abandoned a territory elsewhere.

It is difficult to determine how many males held territories prior to or after holding territories on the tract. Usually before abandonment, however, males were observed to travel greater distances and exhibit longer periods of absence. Movement of males to and from the area indicated that males travel over quite a wide area. Established territorial males may find more suitable areas elsewhere in which they may take up residence.

Shifting territories may particularly be seen in double-brooded birds such as the Gray Catbird where territories were found to have been

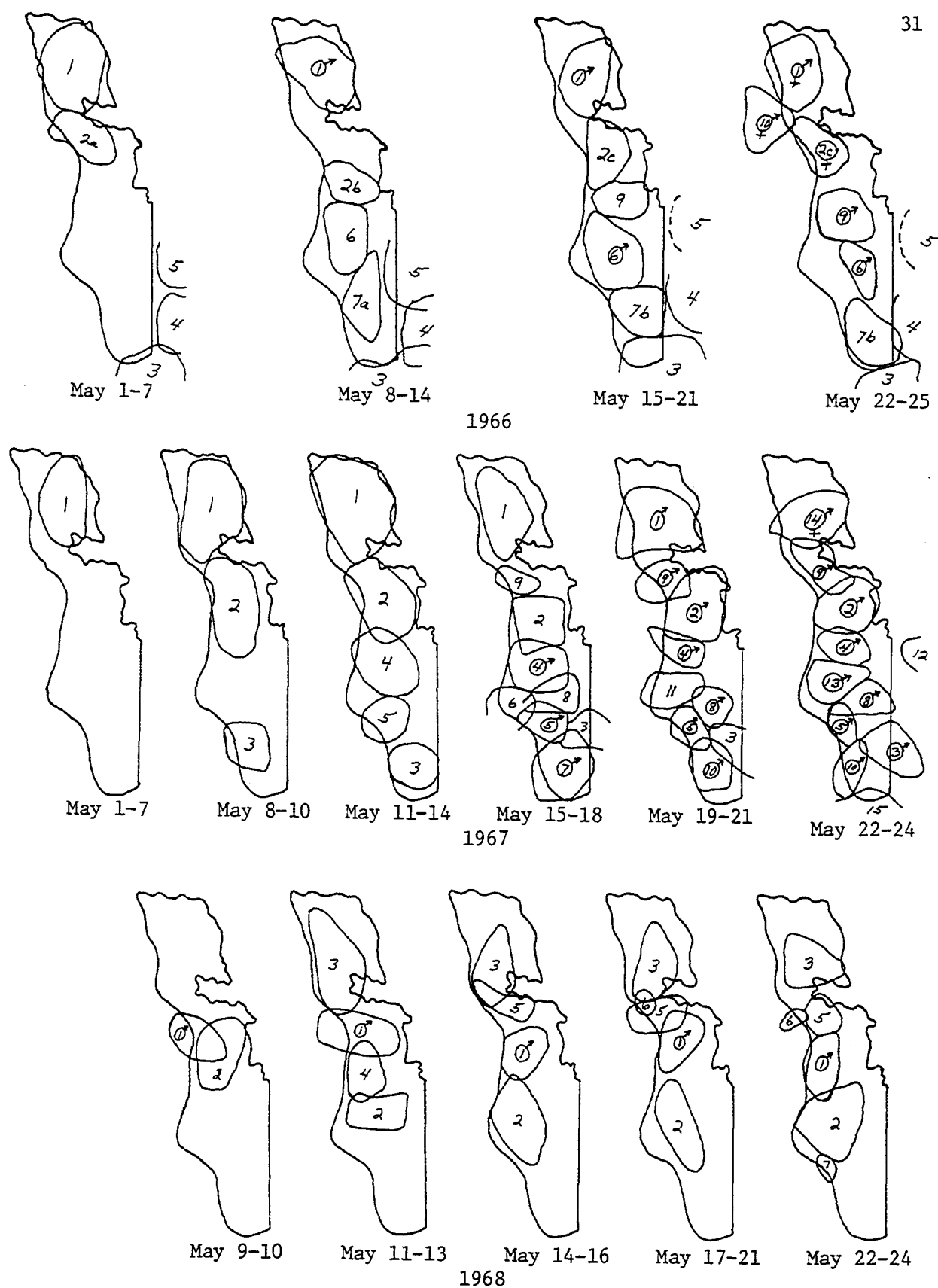


Figure 4a. Bobolink territorial activity areas (areas of territorial and non-territorial activities in territory area). Male or female symbols around numbers indicate color banded individuals. Dots indicate known nests.

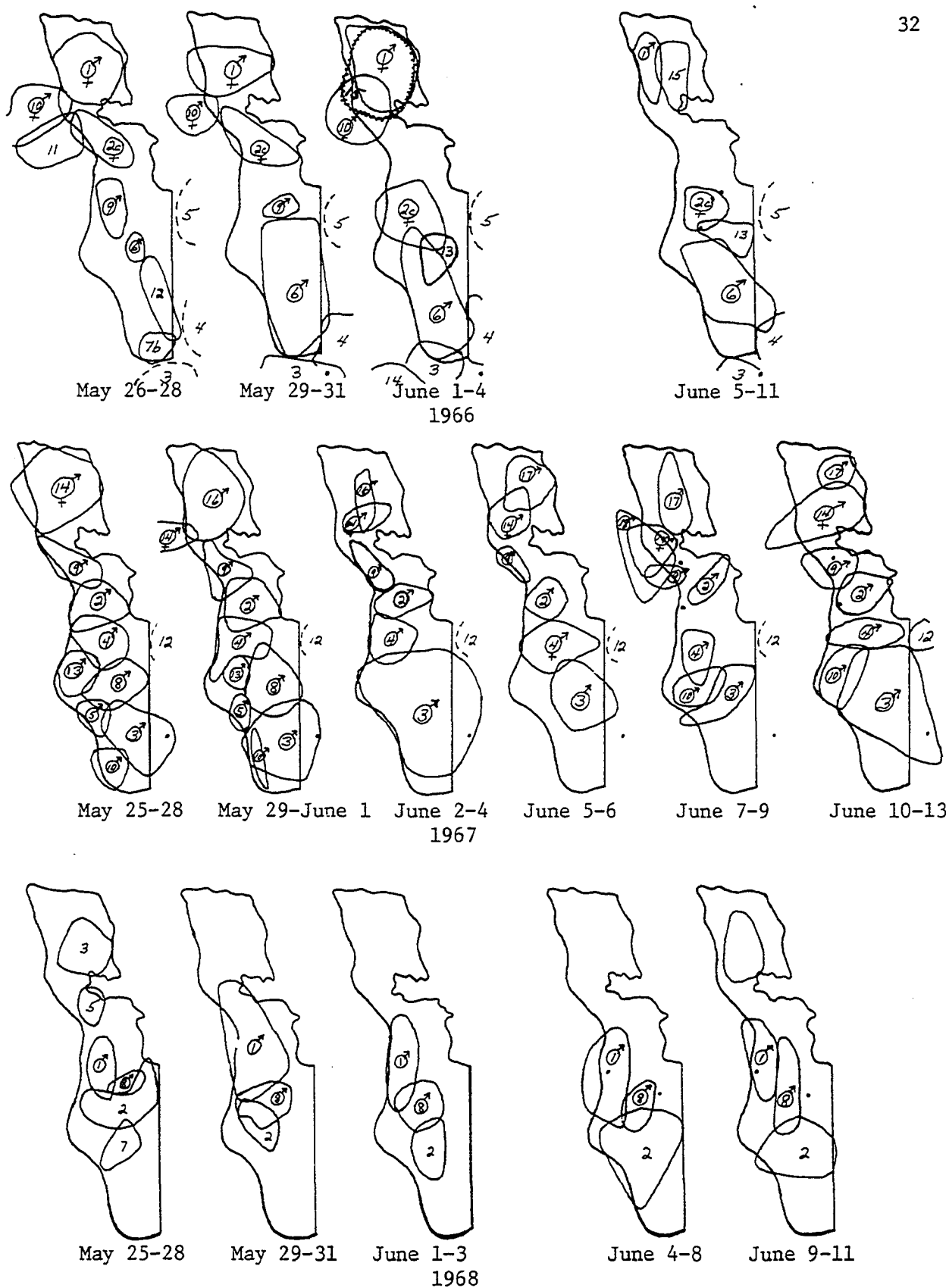


Figure 4b. Bobolink territorial activity areas (areas of territorial and non-territorial activities in territory area). Male or female symbols around numbers indicate color banded individuals. Dots indicate known nests.

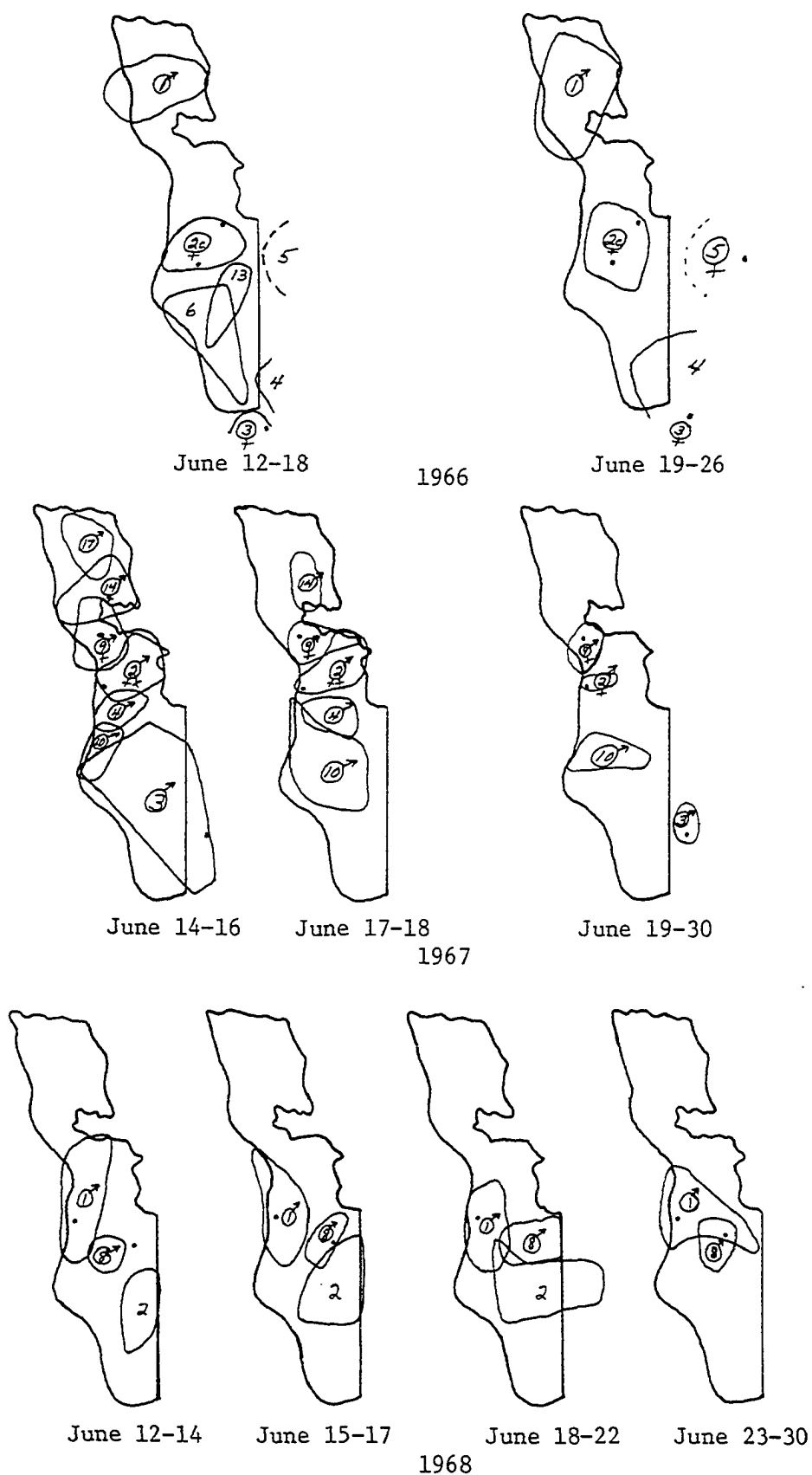


Figure 4c. Bobolink territorial activity areas (areas of territorial and non-territorial activities in territory area). Male or female symbols around numbers indicate color banded individuals. Dots indicate known nests.

set up as much as 800 meters away from earlier abandoned territories (Darley et al., 1971). Many of the abandoned territories were subsequently occupied by new males. Robins (1971) also found that shifting of territory, disappearance of singing males, and establishment of new males on the Colony Farm Tract were common among Henslow's Sparrows.

Shifts of boundaries were numerous. Three males (2-66, 6-66, and 3-67) greatly enlarged their territories by adding newly vacated areas (?) into their territories, as is often observed in Red-winged Blackbirds (Peek, 1971). In some cases (6-66 on May 31) parts of these newly acquired areas were subsequently lost to new males trying to set up territories. Such enlargement of territories happened more during the middle and last part of the breeding season when fewer males were trying to set up territories relative to those being vacated.

Five territories exhibited short-term shifts. These appeared to result from new males trying to gain all or part of a territory over a period of days before being repulsed or victorious. Such shifts are similar to other cases of territory eviction and defense with the exception of being spread over a longer period of time.

Three territories seemed to change shape as a result of pressure from neighboring males. Small shifts seem to result from low intensity territorial conflict in which the defending male, after a period of conflict, may begin ignoring the aggressive male, thereby allowing some shift of territory boundaries. Similar shifts are exhibited when new males form a territory by carving out an area between established territories. The gradual giving of ground with repeated invasion of a

neighboring male is widespread among birds (Drury, 1961; Gould, 1961; Kendeigh, 1941a; Michener and Michener, 1935; Nero, 1956; Snow, 1956; Tompa, 1964; Zimmerman, 1963). This boundary flexibility would help to stop fighting over a small area. Prolonged fighting could reduce nesting success by diverting attention from such important matters as feeding, avoidance of predators and caring for young (Ripley, 1961; Tompa, 1964). Yielding to pressure would also tend to equalize territory sizes by allowing males with small territories to enlarge them at the expense of larger territories without one male being completely driven out.

In many species in which the female does not seem to recognize territory boundaries nest locations often seem to precipitate territory shifts. In such cases the male may extend his territory boundaries to encompass the nest (Ficken, 1962; Barlow, 1962; Marler, 1956; Lanyon, 1956), often taking a part of a neighbor's territory. Though only a few successful nests were found each year in the present study, their possible effect will be considered. During most of May, male 2-66 was not in possession of the area in which his two apparent female mates (one of two marked) eventually nested in early June though his activities bordered the one nest site. A southward shift seemed to take place after the disappearance of 9-66 from the area. The territory shift may have been brought about by selection of the nest site at the edge of the territory. The second nest site, which presumably was selected about June 3, was quite remote from the pre-shifted territory. Since the nest site was within the sphere of the male's activity

from June 2 until the end of the breeding cycle, it is uncertain whether site selection stimulated boundary change or came after it. Other nests during 1966 were off the tract so sufficient data are unavailable for generalization.

Nests found in 1967 involved males whose territories were wholly or mainly on the tract. Territory 2-67 shifted somewhat during the first week but essentially encompassed the area all season in which the one nest found was located. The nest was located near the west edge of the territory. The nest of another female believed to have been in the territory was never found but was thought to have been near the center of territory 2-67.

The nests of males 3-67, 9-67, 1-68, and 8-68 (Figures 4b and 4c) were established within the area defended by the appropriate males, though on some days the males were not observed to be active in their nest areas. It appeared nests were always built within their males' territory boundaries, though the relative nest position sometimes changed due to movement of territory boundaries. Nest location did not seem to restrict territory shifts away from nests, though there was no indication a male would abandon his nest site and female. Martin (personal communication) indicated in his dense Bobolink population the nest of a female may come to lie within the territory boundaries of a neighboring male due to territory shifts.

Each year over half of the males remained on their territories less than three weeks, some remaining only a few days. In general, the earliest territories exhibited much greater tenure on the area than

did males arriving later. The reasons for abandonment probably vary with the territory. Probable causes include loss of mate, nest failure, failure to mate, eviction by an intruding male, and possibly disturbance from banding and observation.

The most frequent cause of territory abandonment was probably failure to mate. This was believed to have been the main cause of eight territories being abandoned. Other territories which were only briefly maintained appeared to be held by unmated birds, but in many cases unequivocal data were lacking. In no case did an apparently unmated male remain more than three weeks. An example of this in the present study was male 10-67 which had two territories on the tract at different times and different locations but was never observed to court or to be mated. Nearly all of the short-term territory males were believed unmated.

First-year unmated Plain Titmice males were reported by Dixon (1956) to shift residence frequently and have transitory territories. Shrikes leave their territories if they do not find a mate (Durango, 1956). If a first year American Redstart does not get a mate, it abandons its territory in two weeks or so (Ficken, 1962). Mockingbirds will desert if they fail to find a mate (Michener and Michener, 1935). Tompa (1964) found only unmated male Song Sparrows deserted their territories. Lanyon (1956) found that Meadowlarks which failed to mate did not maintain their territories. Unmated Gray Catbirds were reported to maintain territories for various lengths of time (Zimmerman, 1963) but for only part of the season (Darley et al., 1971). Kendeigh (1941a) reported some House Wrens held only temporary territories.

The second most common reason for abandonment probably is nest failure or loss of mate. Abandonment because of nest failure appeared likely in four (6-66, 4-67, 14-67, 3-68) territories and possibly in four more (1-66, 13-66, 5-67, and 5-68). (See Figure 2.) The female appeared to disappear in territories 1-66, 10-66, and 5-67 (of course, it is possible in these cases that the females left the area as a result of nest failure). Whether these males set up another territory at another site to try re-nesting is not known. In double-brooded birds, such as Gray Catbirds, most desertions were by mated birds which experienced nest failure (Darley et al., 1971) as was also true in Blackbirds (Snow, 1956). It may be that 8-68's late arrival (Figure 4) was a result of such a nest failure on another area. Abandonment of an earlier, perhaps poor, territory might increase the chance of successful nesting if a better territory were selected.

It might seem that such late establishment of a territory would not give the time necessary to complete the breeding cycle. It appeared, however, that any schedule that achieved egg laying by mid-June could be adequate (see, for example, 9-67, Figure 2 which was able to raise young successfully despite its late nest. Some of its banded young were observed a month after fledging.) The biggest handicap in late territory establishment would appear to be in obtaining a mate. Excess females earlier available would probably be mated to polygynous males leaving some males without mates. The necessity to find a new mate would be alleviated if the mated female remained with the male when he abandoned one territory for another site. Whether this happens

is unclear, but in all cases in which a territory was abandoned and both the male and female were marked, the female either disappeared first or simultaneously with the male. This was also true of Catbirds (Darley et al., 1971) and Blackbirds (Snow, 1956). The late arrival of 8-68 also indicates the possibility that 8-68 was mated upon arrival.

Males being evicted from their territories appeared to be fairly common, though possibly not as frequent as abandonment. Though the intruding male's aggressiveness is generally considered the cause of eviction, some of the factors already mentioned could also cause a male to decrease territorial defense. Several males were thought to have been evicted. Males 9-66, 4-68, and 6-68 may have been evicted or just quickly replaced after abandonment because of lack of a mate. Males 1-67 and 7-67 were believed evicted because they were known to have been involved in territorial conflicts just prior to disappearance.

The replacement of less aggressive males by more dominant males would probably lead to greater stability of the breeding population by their ability to resist the pressure of new or "floating" males. Occasionally some males, though evidently less dominant, remained by sheer persistence. This appeared to be the case with male 14-67. Males 16-67 and 17-67 tried to take over, one at a time, 14-67's territory with apparent early success. Later each male disappeared, leaving 14-67 with his territory intact. A similar situation had been observed between 1-66 and 15-66. Persistence may be of equal importance

with aggressiveness in maintaining territories (Young, 1956). Whether the disturbance of watching and searching for Bobolink nests played any part in any of the abandonments in 1966 and 1967, when most of the field work was done, is uncertain. Territorial behavior was probably only minimally affected, but some nests may have been accidentally destroyed or abandoned due to nest searching. Little or no disturbance probably took place during 1968 due to the decreased human activity on the area.

It appears there is generally a "floating" non-territorial population. This may be composed in part of some of the short-term territorial males which would spend less and less time in their territories and eventually cease to visit them. It is especially difficult in Bobolinks to make any precise estimate of the size of this segment of the population because of the long-distance feeding flights which would bring to the area distant territorial males which could not be distinguished from floating non-territorial males.

Territory Sizes and Breeding Densities

Territory sizes varied over the course of the season. To facilitate comparison with other Bobolink studies, yearly averages were computed from average sizes for the third to the fifth week. The average in 1966 was 3.4 acres (1.37 hectares), in 1967 3.4 (2.9 if territory 3-67 is omitted) acres (1.38 hectares), and in 1968 2.7 acres (1.08 hectares). (See Tables 1-3.) Densities in males per 100 acres for the three years were 14.8, 22.5, and 12.7.

Table 1

Changes in Numbers and Average Sizes of Territories in 1966

Week	Date	Number Territories	Average Territory Size	Number New Territories	Number Old Territories
May					
1	(1-7)	2	3.5	2	0
2	(8-14)	4		2	2
3	(15-21)	5	2.8	1	4
4	(22-28)	8	2.1	3	5
June					
5	(29-4)	4	5.2	1	3
6	(5-11)	5	2.0	1	4
7	(12-18)	4	1.1	0	4
8	(19-25)	2	2.1	0	2

Table 2

Changes in Numbers and Average Sizes of Territories in 1967

Week	Date	Number Territories	Average Territory Size	Number New Territories	Number Old Territories
May					
1	(1-7)	1	1.9	1	
2	(8-14)	5	3.9 (4.4)*	4	1
3	(15-21)	9	3.3 (3.3)*	4	5
4	(22-28)	9	3.0 (2.8)*	2	7
June					
5	(29-4)	6	4.0 (2.3)*	1	5
6	(5-11)	7	2.8 (2.0)*	2	5
7	(12-18)	6	5.3 (3.9)*	0	6
8	(19-25)	1	0.4	0	1

* Averages with territory 3-67 which during week 5-7 was 2-4 times as large as the next largest territory (see Appendix 3).

Table 3

Changes in Numbers and Average Sizes of Territories in 1968

Week	Date	Territories	Average Territory Size	Number New Territories	Number Old Territories
May					
2	(8-14)	4	4.2	4	
3	(15-21)	4	2.8	1	3
4	(22-28)	7	2.1	3	4
June					
5	(29-4)	3	3.1	0	3
6	(5-11)	4	3.4	1	3
7	(12-18)	3	4.1	0	3
8	(19-25)	2	2.5	0	2

Territory size (Table 4), in general, went down during the incubation phase of the nesting cycle. Some territories showed great fluctuation (Appendices 2-4). These great changes affected the averages less than might be expected because the dropping out of some of the smaller territories and increase in size of some territories off-set the decrease in other territories. In general, territories were smaller when more Bobolinks were on the tract and larger when fewer were present (Tables 1-3). When several territories were concentrated into one part of the tract, they tended to be small even though the total territories on the tract were few.

Martin (1967), using the multiple flush technique of Wiens (1969), in late May and early June determined territory size on his lush bottomland where Bobolink density was 54 males per 100 acres. Territories were small, averaging 1.1 acres (range 0.7-1.7) for 15 males.

Wiens (1969), using identical techniques on a dry, more sparsely vegetated grazed upland area a few kilometers from Martin's study area, had averages of 9.2, 5.9, and 4.9 acres for 1964, 1965, and 1966, respectively. Densities were 6.25, 11.25, and 10.0 males per 100 acres for the three years. These data suggest habitat differences may cause the differences in density on the three areas.

Martin's (1967) area was fairly wet and occasionally had standing water after rains. The main plant species were Kentucky bluegrass (Poa pratensis) in association with timothy (Phleum pratense), ticklegrass (Agrostis scabra), and redtop (A. gigantea). Meadow rue (Thalictrum dasycarpum) was the dominant forb with fleabane (Erigeron pilosus) present.

Table 4

Change in Territory Size Throughout the Breeding Season of Males
Present at Least Thirty Days

Territory	1966							
	Before Incubation				Week After start of Incubation			
	4	3	2	1	0	0	1	2
1		2.9	3.0	0.6	4.4	2.2	0.6	5.8
2	1.1	2.3	2.6	4.2	1.0	1.6	2.0	
6		1.2	4.2	8.6	7.1	1.1		
Average	1.1	2.1	3.3	4.5	4.1	1.7	1.3	5.8

Territory	1967							
	Before Incubation				Week After start of Incubation			
	4	3	2	1	0	0	1	2
2			3.9	3.9	3.0	1.6*	1.4	3.5
3			3.6	3.3	3.9	15.0	9.0	8.9
9	1.3	3.4	2.2	0.6	2.9	1.9		
14					6.7	2.2	4.7	3.0
Average	1.3	3.6	3.2	2.3	3.6	5.1	5.7	6.0

Territory	1968							
	Before Incubation				Week After start of Incubation			
	4	3	2	1	0	0	1	2
1		4.9	2.7	3.2	2.6	5.6	3.9	
2			6.5	3.4	6.7	3.4	5.8	6.0 3.0
8			0.4	2.5	2.4	0.9	2.1	
Average		4.9	3.2	3.0	3.9	3.3	3.9	6.0 3.0

* Male 3-67 was thought to have been mated to two female Bobolinks, which were thought to have started incubation a week apart.

Wiens' (1969) study area, however, was a permanent pasture of Kentucky bluegrass and timothy. Fleabane, clover (Trifolium pratense and T. repens) and dandelions (Taraxacum officinale) were the most common forbs.

Wiens (1969) found a number of subtle differences in the areas occupied by Bobolinks compared with other grassland species (Eastern and Western Meadowlark, Savannah, Grasshopper, Vesper, and Henslow's Sparrows) on the area he studied. Litter depth was deeper or equal to most other species. The mean effective height of vegetation was greater than in territories of most other species. There was slightly more unvegetated ground than in most other species. Forb coverage was comparable to that in territories of other species. This compares to Martin's (1967) study where males preferred dense accumulations of tall forbs over the sedge while females nested under the meadow rue. Martin (1967) did not observe fleabane and sparse low bluegrass to be used for foraging or nesting while wet regions also received light use.

Tester and Marshall (1961) had suggested litter depth was important with intermediate litter preferred. If such were the case, too much litter may have been present in the north part of the Colony Farm Tract and too little in the south end, much of which was burned in 1968. Martin (1967), however, found high Bobolink densities in upland alfalfa fields where there was practically no ground litter and believed Bobolinks selected sites with less than normal litter for nests. Graber and Graber (1963) also found highest densities in oat fields where little litter would be present and in ungrazed grassland which would probably have heavy litter.

Grass height differences are difficult to assess because of differences throughout the growing season. In the present study vegetation height and density was much greater (waist high in many places) in early June than on Martin's area (personal observation). Bobolinks could be observed walking on the ground and litter in Martin's area while this was impossible in the present area. Wiens (1969) indicated the vegetation was about 30 centimeters or less in height with a light penetration of 88-89 per cent 15 centimeters above the ground. No good correlation, therefore, seems possible with density or height.

Kingsbury (1933) believed Bobolinks favored fields of mixed timothy and clover with trees, bushes, or other look-out perches available and with water close by. Wiens (1969) felt Bobolinks were characteristic of open fields with lush grass and forb cover. Martin (1967) found little use of woody trees and shrubs for perches. In the present study they were used extensively. This difference could possibly be due to the many strong forb perches available to Martin's birds. Martin felt that in open fields with high populations, weed perches were common. The lack of weed perches and the relative sparseness of grazed vegetation might help explain the low populations in Wiens' (1969) study.

If perch sites are of great importance, the addition of stakes such as were used to mark grid intersections may increase the desirability of the tract. Some Bobolinks seemed to favor stakes while others favored shrubs, hedges, and forbs. Most males used all of them. Stakes were used more where tall forbs and shrubs were absent such as the north third of the area. Most of the successful males were in

areas of more concentrated perch sites. It might be noted, however, that on neither this area or Wiens' (1969) area were there more than a fraction of the many perch sites supplied by meadow rue on Martin's area.

The average territory size appeared to change throughout the season. The great fluctuations of some individual territories make it difficult to know if the changes noted have any foundation in the breeding cycle (Appendices 2-4). With the exception of the largest territories, which fluctuated widely in size, territories in general become smallest toward the end of the breeding season in 1966 while declining mid to late in the breeding season in 1967. There are several possible reasons for these apparent results: (1) the size of the territories may be determined by the number of territories present, i.e., density; (2) a male may defend or utilize a larger area during certain phases of the breeding cycle than at others; (3) the behavior of Bobolinks at certain times in the breeding cycle may have made it appear that smaller territories or utilized areas were used than actually was the case.

It appears that within each breeding season up until mid season (Tables 1-3) increased density correlates with decreased territory size. Succeeding territories (Figure 3a and b) seem to be smaller than the earlier ones particularly in 1967 when the greatest density was noted. Tables 1, 2, and 3 indicate that the latest starting territories were nearly all below the average territory size. The general trend toward smaller territories with greater density is distorted by the very large increases in size in some territories (e.g. 3-67) which appear to be

the result of some males greatly expanding their territories as a result of other males abandoning their territories. The subsequent decrease in size of such large territories can, in many cases, be explained by the resident male being unable to hold all the area against males trying to secure a territory or from neighboring territorial males trying to enlarge their territories. This appears to be the case with the 6-66 male and 3-67 male. Other males such as 9-67 and 2-68 also extended their territories, but since there were no territories bordering on most sides, there was no pressure to reduce territory size.

To consider the second alternative, the sizes of the territories during the different parts of the breeding cycle need to be compared. Using this technique it is necessary to omit those males which were not in the area long enough for them to have passed through most of the breeding cycle. In most cases Table 4 indicates a decline in territory size during incubation. This is a low point in territory size with the exception of the largest territories 3-67 and 1-68. In nearly all of these territories an increase is noted after this low point. Similar changes were observed in the Black-capped Chickadee by Stefanski (1967) in which territories were largest during nest building. He found a decrease after territory establishment with an increase during the nestling stage. Weeden (1965) found the maximum activity space for the Ovenbird during courting and the smallest size between nest building and egg laying. Zimmerman (1963) suggested that the apparent utilized territory of the Gray Catbird was smaller than the

maximum territory and shifted in relation to the second nest site. Davis (1959) also found that territory size became much smaller during the feeding cycle. Elliott (1969) said that in the Red Warbler the defended area was reduced in size concurrent with demands to bring off the brood. Harrison and Buchan (1935) indicated that the St. Kilda Wren feeds on only a small part of its territory. Zimmerman (1966) indicated that the Dickcissel territory changes size and shape throughout the season. Yarrow (1970) found the utilized territory of the American Redstart decreased in size during nest feeding and then increased in size during territory break-down.

No decrease in defended area was found in the Palm Warbler (Welsh, 1971) or in Red-winged Blackbird Type B territories (Nice, 1941) which are maintained within a few feet throughout the season (Nero, 1956). This apparent difference between species may partly be a result of males utilizing only a small part of their territory in feeding but seeming to defend the whole area when an intruder is noticed, as in the Mourning Warbler (Cox, 1960). This type of behavior would account for fluctuations such as noted in territory 1-66.

The third alternative may also have some validity. Male Bobolinks do not seem to patrol their boundary as do many passerines (Barlow, 1962). When holders of large territories were watched continuously all day, they did not sing or display in some parts of their territories, even those parts containing the nests, for several hours at a time. This has been observed also by Zimmerman (1963) in Gray Catbirds. Most defense time seemed to be spent where boundaries abutted

other territories with defending males. An observer has difficulty in determining true territorial boundaries when no intruder or intruding neighbor is present. The decreased feeding of Bobolinks within the territory and frequency of males making long flights off the area also decreases the individual contact. This often allows neighboring males to wander over a wider area with increased overlap over extended periods than would be permitted were the neighboring males present. Without more stable long-term territories, it is difficult to make any solid conclusions as to why the sizes of territories appeared to fluctuate as they did.

Mating System

Of the 19 males considered mated, 16 were thought to be monogamous; 3 males apparently had 2 females each. Owing to the secrecy of female Bobolinks and the low number marked, some polygynous mating of short duration may have escaped detection.

Polygamy in Bobolinks has been mentioned by Buttrick (1909), Ken-deigh (1941b), Kingsbury (1933), and Martin (1967). Martin (1971, 1974) gathered conclusive evidence that polygamy exists in the Bobolink. It appears that Bobolinks, like Red-winged Blackbirds, will mate with as many females as possible (Nero, 1956; Payne, 1969; Peek, 1971). In this study monogamy seemed the general rule with polygamy practiced only by a minority. This has also been reported for House Wrens (Ken-deigh, 1941a), Pied Flycatchers (von Hartmann, 1956) and Brewer's Blackbirds (Williams, 1952). The apparent lack of defense by female Bobolinks against other female Bobolinks would allow polygamy to take

place. This would allow the male to attract as many females as were willing to mate. A limit would probably be imposed by the number of mates a male could court at a time as with Red-winged Blackbirds (Payne, 1969), Pied Flycatchers (von Hartmann, 1956), Brewer's Blackbirds (Williams, 1952), and House Wrens (Kendeigh, 1941a). If only one female could be courted at a time, all males holding territories at any one time would have a near equal opportunity to obtain a mate, other things being equal. When more females were available, the opportunity would be open for males subsequently to seek another mate. A lack of females, suggested by the inability of later arriving males to pair, may be responsible for the low frequency of polygamous mating.

Non-territorial Social Interactions

Often males were observed off their territory with a group of other territorial males. Sometimes these groups were largely silent or giving only a "chip" note. At other times all, or most of the three to five males in a group, would sing in a bush or tree without any apparent antagonism among them. These groups appeared to be essentially social groups. Often such groups would fly around together far off the area, eventually coming back to their respective territories.

During the height of territorial defense groups of two or three males were sometimes observed within a territory showing no obvious antagonism. When such groups were watched at length, periodic territorial behavior was usually seen. Territorial males were sometimes seen in other males' territories in which territorial conflict was

taking place but were seemingly ignored and did not take part in the song flights and chases occurring. Such males preened or fed without singing or displaying in any noticeable way, though occasionally seeming to watch the conflict.

Though female Bobolinks were generally not seen in groups, on several occasions two females were seen together. In territory 2-67 the two presumed female mates (both marked) were frequently seen together before the disappearance of one. Females, and occasionally males, were observed coming to nests of other Bobolinks without any apparent disturbance to owners feeding the young. Kendeigh (1941b) mentioned that neighboring males frequently stopped by the nest of another male before going on to procure food.

Nesting Cycle

The following highly condensed summary of a great volume of observations on the nesting cycle is restricted to material considered useful as a context for interpretation of population structure.

Nest building. In the present study nesting material was never observed to be carried for more than one day by a given female. Kingsbury (1933) and Martin (1967) thought that two days were spent in nest building, and it is possible that, owing to the tall grass on the Colony Farm Tract, gathering of nest material close to the nest (as reported by Kingsbury, 1933, and Karr, 1963) was not seen.

The nine nests found were built in slight natural depressions. All were constructed of grasses arranged in the shape of a cup. Of 20 nests

found by Martin (1967), 18 were open-top nests and two were slightly domed. All of the nests Kingsbury (1933) found were open top.

Seven of the nine nests were in areas of sparser grasses with at least some forbs present. Nests in the more sparse grasses were either between several forb stems or under an overhanging forb. Nests in dense grass were generally semi-covered by grasses hanging over the nest. Kendeigh (1941b) found Bobolink nests were well concealed in the bases of Andropogon or less so in Kentucky bluegrass.

The nest completion dates appeared to range from May 19 to June 13 in 1966, May 22 to June 11 in 1967, and May 21 to June 27 in 1968 (Figure 2). It is assumed that some of the late nests were renesting attempts, though Kingsbury (1933) felt Bobolinks rarely if ever renest. Martin (1967) found an average date of May 22 (May 16 - June 1) for 11 nests in Meadow Rue and June 2 (May 19 to June 23) for 9 nests located in grass-sedge.

Egg laying and copulation. Egg laying started two days after completion of the nest with one egg being laid per day until clutch completion (Martin, 1967). Eggs and flightless young indicated that three nests had four eggs, three had five, and one had six. Late nest 9-67 had one egg (of four) disappear during incubation indicating the possibility that some of the above nests could have had more eggs in the complete clutch. Martin (1967) found that three to seven eggs were laid, five being the usual number.

Copulation took place over a several-day period from the beginning of nest building through the middle of egg laying (Martin, 1967). Male

Bobolinks frequently gave a "we ju we ju" call before and after copulation. The female generally answered by the "zoo" call (thought to be synonymous with "zeep" by Martin, 1967, and "chirr" by Kingsbury, 1933) of the female. When copulating, a male mounted the female for a few seconds, remounting up to six times in succession with an interval between mountings of one-half to five minutes.

Incubation. The incubation period is reported to be twelve days (Martin, 1967). Only one nest was found early in incubation. In the few hours of observation three days before hatching only the female incubated the eggs as was also reported by Kingsbury (1933) and Martin (1967). Average periods on the nest were 10.3 minutes in the morning to 19.8 minutes in the afternoon. The average period off the nest was 5.7 minutes for both morning and afternoon. These were somewhat shorter than the average attentive and inattentive times of 22 and 12.3 minutes found by Martin (1967) when the female fed on her territory.

During incubation the male was occasionally observed to go to the nest and sometimes brought food. Since the nest could not be seen well, it was not certain that the male fed the female. Karr (1963) made a similar observation of a male bringing food to the nest.

Care of nestlings. Feeding of young on the first day after hatching was slow (Table 5). The rate increased to day six or seven and was maintained at a fairly high level after that time (with some daily variation: Table 6). Yellow-headed Blackbirds (Willson, 1966) show a similar pattern. The male was always observed to do some feeding, though at some nests his participation seemed slight. In one pair

Table 5
Feeding Rate of Male and Female Bobolinks*

Days after hatching	No. of hours watched	Nest feeding visits per hour		
		Male	Female	Total
1	1 1/3	3.3	2.2	5.5
2	2 1/2	4.1	4.1	8.2
3	2	6.5	5.0	11.5
4	3/4	6.2	7.0	13.2
5	1 1/2	8.7	6.0	14.7
6	2	12.9	10.6	23.5
7	9 1/2	8.9	8.7	17.6
8	5 3/4	8.0	7.4	15.4
9	2 1/2	14.9	18.1	33.0

* 1-8 day 9-67 pair with three young; ninth day 2-67 with five young.

Table 6
Feeding Rate Variation of Seven-day Young
(Nest 9-67, Three Young)

Time	Number Feedings per Hour		Total
	Male	Female	
7:00 - 8:30	5.9	11.5	17.4
12:30 - 14:30	9.1	8.6	17.7
14:30 - 16:30	11.9	10.0	21.9
16:30 - 18:30	10.5	9.1	19.6
18:45 - 20:00	5.7	7.6	13.3

the male made more feeding trips than the female. Kingsbury (1933) and Martin (1967) reported that male and female fed about the same at most nests though some males fed little.

In all icterids for which significant published data are available (Eastern Meadowlarks, Yellow-headed, Red-winged, Rusty, and Brewer's Blackbirds, Northern Orioles, and Common Grackles), except for Boat-tailed and Great-tailed Grackles, males apparently feed their young at least part of the time (Verner and Willson, 1970). In polygamous species such as Red-winged Blackbirds the role of the male usually is slight (Verner and Willson, 1970).

The female approached the nest generally by landing on a bush or forb near the nest (about 2 - 3 feet), and then dropped to the ground. The male also had a set nest approach pattern which was, however, different from that of the female.

Most food brought to nestlings appeared to be gathered outside the territory, usually in the bordering hay strip which was a communal feeding area. Some adults were observed to carry food a quarter-mile and may have gathered food even farther away. Kingsbury (1933) indicated females generally went outside their territories to feed. Martin (1967) reported that about 15 per cent of the males foraging during the incubation period were in their territories with most foraging in the communal feeding areas. Wiens (1969) stated much nestling food came from croplands and a marsh a kilometer away.

The female and male were not usually observed to gather food from the same directions as also noted by Wiens (1969). Wiens felt the males generally obtained food for young at a greater distance than the female.

Fecal sacs were observed to be carried from the nest from three days after hatching until fledging.

Protective measures of parents were occasionally observed. The female usually left the nest very reluctantly after allowing approach to six feet without fleeing. Kingsbury (1933) mentioned "the female remains on the nest until nearly stepped on". The female was thought generally to leave the nest through the grass when danger was present. A male was observed to flutter through the grass away from a nest with newly hatched young when the nest was almost stepped on accidentally. Nero (1955) observed distraction display in a female and Martin (1967) observed it frequently in both sexes when quickly approaching a known nest.

When disturbed close to the nest, males and females gave a "dic" note (probably the same as the "chunk" described by Martin, 1967, and "chut" by Kingsbury, 1933) which was generally accompanied by wing and tail flicking. Several times adults were observed hopping up and down with wings over their back. A hog-nosed snake (heterodon nasicus) one and a half feet from an incubating nest and a blue racer (Coluber constrictor) with a live fledgling in its expanded mouth were evidently the cause of the disturbance on two occasions. This type of behavior by adults was also shown by Gray Catbirds in the presence of snakes (Zimmerman, 1963).

Nestling development. Hatchling Bobolinks were blind and bare except for down. The first pin feathers appeared two days after hatching on wings and tail. The eyes had begun to open on the third day. By the

fifth day wing and tail feathers had begun to break from the sheaths. By the eighth day most feathers of the head and back had broken out of their sheaths, and wing feathers were about 40 mm. in length. The young Bobolinks may leave the nest shortly after this time. By the twelfth day the young were well feathered and had wing lengths of 67 mm. and tail lengths of 17 mm.

The young left the nest before they were able to fly, as is true of many ground-nesting birds (Cox, 1960). They were able to move rapidly through the grass and were difficult to catch even the first day out of the nest. By about the sixth day out of the nest, young were able to fly distances up to about 50 feet and by the following day were able to fly up to 200 feet. Martin (1967) stated that young were capable of sustained flight at 16 days of age.

Reproductive Success

The foregoing section describes the nesting cycle from nest building to the time the young leave the nest; success in completing the cycle, however, was achieved by only a small proportion of the pairs. Of 17 territories (20 nests), in which events proceeded as far as nest building, only 7 (41 per cent of the territories and 35 per cent of the nests) produced young which left the nest. A more meaningful figure would be the percentage of completed clutches which were successful; owing to the difficulty of finding nests before the young had hatched, this figure is not available.

About half of the territories present at any particular time were short-term (one in 1966 and 1967 was thought to have resulted from nest

failure). Six, five, and four territories were present up to 30 days in 1966, 1967, and 1968, respectively, with 3 (50 per cent), 3 (60 per cent), and 1 (25 per cent) fledging young. Kingsbury (1933) for 28 nests found a success rate of 67.8 per cent. Since half the nests were found after hatching, many unsuccessful nests may not have been found. Out of 14 nests found before hatching, only 5 (35.7 per cent) fledged some young. Karr (1963) found a success rate of 12.5 per cent for 8 nests. Karr's low success rate probably was a result of disturbance caused by his daily weighing of young (Martin, 1967). Out of 20 nests found by Martin (1967), 18 of which were found with eggs, 65 per cent were successful.

It appeared in the present study that most of the nesting birds experienced nest failure. Though human disturbance may have been a factor, evidence indicated nest predation was the main reason for failure as also found by Zimmerman (1971) for the Dickcissel. Snakes were the only known predators. Mammals such as the thirteen-lined ground squirrel (Citellus tridecemlineatus) may have preyed on Bobolink eggs or young as mentioned by Robins (1971) for Henslow's Sparrows on the same study area. Kingsbury (1933) thought snakes were the principal enemy to eggs and young on her area, though she believed her data may be biased because many or most early nest failures were not found. Kingsbury calculated 64 per cent of eggs and young lost were taken by snakes, skunks, or possibly crows. Martin (1967) reported that of 101 eggs a minimum of 18.8 per cent were lost due to predation. Losses were attributed to mammals and Red-winged Blackbirds.

Breakdown of Territories and Post-territorial Behavior

Territory breakdown began during egg-laying or the beginning of incubation. As time progressed, males gave less time to song spread and song flight display while being absent from their territories longer and more frequently as also noted by Wiens (1969). Even in the hours of the morning when territorial activity had been greatest, males were frequently absent. Males (and sometimes females) were frequently observed to fly to one of the neutral hay strips west of the tract and land, circle a quarter-mile away and return, or fly out of sight of 7 x 35 binoculars. These males were gone up to 20 minutes and possibly longer on some occasions. Martin (1967) mentioned that in early June, 5-7 minutes would elapse without a sound from territorial males giving the impression of vacant or undefended territories. He felt that males were generally flying to an upland feeding area a kilometer away. The amount of time males spent in such areas was difficult to determine since males frequently left these apparent feeding spots without detection.

When young leave the nest, territory breakdown seems complete. The male then sings little or not at all. Occasionally renewed singing and female chasing was observed by a male. This did not seem to be site oriented but rather oriented around the female. Kingsbury (1933) and Martin (1967) likewise found no territory defense after fledging.

Though two or more of the fledged young sometimes remained together for a day or more, the group generally split up. Both parents

fed the fledged young and followed their movements which appeared to be random. After the young were able to fly, but still obtaining food from their parents, formerly widely separated family groups were frequently found in the same area. Martin (1967) called these "nursery flocks" which he felt remained together until leaving the field. Data from 1966 and 1967 in the present study only partially support this.

In 1966 two or three such family groups were often seen together between June 30 and July 4; thereafter they spread out until only one family remained after July 9.

In 1967 during late June two families moved around the tract but remained 200-500 feet apart. During early July both families moved around the south part of the tract in what appeared to be a random pattern, though they often were in the same general area. When feeding their young in the same area, the male of one family was observed to dive at and chase the female in the other family. Three of the four feeding adults (two males and a female) were last seen July 11, and the fourth July 21. The late-nesting pair moved around most of the southern two-thirds of the study area and adjacent hayfield to the west before the male, last seen July 23, and female, last seen with some of her banded young August 1, disappeared. The general later disappearance of the female corresponds with Kingsbury's opinion that the majority of the time the females continue feeding their young out of the nest longer than males which flock early.

Since male fall plumage differs from breeding plumage, time of molt is easy to observe. On June 25 in 1966 what looked like a female with black breast markings was observed around a nest with young.

Neither of the nest's adults showed any molting. Some ragged looking males with some yellow feathers coming through black feathers were observed during early July in flocks, although other males showed no signs of molting. In 1967 the first sign of molt was July 10 when a male was seen with yellow feathers in the center of black breast feathers. No adults that were caring for young were ever observed to show any signs of molting. The last identifiable male in 1967 was observed August 13.

The first possible evidence of flocking appeared June 19 in 1966 when, with five territories still active, many singing Bobolinks were observed at the south end of the tract. On the following day several males were observed to fly over together. These males were assumed not to have nested successfully due to natural causes or to hay mowing taking place during mid-June in some Bobolink breeding areas. All birds still resident on the study tract were involved in the rearing of young at this time.

No further flocks on the tract were noted until July 11 when some small flocks were seen on the north part. Some flocks of 15-20 were present and some larger flocks were passing over. After July 22 Bobolinks were never observed singly. Flocks up to 50 or more individuals were observed by late July in 1966 while in 1967 only small flocks (of less than 10) of Bobolinks were observed throughout August of 1966. Only occasional Bobolinks were observed in late August in 1967. Few were observed during September during both 1966 and 1967 with the last Bobolinks observed October 4 in 1966 and September 21 in 1967.

It appeared that at least some of the flocking Bobolinks returned on successive days to the same place to feed or roost. A female which was banded and marked July 18 on the Colony Farm Tract was again observed on August 3 in a flock of 10-20 birds.

Characteristic of flocking and migration is a "pink" (described as "chink" by Kingsbury, 1933, and "pink" by Martin, 1967) flight call. This is generally the only call heard in late summer flocks.

General Discussion

As expected, the territorial and mating system of the Bobolink proved complicated and some aspects remain unclear. Several features, nevertheless, have been established in the foregoing sections. Males establish territories, but territory defense declines markedly about the end of egg laying or shortly after copulation ceases. Males appeared on the study plot and established territories over an unusually extended period; the time from the beginning of territorial behavior to the last male to establish a territory was on the order of a month. Many territories were defended only briefly and then abandoned. As a consequence of these two conditions, the number of territories varied greatly through the spring, the general pattern being a build-up over two to four weeks to a peak, a rather sharp drop to a nearly stable number for about three weeks, and then a rapid decline as young left the successful nests and adults no longer showed any tendency to focus activity around the former territory. On this area polygyny occurred, but monogamy was the usual situation. The female Bobolink did not defend a territory, even against other female Bobolinks.

This discussion will concentrate on four questions. The first is the practical one which first suggested this study: How can numbers in an unmarked population of Bobolinks be censused? The second and third questions are possibly interrelated: Why did territorial establishment occur over such a long period and why was there so much abandonment? The fourth question is, what is the role of territoriality in the Bobolink?

Censusing Bobolinks. The standard Williams spot map method of censusing birds (Williams, 1936) is based on the assumption that the numbers of territories and their boundaries will remain relatively stable throughout the season or census period. It is expected that by compiling weekly or periodic maps of territorial adjacent males, the outlines of territories can be determined and hence, the location and numbers of territories on the census area. This appears to hold true for Bobolinks only in high densities in what probably is near optimal habitat (Martin, 1967). Lower densities found in this study and Wiens' (1969) seem less stable. The compilation of periodic maps representing different numbers and locations of territories are difficult to interpret accurately.

I believe two methods are available for accurately assessing the Bobolink population: (1) a series of closely spaced (preferably consecutive days) early morning censuses in mid-May. Unless a great amount of fluctuation is taking place, three consecutive mappings should give a good idea of where the territories are located at any one time. To separate short-term territories from long-term territories

a second three-day series at least two weeks later, probably around the first or second week of June, would be necessary. Weekly visits would confirm the continuing presence or absence of territorial males found to be present during the series censuses. The determination of the pairing status would be more difficult, though some indication of a male being paired probably would be apparent. Evidence of polygyny would be more difficult to determine. Unmated males, besides not being observed with females, probably would not remain on the study tract more than two or possibly three weeks.

(2) Another possible method of censusing Bobolinks is described by Wiens (1969). It is based on the assumption that a territorial male will not leave its territory or activity area when flushed. A singing male is flushed and its position and activities continuously mapped. The male is flushed at least twenty times during several minutes while mapping elevated singing perches, aggression from adjacent territorial males, flight paths and landing sites. It was believed by Wiens that these flush areas were equivalent to actual territories because they did not overlap in areas of high density and because conspecific birds were frequently observed to give aggressive displays at flush-determined territory boundaries. This technique, when time is available, should give a good idea of the size and number of territories present on any one day. To determine the average number of males throughout the season, at least two or three flush censuses probably should be performed.

The long period of territory establishment. There appear to be three general possibilities for the source of late arriving birds. (1) The population arrives from its wintering ground over a long period of time; (2) some males may spend a considerable amount of time in the region before establishing a territory; and (3) some of the late arrivals may be males which have set up territories elsewhere and abandoned them. There is some evidence that both possibilities 1 and 3 may be true. Stoddard (1962) gave data on Bobolink migration from television tower kills in northern Leon County, Florida. The range of dates involved (for a period of six years) was April 5 to May 20; however, most (24) of the 27 birds killed were between May 1 and May 20. Bobolinks do not breed nearer to northern Florida than Pennsylvania, so these birds were all migrants with some distance yet to travel. These data suggest that, despite the regularity of first return of Bobolinks (see Arrival of Bobolinks), the span of time over which birds return may be rather broad.

The pattern of abandonment shown on the study tract, along with the observations of the activities of such birds as 10-67 and 16-67, described earlier (territorial stability and population size), suggests that some of the late appearing males were almost certainly ones which had earlier set up territories elsewhere.

Why were territories abandoned? There is a clear temporal difference in the major cause of abandonment: Abandonment of early established territories was associated with nesting failure (possibly sometimes resulting from loss of the mate); abandonment of late established

territories was associated with failure to attract a mate. There is an indication that Bobolink territorial abandonment was more frequent here and in Wiens' (1969) study than in Martin's (1967) area. This difference apparently is real since Martin's techniques should have detected any significant number of abandonments.

As mentioned earlier, density on Martin's (1967) area was much greater (54 per 100 acres) than in either Wiens' (6.25 - 11.25 per 100 acres) or the present study (12.7 - 22.5 per 100 acres). Martin's area (a few kilometers from Wiens' area) may represent optimal or near-optimal habitat while Wiens' (1969) area and the Colony Farm Tract may be more marginal breeding areas. Brown (1969a) suggests since good habitat would be occupied first, its population would probably remain fairly uniform from year to year as long as the population maintained a certain minimum necessary to occupy the most desirable habitat. Variations in numbers and sizes of territories on good sites would not be proportional to the overall magnitude of possible population change from year to year (Brown, 1969a) as found by Kluyver and Tinbergen (1953). More marginal areas (such as Wiens' and the Colony Farm Tract) would be used during years of medium or high populations but would be little used during years of low populations (Brown 1969a, 1969b; Kluyver and Tinbergen, 1953). Marginal areas under medium populations would be subject to great fluctuations in territory size and number from year to year as the population rose and fell (Brown, 1969b). Under low-medium populations few birds would probably use marginal areas while under high-medium to high populations many breeding birds would use marginal areas (Brown 1969a, 1969b). During high populations

when marginal areas were maximally utilized, the remaining excess would be floaters (Brown, 1969a). The fluctuation in numbers on the Colony Farm Tract and Wiens' area would indicate Bobolink populations in both areas would fall in the medium range with breeding populations being determined by breeding success and mortality from the previous year. These birds on marginal land would serve as a buffer for the population (Brown, 1969b). This would explain the great amount of in-season fluctuations observed on Wiens' (1969) area and in the present study. Short-term territories on marginal habitat could be a result of shifting to more favorable sites or replacement of males on more nearly optimal habitats. These individuals would form a semi-floating population which could quickly fill in when optimum space was available.

A large portion of territory abandonment is attributed to failure to pair. This could partially be attributed to the apparent polygamous nature of female Bobolinks (Martin, 1967) and the apparent habit of female Bobolinks selecting a mate on the basis of habitat suitability (Martin, 1971; Zimmerman, 1966). If optimal habitat was available within the search range of the female, most females would be expected to select mates on more optimal territories causing the ratio of females to males to be much greater than unity. Unless the male-female ratio differed markedly from unity, the number of females available to mate with males on marginal habitat would then be limited. Though marginal habitats would be expected to show a continuum of suitability so that some quite suitable sites may be available, the lower quantity of near-optimal habitat would decrease the chance of attracting females to the area. On marginal habitat, polygamy would therefore be much reduced

as compared with optimal areas. Many males under medium population conditions would not attract mates and this in turn would lead to early territory abandonment.

Habitat-altering activities (e.g., mowing) and loss of males and/or females would also increase the territory fluctuations experienced on suboptimal areas as compared with optimal sites. Losses on optimal sites up to midway into the season would probably be quickly filled by individuals from more marginal areas, leaving vacancies in the marginal areas except when the population was quite high.

The role of territoriality in Bobolinks. The sizes, types, and roles of territories have been studied extensively since discussed by Howard (1920). No one set of explanations can be assigned for all species. Several general explanations have been advanced for different species which may be applicable to the Bobolink.

Food is often suggested as the ultimate reason for territoriality in those species which gather most or all of their food within their territory. If food were the ultimate factor in the Bobolink, territory defense should not be expected to decrease when food needed for feeding young was greatest (Drury, 1961; Hinde, 1956). The apparent increasing number of far-reaching flights and off-territory food flights would also indicate food is probably not the ultimate factor in territory formation, though its presence in a territory may be important in pair formation early in the breeding cycle. Many territorial passerines with fair sized territories do some food gathering (particularly for nestlings) off their territory (Andrew, 1956; Coutlee, 1967; Gibb, 1956a;

Hinde, 1956; Lack, 1935, 1939; Simmons, 1956; Snow, 1956; Southern, 1958; Tompa, 1964; von Hartmann, 1956; Young, 1956). Food could be related to the decreased territorial defense, however, in that time and energy required for finding food during certain periods of the breeding cycle may not leave sufficient time or energy to defend a territory as was available at the beginning of the season.

Several authors (Armstrong, 1956; Beer et al., 1956; Conder, 1956; Evans, 1970; Gibb, 1956b, Gibson, 1971; Hinde, 1956; Marler, 1956; Mayfield, 1960; Mayr, 1935; Snow, 1956; Stefanski, 1967; Tompa, 1962; Young, 1956) have suggested that territories in some species may function primarily in assisting mating, preventing interference in copulation, and in maintenance of the pair bond. Bobolink males seemed interested in any female which passed by. This was particularly evident when five or six males were observed following one female around the area. Intruding males also did not seem to show any hesitancy to court or chase a mated female in another territory if the opportunity presented itself. The Bobolink territory may be an area in which a male could attract a mate and keep other males from copulating with his female. By the male maintaining as large a territory early in the season as can successfully be maintained, an area would be available for attracting females to mate while preventing other males from interfering with mating and copulation. Having a large territory and staying within the territory early in the season would strengthen the pair bond by allowing the pair to feed in close proximity without interference. Territorial behavior that reduces density may prevent continual conflict which would prevent a pair bond from forming or that

would destroy it (Tompa, 1964). Formation of the pair bond may not be an immediate thing (Hinde, 1956) as appears to be the case in Brewer's Blackbird (Williams, 1952) and may gradually be strengthened over a period of days during which a territory is essential to allow subsequent successful mating and raising of young. A territory would protect females from the attentions of other males (Andrew, 1956; Ficken, 1962; von Hartmann, 1956). This need to be protected corresponds with defensive behavior which generally reaches a maximum at egg laying and decreases throughout the rest of the breeding cycle (Conder, 1956; Drury, 1961; Gibb, 1956a; Hinde, 1956; Kendeigh, 1941; Mayfield, 1960; Mountfort, 1956; Schartz and Zimmerman, 1971; von Hartmann, 1956; Williamson, 1971) when the need to protect the female from foreign copulation is absent. After copulation is completed, the need for defense of an area to protect the female would be past. The male's presence would no longer be required so partial absence and overlap could be tolerated. Territorial behavior would limit the density in any one area, but this limiting effect would be a consequence of the territorial behavior which resulted from the need to isolate the breeding pair from interference from other Bobolinks.

Protections against predators is sometimes mentioned as a function of territoriality (Krebs, 1971; Simmons, 1956). Since predators seem to be the main reason for nest failure, this may be important. It is, however, difficult to determine its significance without being able to compare the relative predation rates for various densities. There is evidence for increased predation at higher densities in some birds (Krebs, 1971), but Fretwell's (1972) data suggest that predation

rate on nests tends to be correlated with the total open nesting population (all species). Individual species seem to gain little advantage by being rare; consequently, predation seems unlikely as an important selective force in intra-specific territoriality.

Food is probably secondarily important (Conder, 1956; Mayfield, 1960; Young, 1956). It could be important that enough food is available during pair formation so the male could generally remain on territory during mating. A food supply would allow the pair to do most of its feeding within the territory, thereby decreasing the possible distraction of other species' members during bond formation. This secondary importance is also true of any prerequisite found in the territory which would decrease the need of a pair coming in conflict with or being interfered with by other males during the breeding cycle, (Mayfield, 1960; Nice, 1941).

Summary

Bobolinks were studied over a three-year period on a 40-acre tract containing 33 acres of grassland. The first Bobolinks arrived at the beginning of May each year, but most were spread out over at least the first half of May. The establishment of territories was spread over a period of a month. This was attributed possibly to late arrival but primarily to long-term presence in the area prior to territory establishment on the study tract (possibly due to previous territory establishment elsewhere). In general, the number of territories built up over two to four weeks, then there was a rapid decline to a stable number for three weeks before the final break-up of

territories as the young left their nests.

Territory defense, which consisted mainly of song flights and displays, was solely a male function. The Red-winged Blackbird was the dominant passerine of the tract with the Bobolink the next most dominant passerine. Territory defense was greatest at the onset of territoriality, declining greatly after egg laying and disappearing completely upon fledging of young.

Fluctuations in territory size, location and number were greater intraseasonally and interseasonally than observed in most other detailed Bobolink studies. About half the males holding territories did not mate, apparently resulting in early territory abandonment. Some males were observed to set up territories widely separated in space or time. The lack of stability was attributed partly to a lack of female mates and ultimately to the study tract being sub-optimal Bobolink breeding habitat.

Monogamy was the common mating pattern though a few cases of polygamy were observed. One nesting per season was the usual case though renesting after nest failure may have occurred. The nesting cycle required about 30 days. The female alone incubated the eggs, but the male helped in rearing the young. Nesting success of observed nests varied from 25 to 60 per cent over the three-year period.

Two special census techniques are suggested for determining the number of Bobolinks on such marginal areas. Both require some concentrated effort centered on Bobolinks. One involves a series of consecutive daily visits while the other involves mapping the movements and behavior of flushed individuals.

The various possible roles of the territory in Bobolink behavior were discussed. The data suggested its main function may be to prevent interference with successful mating.

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APPENDIX

Appendix 1

Detailed Account of Territory Shifts

During the first week after arrival in 1966, the northeast was held by Male 1-66 while territory 2-66 fluctuated considerably from day to day causing some question as to whether the same male was present (therefore referred to as 2a, 2b, 2c, etc.). Territories 3-66, 4-66, and 5-66 were located off the area. Few territories were set up on the south half the first week in 1966. Only one territory was evident the first week in 1967, and none in 1968.

The second week showed a great increase in the number of new territories. Territories 1-66, 3-66, 4-66, and 5-66 remained and 2b-66 evidently shifted south. Territory 8-66 seemed to be a one-day territory.

In 1967 1-67 remained and 2-67 through 6-67 started. Territory 2-67 seemed to shift south in midweek possibly because no males were present in the area. After some conflict, 2-67 and 4-67 were established where 2-67 previously was alone causing some uncertainty as to which were the new males. A new one to two day territory may have started on the 12th and 13th in what was to be 9-67.

In 1968 the first four territories were set up during the second week. Male 1-68 was banded the previous year (2-67). Territory 1-68 was in approximately the same location as the previous year. The

north territory was settled third in contrast to being occupied earliest in each of the previous years. There was a shifting south of 2-68 and a short-term 4-68 territory forming where 2-68 had previously been.

The second week seemed to also be the time of major build-up on Martin's (1967) study with five territories evident May 7, nine on May 8, twelve on May 10, fifteen on May 14, and sixteen on May 15.

The third week added one or two territories in 1966 and 1968, and several in 1967. Territory 2b-66 was not observed for sure during a rainy period so the male may have left. Male 9-66 moved in between 2c-66 and 6-66. Other territories showed little change.

In 1967 four or five territories were started with some males being replaced. 1-67 disappeared after being observed defending against an unmarked male (14-67) which evidently replaced 1-67. Male 2-67 shifted in correspondence with the shifts of 4-67 to the south. Male 3-67 was partially off the tract. Male 6-67 was of short duration, evidently being replaced by another short territory 11-67. Male 10-67 was observed being quiet on the central part of the tract the two days prior to pushing 7-67 gradually off his short duration territory. Male 7-67 was observed behaving quietly after being pushed out of its territory.

Male 8-67 pushed between 3-67 and 4-67 possibly moving in from east of the tract. Male 9-67 formed though possibly having appeared off and on in the area previously. Male 12-67 may have started earlier, but was not observed before since off the tract to the east.

In 1968 4-68 disappeared during the third week. Males 5-68 and 6-68 started between 1-68 and 3-68 with 1-68 shifting south. Male

6-68 subsequently deserted after always being less active than 5-68.

During the fourth week a few new territories were started each year. In 1966 little change was noted except for the addition of three territories: 10-66 and 11-66 bordering the tract on the west; 12-66 a short time territory disappearing about the same time as 7a-66.

In 1967 14-67 replaced 1-67 at the beginning of the week. Male 13-67 also appeared with 15-67 appearing off the tract and deserting within the week.

In 1968 7-68 was observed on the area only a few days. Male 8-68 appeared setting up a territory between 1-68 and 2-68. Male 8-68 was a banded male from the previous year (14-67).

The fifth week had several males disappearing with some of them being replaced by new males. In 1966 15-66 apparently tried to usurp part of 1-66's territory resulting in the north area being divided into separate territories. On some days, 1-66 was seldom observed. Male 2c-66 shifted south to area left vacant by 9-66. The vacancies allowed 6-66 to defend most of the south area which subsequently came under pressure from several new males. New Males 13-66 and 14-66 evidently started territories as a result of this pressure, though 14-66 proved to only be of short duration. Males 10-66 and 11-66 disappeared.

In 1967 2-67 covered less area while 3-67 defended a much greater area at least partially as a result of 8-67's disappearance. Males 5-67, 10-67, and 13-67 disappeared leaving 3-67 the only south male. In the north 16-67, which evidently tried to replace 14-67, eventually left.

In 1968 no new males were observed and 5-68 disappeared. On some days males appeared quite active, and on other days quite inactive.

During the sixth week less change was noted. Territory 6-66 became much smaller and 15-66 disappeared with 1-66 again controlling the whole north area.

In 1967 two new Males, 17-67 and 18-67, arrived in the north. Male 17-67 took over part of the north area much as 15-66 had done in 1966. Male 18-67 subsequently disappeared. The 10-67 Male, which had been gone five days, returned setting up a territory in an area north of its former territory and in an area formerly occupied by 3-67.

In 1968 a new Male, 9-68, with a distinctive song was quite active in the north area. The 3-68 Male had not been observed to sing in the area for a couple of weeks and seldom was observed. Male 9-68 subsequently disappeared.

During the seventh week little change was noted except for a few birds leaving their territories. Most remaining birds were well along in breeding. The non-breeding adults seemed to lose interest in their territories and left the area. Nest failures may have played a part in some desertions, such as that of 6-66 whose activity had previously become much less.

In 1967 the Males 17-67 and 12-67 disappeared, and 14-67 regained his area only to disappear the following week. In 1968 no change was noted.

The eighth week found more males disappearing. A flurry of activity was noted on June 19 in 1966 with no apparent order and no males in the area the following day. Male 2d-66 had young hatch with the young disappearing and males feeding young no longer remained territorial.

In 1967 activity diminished with the raising of young or non-success. Male 3-67 confined self to raising young. Male 2-67 did not sing after young hatched. Male 4-67 evidently experienced nest failure. Male 10-67 disappeared leaving 9-67 with a late hatching nest being the only male still acting territorial.

In 1968 the eighth week saw hatching of young from 1-68 nest, while 2-68 and 8-68 were last seen the following week after nest failure.

Appendix 2

Weekly Territory Sizes During 1966

Territory	Territory Size in Acres							
	Weeks (Date)							
	1 (May 1-7)	2 (8-14)	3 (15-21)	4 (22-28)	5 (29-4)	6 (June 5-11)	7 (12-18)	8 (19-25)
1	5.2	2.8	3.7	1.7	4.1	1.3	1.4	5.5
2	1.8	1.1	2.3	2.6	4.2	1.0	1.6	
6		3.4	4.1	1.2	11.4	5.1	1.0	
7		1.2	2.6	2.8				
9			1.4	2.2				
10				3.3				
11				3.0				
12				0.9				
13					1.2	0.9	0.4	
15						1.6		

Appendix 3

Weekly Territory Sizes During 1967

Territory No.	Territory Size in Acres							
	Week							
	1	2	3	4	5	6	7	8
1	1.9	8.4	6.9					
2		3.9	3.9	3.0	1.6	1.4	3.5	
3		2.2	3.7	4.2	12.2	7.7	12.6	
4		3.4	4.3	1.5	2.3	3.2	2.5	
5		1.9	1.6	1.1				
7			3.4					
8			1.8	2.7				
9			2.7	3.2	1.4	1.0	2.9	0.4
10			1.7	1.8		2.4	5.7	
13				2.3				
14				7.0	3.1	2.2	5.1	
16					3.2			
17						1.6		

Appendix 4

Weekly Territory Sizes During 1968

Territory No.	Territory Size in Acres							
	Week							
	1	2	3	4	5	6	7	8
1		4.1	2.5	2.3	3.4	3.2	5.5	
2		6.5	3.4	6.7	3.4	5.9	6.0	3.0
3		4.3	3.2	2.7				
4		1.8						
5			2.0	1.3				
6				0.3				
7				1.1				
8				0.4	2.5	2.4	0.9	2.1
9						2.1		

Appendix 5

Bird Species Cited

Eastern Kingbird Tyrannus tyrannus
Traill's Flycatcher Empidonax traillii
Pied Flycatcher Ficedula hypoleuca
House Wren Troglodytes aedon
St. Kilda Wren Troglodytes troglodytes
Mockingbird Minus polyglottos
Gray Catbird Dumetella carolinensis
Starling Sturnus vulgaris
Palm Warbler Dendroica palmarum
Red Warbler Ergaticus ruber
Mourning Warbler Oporornis philadelphia
American Redstart Setophaga ruticilla
House Sparrow Passer domesticus
Bobolink Dolichonyx oryzivorus
Eastern Meadowlark Sturnella magna
Western Meadowlark Sturnella neglecta
Yellow-headed Blackbird Xanthocephalus xanthocephalus
Red-winged Blackbird Agelaius phoeniceus
Northern (Baltimore) Oriole Icterus galbula
Rusty Blackbird Euphagus carolinus
Brewer's Blackbird Euphagus cyanocephalus
Great-tailed Grackle Cassidix mexicanus
Boat-tailed Grackle Cassidix major
Common Grackle Quiscalus quiscula
Brown-headed Cowbird Molothrus ater
Dickcissel Spiza americana
Savannah Sparrow Passerculus sandwichensis
Grasshopper Sparrow Ammodramus savannarum
Henslow's Sparrow Ammodramus henslowii
Vesper Sparrow Pooecetes gramineus
Song Sparrow Melospiza melodia