



**Male Bobolink performing pre-copulatory
Crouch display (see Breeding Behavior)**



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BREEDING BIOLOGY
OF THE BOBOLINK

BY
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I. INTRODUCTION

Despite the importance of the Bobolink (Dolichonyx orizivorus) as a subject of migration (Hamilton, 1962a, 1962b) and physiological studies (Engels, 1959, 1962a, 1962b, Wolfson and Westerhoff, 1960), the species has received scant attention from ecologists and ethologists. This study has concentrated on describing the breeding ecology of the species and display sequences used on its breeding grounds, particularly with reference to agonistic and courtship situations.

The family Icteridae, to which the Bobolink belongs, lends itself admirably to a variety of ecological and ethological studies. Within the family is a broad spectrum of mating types (Lack, 1940a), from strictly monogamous pair bonds (Ficken, 1963) through various forms of polygamy (Verner and Willson, 1966) to promiscuous breeding (Selander and Giller, 1961). Nesting habits and nest construction are also extremely variable, from the elaborately woven hanging nests of the oriole group, through various types of supported and suspended cups in blackbirds and the domed ground nests of meadowlarks to none at all in parasitic cowbirds. The family shows a variety of distinctive displays, offering opportunities for comparative study and speculation on phylogenetic derivations. Furthermore, since most icterids inhabit marshes, prairies and savannahs (Verner and Willson, 1966), these displays are in many instances performed under

easily observable conditions.

Most North American icterids have received considerable study. The behavioral repertoire and ecological relations of the Red-winged Blackbird (Agelaius phoeniceus) were investigated by Beer and Tibbitts (1950) and Nero (1956a, 1956b). Ficken (1963) described the behavior of the Common Grackle (Quiscalus quiscula) and Wiens (1965) and Snelling (1966) considered behavioral interactions and competition between the two species. Willson (1966) examined the ecology of the Yellow-headed Blackbird (Xanthocephalus xanthocephalus), and Willson and Orians (1963) compared Yellow-headed Blackbird ecology with that of the Red-wing, while Nero (1964) compared the behavioral displays of the two species. Lack and Emlen (1939) recorded preliminary behavioral observations on the Tricolored Blackbird (Agelaius tricolor); Orians (1961) extensively compared the ecology of the morphologically similar Tricolored and Red-winged Blackbirds, and Orians and Collier (1962) explored interspecific interactions between these two species. Lanyon (1957) investigated and compared the biology of the Eastern Meadowlark (Sturnella magna) and the Western Meadowlark (S. neglecta). Williams (1952) studied the breeding biology of the Brewer's Blackbird (Euphagus cyanocephalus). The ecology and behavior of the Brown-headed Cowbird (Molothrus ater) was recorded in Friedmann's classic work (1929); Laskey (1950) elaborated on this paper, supporting its much ques-

tioned views on the cowbird mating system and adding descriptions of displays. McIlhenny (1937), Selander (1960) and Selander and Giller (1961) explored the behavior and ecology of the Great-tailed Grackle (Cassidix mexicanus).

Ignoring the oriole group, two North American species remain largely unstudied, the Rusty Blackbird (Euphagus carolinus), and the Bobolink. Kennard (1920), presented a few notes on the former, but the only substantial study of the Bobolink (Kingsbury, 1933) is unpublished and concerns for the most part distribution rather than basic ecology and the ethological analysis of behavior.

Most papers dealing with Bobolink life history are anecdotal, have incomplete behavioral descriptions and lack precise or quantitative ecological information. Many aspects of life history were compiled and summarized by Bent (1958), but he found little on behavior and nesting activities, although Skutch (in lit.) provided a few nesting details. McAtee (1919) discussed the economic status of the Bobolink, but offered no behavioral treatment. Karr (1964) touched on general life history and habitat utilization. Further life history notes are found in Bendire (1895) and Kendeigh (1941). Graber and Graber (1963) and Tester and Marshall (1961) presented information of habitat preferences. An intensive study of a grassland avifauna in southern Wisconsin by Wiens (1966) included information of vegetative preferences, territoriality, foraging and nesting, and gave a brief distributional summary. A few Bobolink displays were commented on

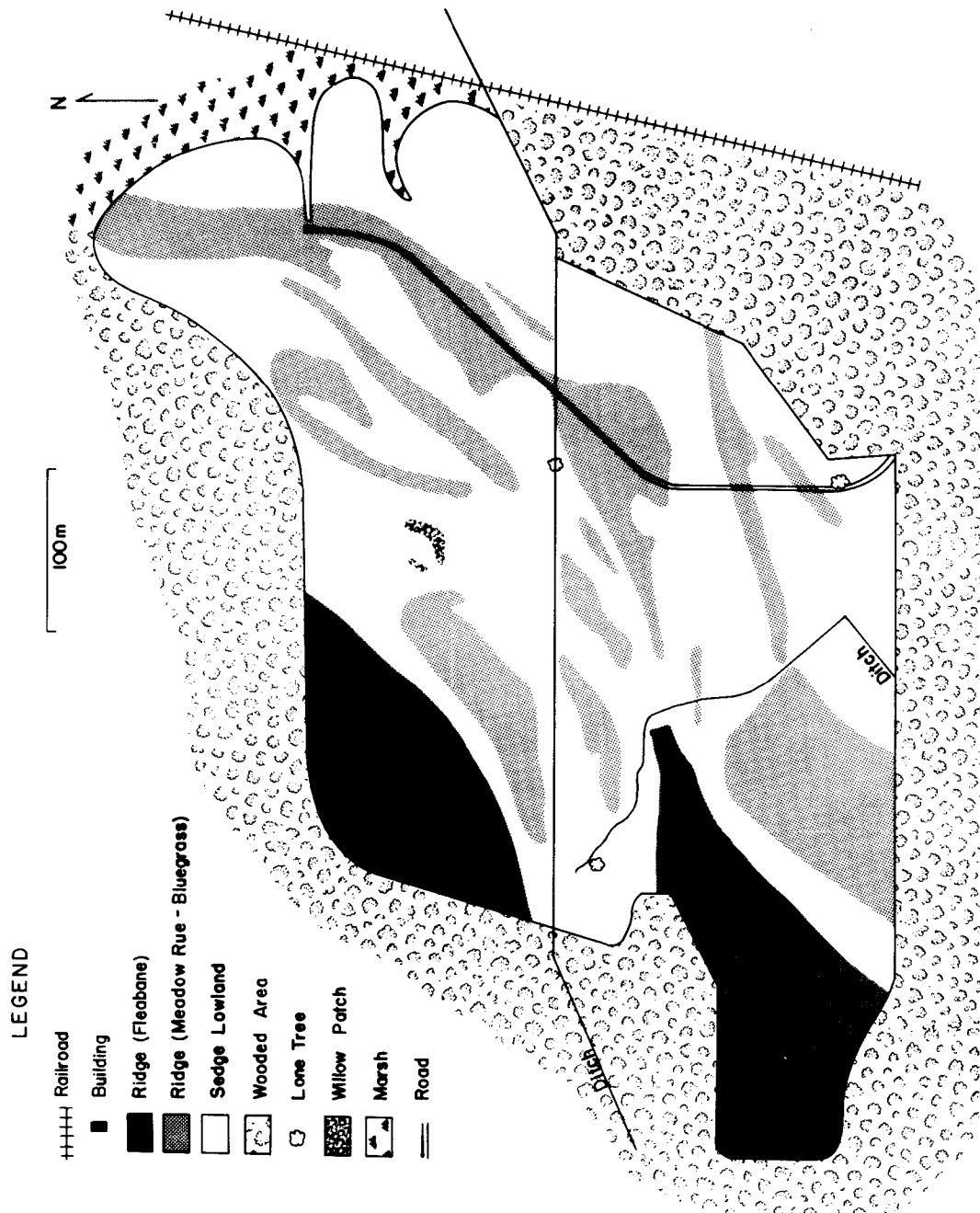
but not described by Nero (1964); this is the only work dealing directly with Bobolink ethology.

II. THE STUDY AREA

The research was conducted on a 28 acre mixed hayfield located on the Wisconsin River floodplain in Dane County, Wisconsin (T9N, R6E, S13). A dense lowland mesic forest (Curtis, 1959) dominated by Silver Maple (Acer saccharinum), River Birch (Betula nigra) and American Elm (Ulmus americana) lies to the south and west, with the river coursing 300 meters beyond. The forest, in a sparser form and dotted with thick clumps of Red-Osier Dogwood (Cornus stolonifera) also extends along part of the eastern border. To the north a dense stand of young Cottonwood (Populus deltoides) grades into the forest. Two small (three and six acres) lowland meadows of similar vegetative composition are less than two kilometers distant and several upland pastures lie about one kilometer to the east. No Bobolinks were resident on these fields.

Figure 1 illustrates the shape, vegetative cover and other salient features of the meadow. From a distance the surface appears level, but at close range the effects of past floods can be seen in the form of long, narrow ridges (Fig. 2 a) shaped by river flow and deposition. This relief, although involving less than one meter variations in elevation, has a pronounced effect on the vegetation of the field. A dam 6.4 kilometers upstream serves a flood control function, but in springs of exceptionally high water the area is sometimes flooded to a depth of up to one meter (O. Ballweg,

Figure 1. Map of the study area depicting salient features and the three major vegetative cover types.



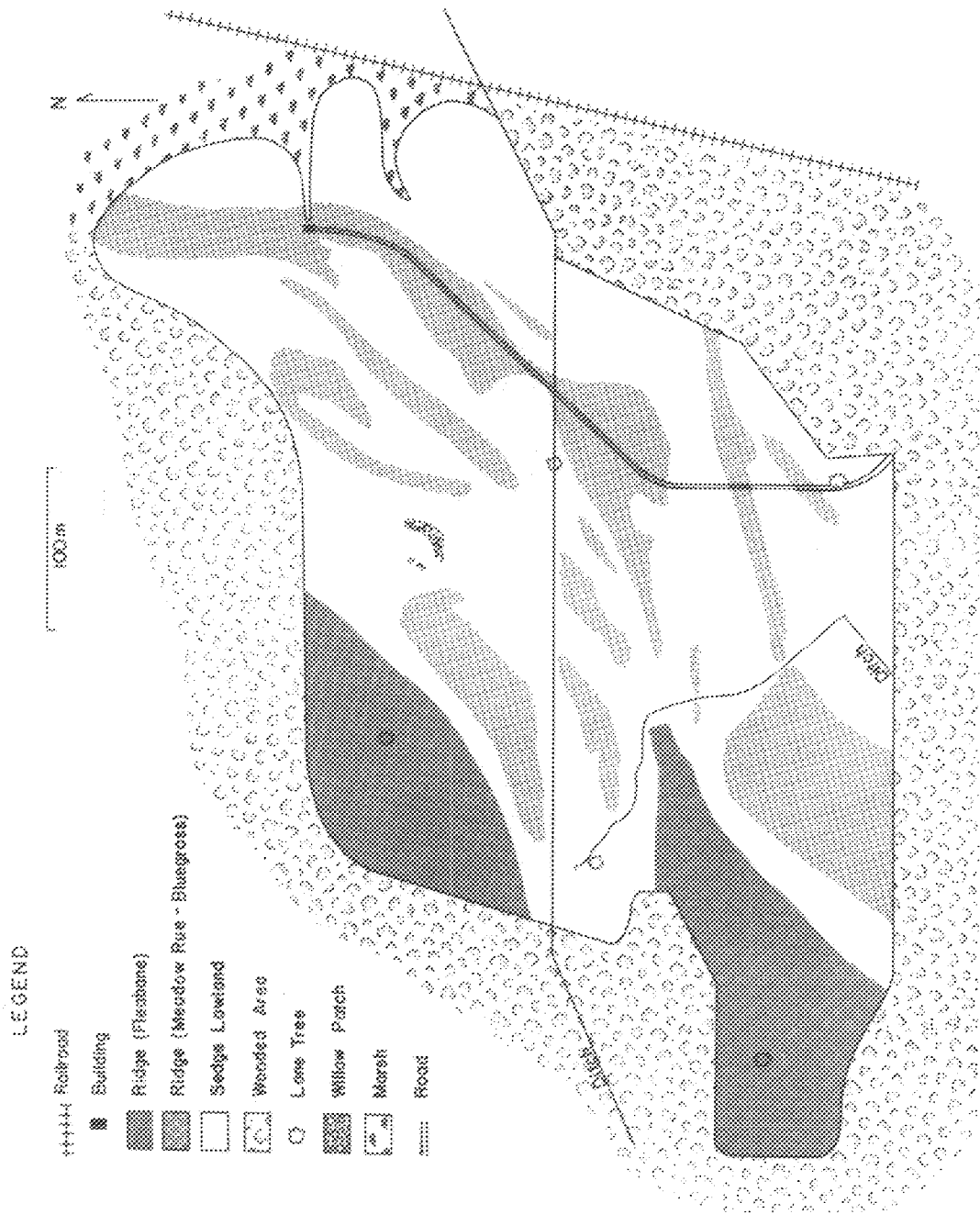
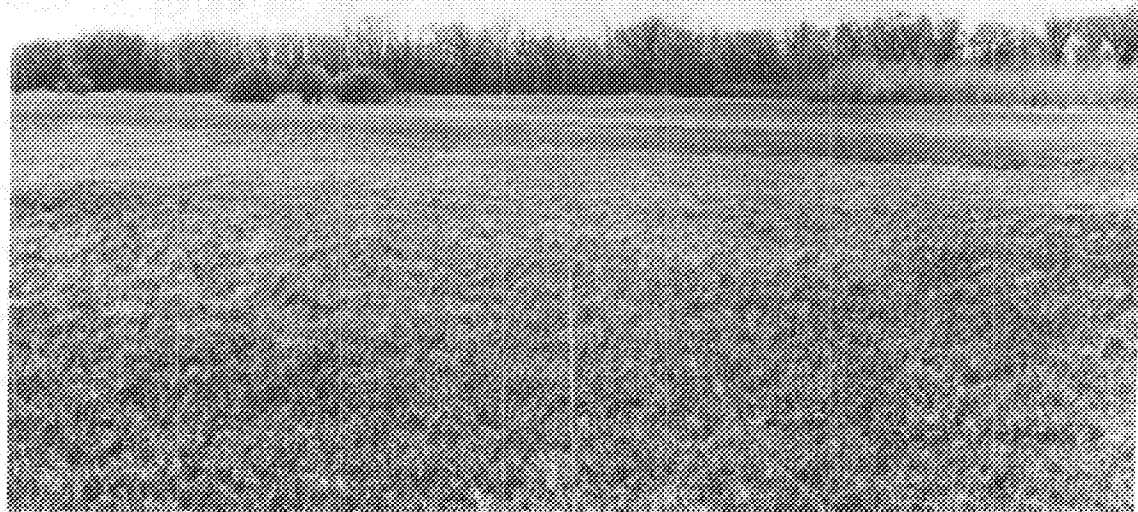
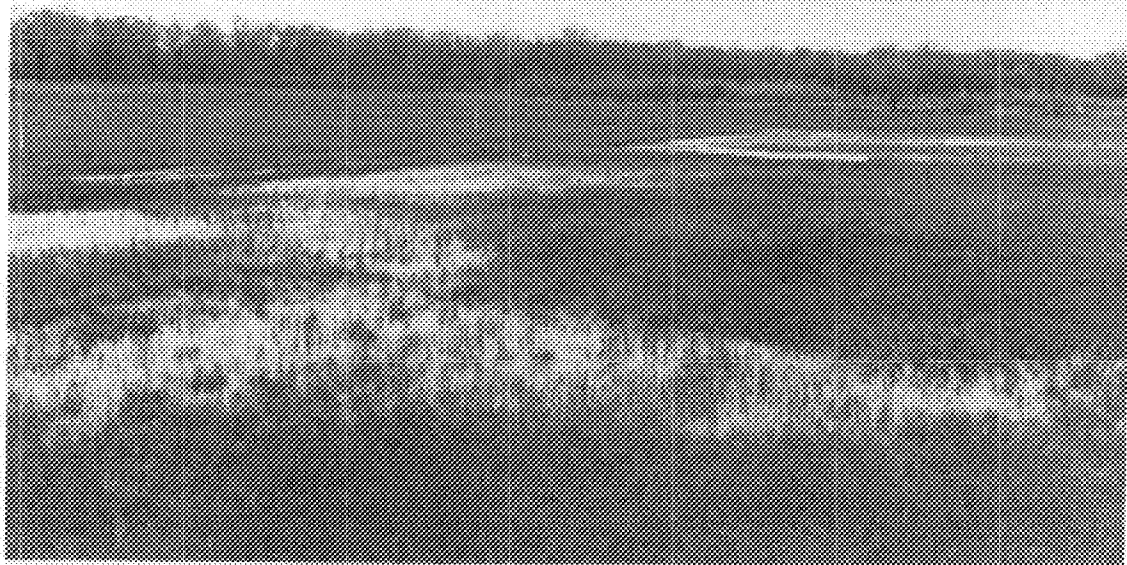


Figure 2. (a) A view looking west, illustrating the form of the long ridges (center). In the left background is the willow patch, and to the right is the Cottonwood stand which borders the meadow. Exposure taken on 1 May, 1967; (b) standing water on 15 May, 1967, two days after a hard rain. A portion of the stake grid system can be seen in the left background. The view is toward the northwest.

**A****B**



A

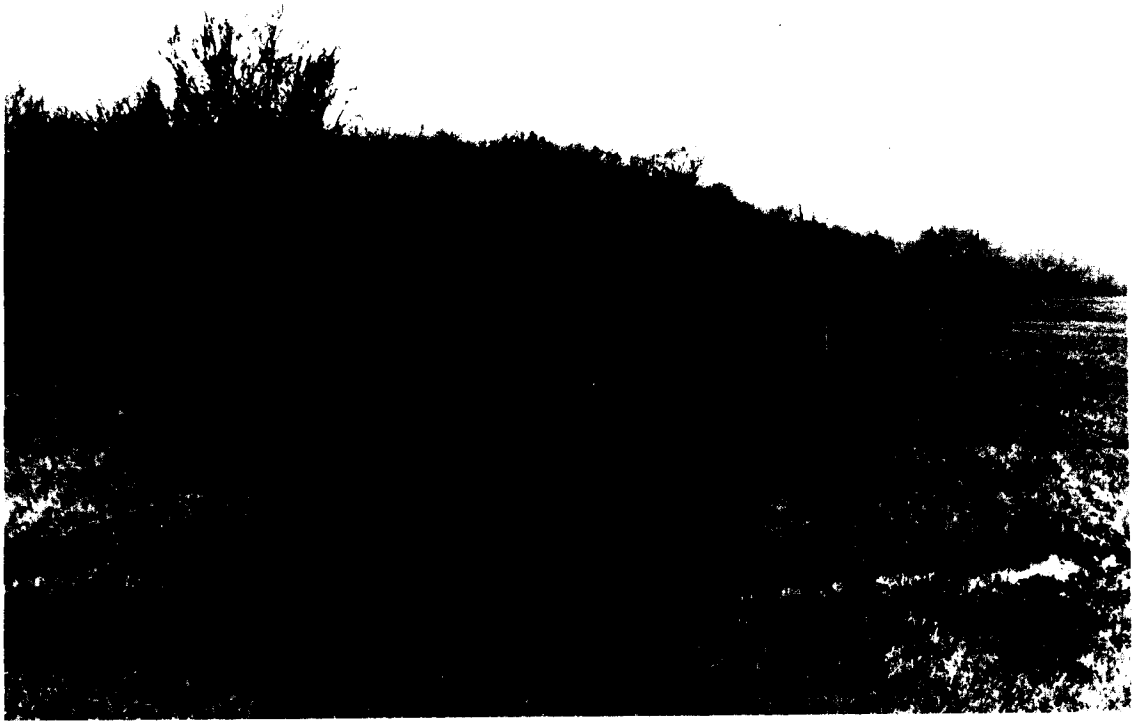


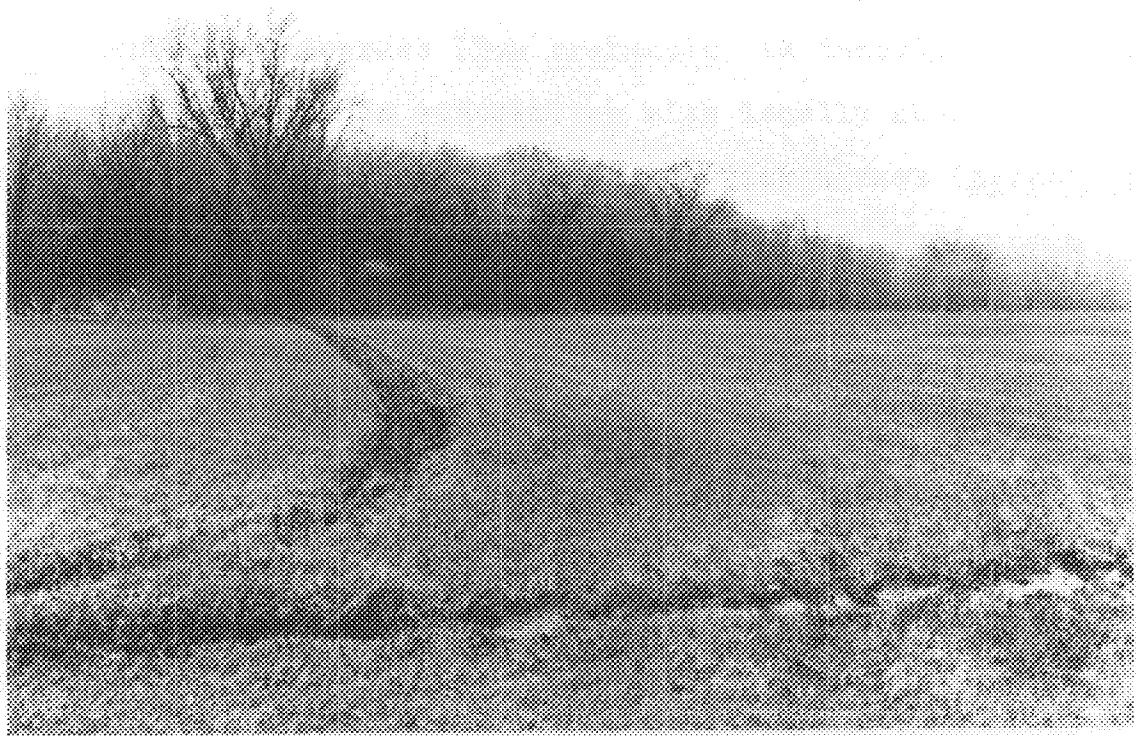
B

pers. comm.). Soils of the meadow are classified as "alluvial soils, undifferentiated"; the ridges are composed of fine sand, becoming coarse at a depth of 1-1.5 meter, overlain by 15 to 20 cm of black top soil. Between the ridges a layer of oxidized muck grades into a deeper peat zone, very rich in partially decomposed organic material; at a depth of about 0.8 meter a thin 8-10 cm layer of clay mixed with small amounts of fine sand is sandwiched between the rich peat and the coarser sand that apparently extends beneath the entire meadow. This sand is very wet and probably is at the water table level of river seepage. The basement zone of clay-fine sand is an exceedingly sticky, plastic mixture which is relatively impermeable. Thus, the peat layers above retain water for long intervals. While the sand ridges are dry by mid-May these lower stretches remain spongy, even in floodless years, until early June, and June rains result in 25-30 cm of standing water in certain portions of the lower tracts for up to five days (Fig. 2b).

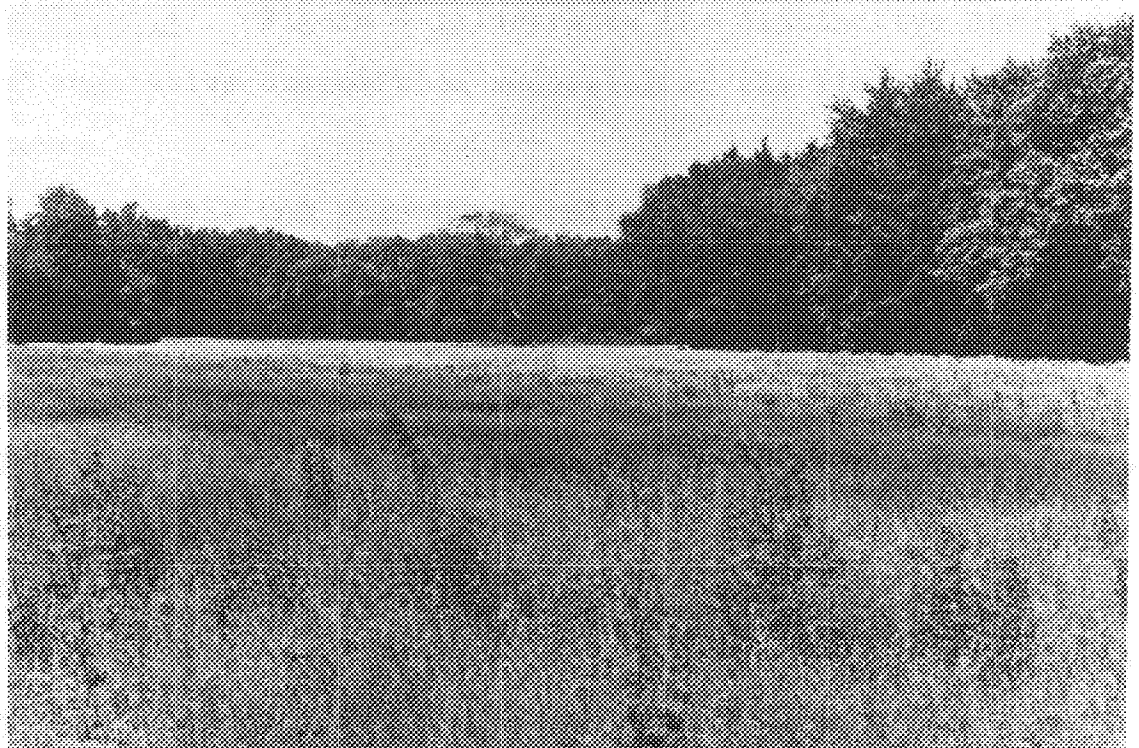
An old drainage ditch, arched at intervals by three to five meter willows (Salix) and low brambles (Rubus) serves as a water supply for birds and divides the field into two parts. Additional shallow ditches (Fig. 3a) providing for increased water runoff traverse the southern portion of the meadow. Within the field are three widely spaced American Elms and a River Birch, all about 20 meters high, and a small patch of five meter high willows.

Figure 3. (a) Looking southwest over a drainage ditch on 29 April, 1967. Note the sparseness of vegetation at this time, just prior to arrival of Bobolinks. (b) A view showing the Fleabane-covered ridge occupying the southwest arm of the meadow, taken in early July. Bobolinks avoided the two large ridges on the study area that were covered with Fleabane. Note that the forbs which offer excellent perches for Bobolinks rise high above the surrounding grass and sedge.

**A****B**



A



B

Kentucky Bluegrass (Poa pratensis) is densely distributed over the ridges in association with locally abundant growths of Timothy (Phleum pratense), Ticklegrass (Agrostis scabra) and Redtop (A. gigantea). Meadow Rue (Thalictrum dasycarpum), the dominant forb is found in thick irregular patches on the ridges, but like Golden Alexanders (Zizia aurea), it is scattered here and there in the moister regions. Fleabane (Erigeron pilosus) covers the elevated portions of a large ridge forming the field's western edge (Fig. 3b). The low areas are densely vegetated with a sedge (Carex), and locally, with a manna grass (Glyceria), Canada Anemone (Anemone canadensis) and Saxifrage (Saxifraga pennsylvanica). Figure 4 illustrates the distinctive zonations of vegetative composition occurring at the ridge-lowland interfaces.

In early May when the Bobolinks arrive the new annual growth is only a few centimeters high and old growth stands as a coarse stubble about 10 centimeters tall over a loose mat of dry grasses. The meadow is usually mowed early in July when the Meadow Rue stands about 1.5 meters tall and the sedges and grasses are .5 to .7 meter tall, and again in September.

In addition to the Bobolink, birds found nesting on the meadow in 1966 were two pairs of Song Sparrows (Melospiza melodia), about ten pairs of Savannah Sparrows (Passerculus sandwichensis), at least six pairs of Eastern Meadowlarks

Figure 4. Two examples depicting the abrupt change in vegetative species' composition which occurs along the base of ridges. Photograph A was taken on 10 July, 1966 after Bobolinks had vacated the field, and B was shot on 1 July, 1967.



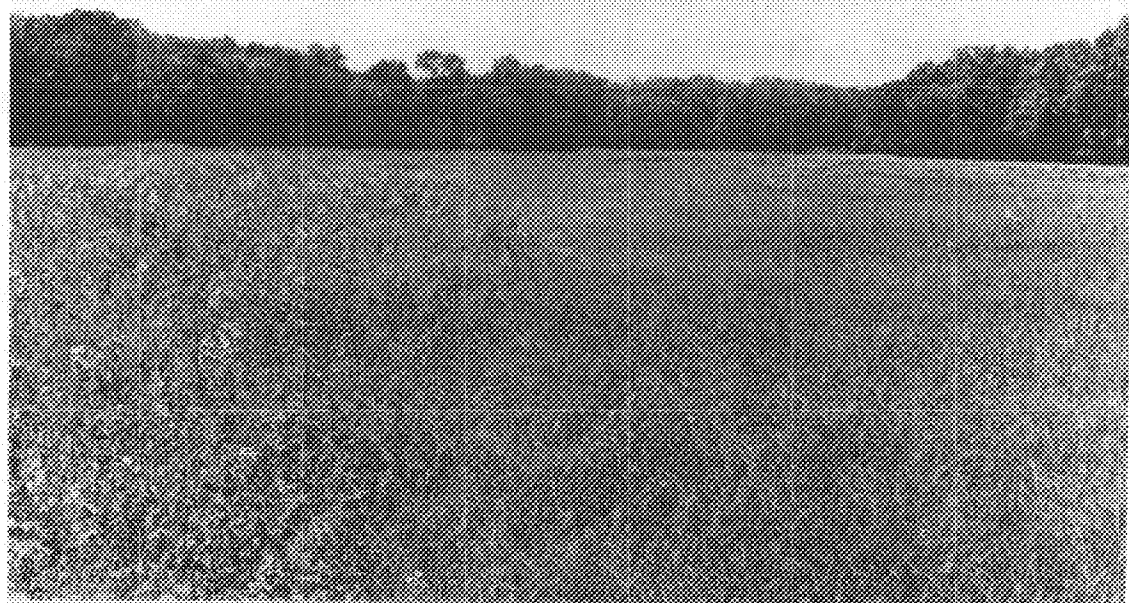
A



B



A



B

and about five pairs of Red-winged Blackbirds. Brown-headed Cowbirds parasitized some of the nests of these species, and Common Grackles and Robins (Turdus migratorius) were often observed foraging in the meadow. At least two pairs of Traill's Flycatchers (Empidonax traillii) and one pair of Bell's Vireos (Vireo Bellii) nested in the Willow patch.

In many respects the meadow is an ideal locality for studying grassland birds. The lack of major relief allows unhindered observation of bird movements over almost the entire field. The ground vegetation has two distinct canopies, the fairly short grass-sedge canopy and the taller forb canopy; the birds utilize the two layers differentially, for the majority of song and display is performed on the fairly rigid tall forbs where the birds are positioned in view. Additionally, the meadow is isolated from roads, the only access being barred from public travel. Thus, extraneous noise and disturbance are held to a minimum.

III. PROGRAM AND METHODS

Field research was initiated on 30 April, 1966 with the arrival of the first male, and terminated on 8 July 1966 when the last Bobolinks left the meadow. Notes were taken on a total of 51 days, with additional trips made after 8 July to verify the birds' departure. Attempts were made to distribute observations evenly throughout the bird-day, but the bulk of field work fell between 0700-1200 hours and 1800-2000 hours. However, all hours between 0500-2030 hours were sampled. Unseasonably cold, rainy weather prevented field work on 9, 11, 12 and 13 May. Supplemental behavioral records and photographs obtained in May and June, 1967, are included in this paper.

Observations were made from elevated vantages on a hay wagon, hay rake and from a tree, as well as from ground level with the aid of 7X35 binoculars and a 20X spotting scope. Throughout the study a battery-operated tape recorder was used for dictating descriptions of display sequences and other pertinent activities requiring the observer's full attention. At intervals throughout the breeding season five to twenty-five minute continuous taped records were made of activities of selected individuals, to provide quantitative data on times budgeted for various activities. Each evening all recordings were transcribed verbatim to a notebook. A 35 mm still camera and a 16 mm motion picture camera were used extensively. Both were equipped with long

lenses (8X and 12X respectively); the latter was particularly valuable for catching rapid behavioral sequences. A Kodak analyst II Stop-motion Projector was used in analysing films.

In mid-May meter-high stakes were placed in a grid system at 125 foot intervals over the south half of the field. In addition to enabling plotting of territorial boundaries, the stakes served as convenient song perches for the birds, facilitating observation and filming. Shorter stakes were placed one meter from nest sites to mark locations. Nests were discovered by chance encounter, by systematic traversing of territories and by prolonged observation of attending females. Once young had hatched adult feeding trips indicated nest positions.

Adults were not banded in 1966. However, of fifteen males remaining through the breeding season seven were recognizable on the basis of plumage or voice: nape patches varied from nearly white to bright gold; intensity of black and white contrasts on the upper surface varied; local areas of white upon black undersurfaces when sufficiently large afforded recognition; one male was very brown below; missing rectrices identified one individual; one male began the Song-spread display with a unique "twangy" note. Females were not recognizable except on the basis of nest and mate associations. Variations in female plumage existed, but their shy and inconspicuous behavior made these difficult to detect. A total of 51 nestlings were banded.

IV. BREEDING ECOLOGY

Habitat Preferences

The Bobolink prefers open fields with relatively lush cover. In Illinois, Graber and Graber (1963) discovered high breeding densities in pastures, ungrazed grasslands, and red clover and alfalfa fields, with highest densities in oat and mixed hay fields. Low numbers or complete absence were characteristic of shrub-grown, forested, marsh or agricultural lands growing spaced crops (eg. soy bean).

Tester and Marshall (1961) suggested that litter depth is an important factor in limiting Bobolink distribution in Minnesota, for at a series of test locations the species inhabited only those regions possessing intermediate litter depths. However, in Wisconsin I have found high Bobolink densities in upland alfalfa fields where there is practically no ground litter. Oat fields, found to have high breeding densities in northern Illinois (Graber and Graber, op. cit.) normally have little or no litter. A preliminary analysis of litter samples taken at and within one meter of Bobolink nests on my study area suggests that females select nest sites where there is less litter than the average litter over the male's territory as a whole. Wiens (1966) determined that litter in Bobolink territories was more variable than in territories of most other species inhabiting his study

area. This is all evidence that an "intermediate" litter depth is not as important a factor in Bobolink distribution as Tester and Marshall thought it to be.

Kingsbury (1933) believed that Bobolinks prefer to nest in fairly small meadows or large fields broken by trees, bushes or fence posts serving as male song perches. "Wide, unbroken stretches of meadow do not appeal to them," she remarked. But Good and Dambach (1943) found Bobolinks more common in large fields than in narrower strips, and Wiens (op. cit.) felt the species is "characteristic of large, open fields" having lush grass and forb cover. Fields lacking trees and shrubs were found to have high Bobolink densities by Graber and Graber (op. cit.). This suggests that woody vegetation is at least not a requisite for good Bobolink habitat. In my study males spent relatively little time singing from trees and bushes. Despite scarcity of trees and shrubs within the Bobolink territories, the meadow had an extremely dense male population (see Table 1 for territory sizes). Perhaps more important than woody vegetation for ideal Bobolink habitat in southern Wisconsin is an availability of forb song perches that rise above the surrounding vegetation. My casual observations suggest that most alfalfa and clover fields with high breeding populations have weed species or grass clumps with this characteristic. On areas lacking such natural perches Bobolink numbers appear to be sparser, and in these situations, I feel, trees and

shrubs may serve as substitutes for song perches. Grid stakes placed on my study field were used extensively by the birds as song perches. These were not introduced, however, until resident males had become established, and therefore were not responsible for the high numbers.

On my study area no Bobolink territories (see Territory Size for methodology of territorial determinations) were contiguous with forest edge. Indeed, an unoccupied "buffer zone" ranging from 10 to 30 meters in width existed between the forest and territory peripheries while the central portion of the area was almost completely occupied (see Fig. 6). No nests were located within 40 meters of the forest edge. I suspect a "psychological" factor limits Bobolink activities to regions distant from dense forests, and that birds that are specialized to conditions of open grassland may be more susceptible to predation in or close to dark woods. There is evidence that a number of such psychological factors operate in the selection of nesting habitat by birds (Lack, 1933, 1937).

Birds have commonly been "assigned" to various artificial categories of "preferred" habitat on the basis of subjective appraisals of association between species' presence and vegetative physiognomy. Species are pigeon-holed in this manner, often with little or no effort made to distinguish between subtle vegetative variations which may be very important in the micro-distribution of the species

within the assigned category. It is requisite that the X number of species occurring in "grassland habitat" must each show specialized utilization of the grassland to prevent excessive competition. Unfortunately, studies analysing differential use by birds of slight physiognomic differences over a fairly homogenous habitat are rare. Wiens (1966), in such a study of grassland birds, discovered the following relationships between habitat and Bobolink presence:

(1) Coverage of forbs in Bobolink territories was comparable to that in territories of most of the other grassland species in his study area (Eastern and Western Meadowlarks, Savannah Sparrow, Grasshopper Sparrow (Ammodramus savannarum), Vesper Sparrow (Pooecetes gramineus) and Henslow's Sparrow (Passerherbulus henslowi); average forb height was greater than in territories of all other species except the Henslow's Sparrow.

(2) There was a slightly greater area of unvegetated ground than in territories of most other species.

(3) Light penetration to the ground in Bobolink territories was less than in territories of all of the other species except the Henslow's Sparrow.

(4) The mean effective height of vegetation was greater than in territories of most of the other species except the Henslow's Sparrow. The effective height was somewhat less variable than in most species.

(5) Litter depth in Bobolink territories was deeper or

equal to that of all species except the Henslow's Sparrow. However, the litter depth was more variable than in territories of other species.

Thus, on Wiens' field Bobolinks selected regions which had thicker (less light penetration) and higher (higher mean effective heights, and higher forbs) vegetation than the regions selected by all but one of the six other species. However, slightly more bare area was present in Bobolink territories than in those of the other species. Other vegetative characteristics of Bobolink territories were comparable to those selected by the other six species.

On my study area males preferred the dense accumulation of tall forbs on the ridges over the sedge in the lowlands for song perches, and females nested beneath Meadow Rue. Vegetation thus influenced the type and degree of use that portions of a territory received, and probably had an important effect on the ability of males to procure mates. For instance, territories containing sparse Meadow Rue provided little suitable nesting habitat, and males occupying them were rarely successful in obtaining more than one mate. Bobolinks apparently never used the western ridge covered with Fleabane and sparse low bluegrass for either foraging or nesting. Similarly, small wet regions were either excluded from territories, or if included, received relatively light use.

Arrival of Birds

Males

In Dane County the average date of first reported observations of male Bobolinks for six years was 30 April (U.W. Zoology cooperative migration charts). On 29 April, 1966 three males were reported on a grazed pasture in Fitchburg Township 39 kilometers from the study area, and the following day I saw two males briefly on my study area. Between 1 and 4 May the number of males observed on the meadow during 70 to 150 minute observation periods varied from two to six; on 5 May none were seen and only two males were noted on 6 May. It is uncertain whether these early arrivals were resident males that failed to settle down or whether some or all were transients. Evidence from observations on color banded individuals in 1967 clearly indicates some of the earliest arrivals in that year remained to breed, and that until these birds settled down on territories their behavior was similar to that of the earliest male arrivals of 1966. In the Red-winged Blackbird, Nero (1956a) found that resident males arrived on the breeding area before transients visited the area.

Early arrivals occasionally spent as little as 50 seconds at the meadow, arriving from and departing toward the direction of the large upland fields to the east. When in flocks, little overt hostility was evidenced, the

birds often flying and foraging as a group. When flushed by the observer a group usually dispersed above the field, usually converging some distance away. A flushed individual commonly landed near another bird or group, showing little tendency to return to its former region.

The behavior of these early arrivals was characterized by four features:

(1) Song-spread (see Visual Agonistic Behavior), although present, was infrequent (mean 0.8 songs/minute, $n=52$ minutes compared to 2.7 songs/minute, $n=56$ in mid-May) and did not appear to be oriented towards other individuals or to lead to encounters and chases. Nero (op. cit.) noted a similar low intensity Song-spread performed by Red-wings under similar circumstances. In the Bobolink these songs were not given consistently from specific perches, but from any elevated position.

(2) Early arrivals usually left the meadow after as few as two flushes, whereas territorial males were never driven from their relatively small territories during 50 consecutive flushes.

(3) After flushing, early arrivals remained aloft for up to one or two minutes, sometimes circling the entire meadow two or three times before re-alighting. This was in contrast to the short duration of the more direct, intra-territorial flights of resident males.

(4) Early male arrivals remained in unsettled, drifting

groups that formed no attachment for a particular locality. Occasionally lone individuals or small groups appeared over the meadow, dropping down to forage and mingle freely and peacefully with those already present.

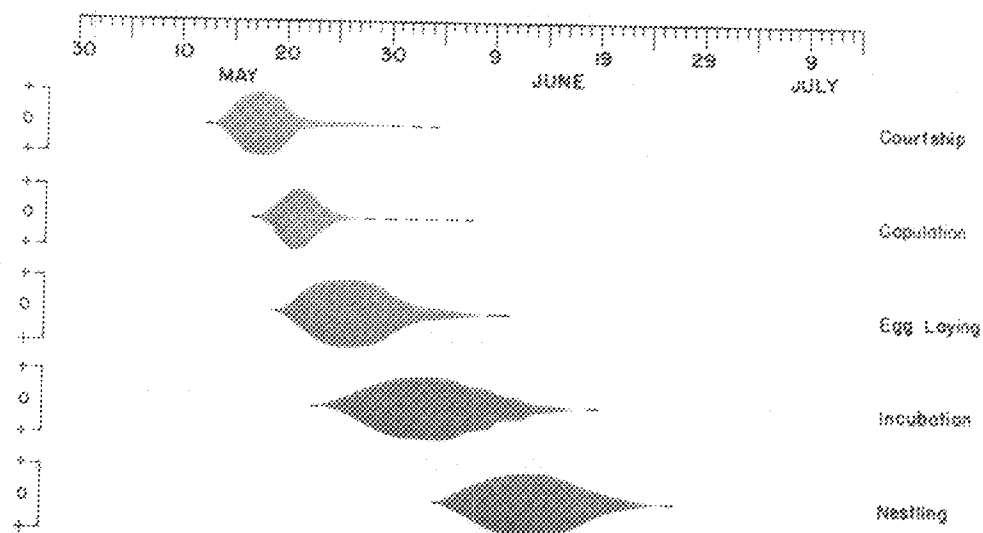
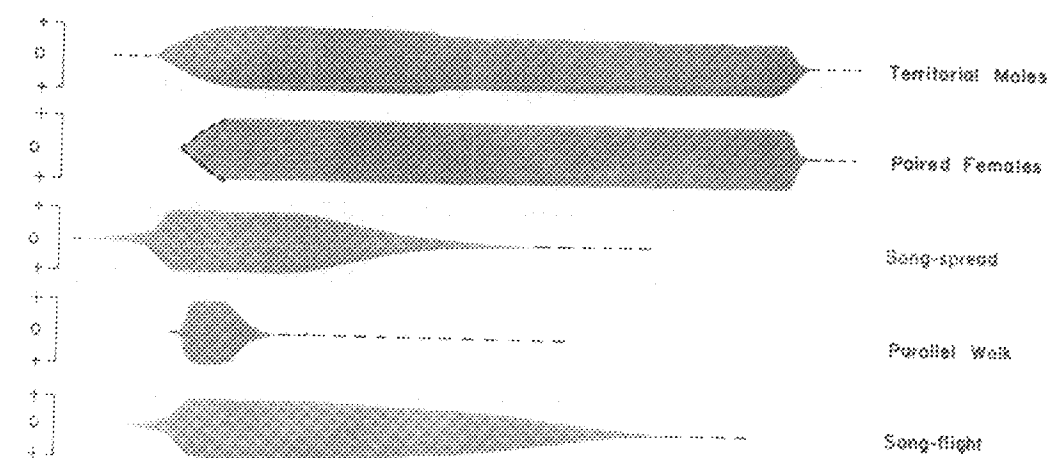
On 7 May an influx of approximately 15 males occurred and several individuals gave first evidence of territorial behavior. Cooke (1888) thought that the main influx of Bobolinks occurs about 10 days after the first arrivals. For five years in Dane County the major influx of males averaged 8 May (Passenger Pigeon back issues). Wiens (1966) found a latency of about 10 days (1964), 12 days (1965) and six days (1966) in territorial establishment following observation of the first male Bobolink on his area. His six day interval in 1966 compares with an eight day latency on my study area.

Of three males identified individually on 7 May two were gone on 8 May and one remained to breed. Four other birds exhibiting territorial behavior on 7 May apparently remained, for on 8 May four birds were noted defending areas at the approximate localities of defense the previous day. Thus, the 7 May wave apparently consisted of both transient and resident males.

The number of males displaying good territorial behavior on the meadow increased from five (7 May) to nine (8 May) to 12 (10 May) to 15 (14 May) to 16 (15 May) (Fig. 5). Fifteen of the sixteen males occupying territories on 15 May

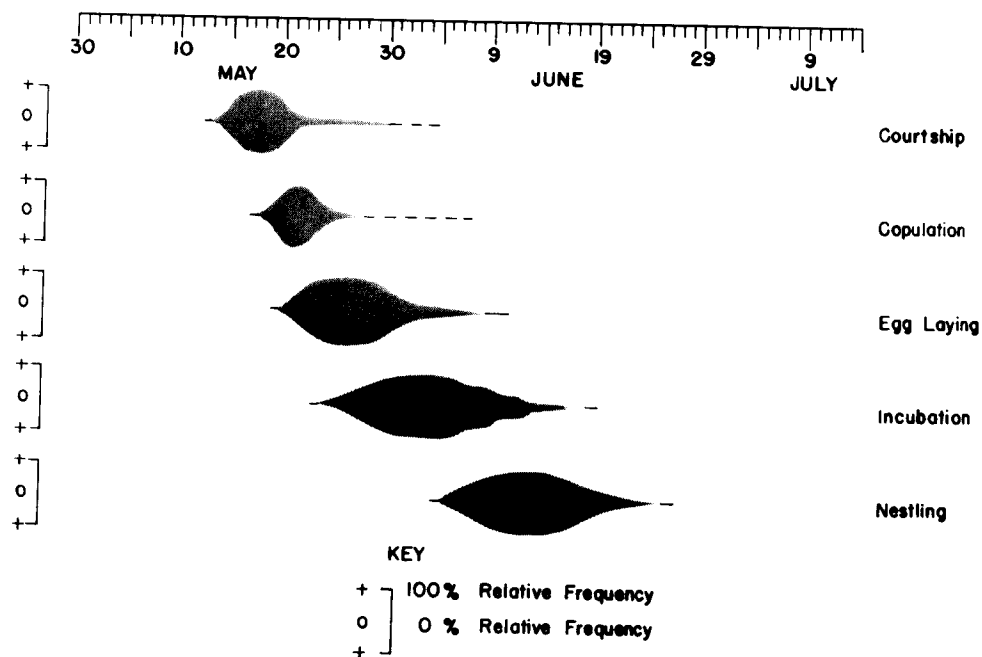
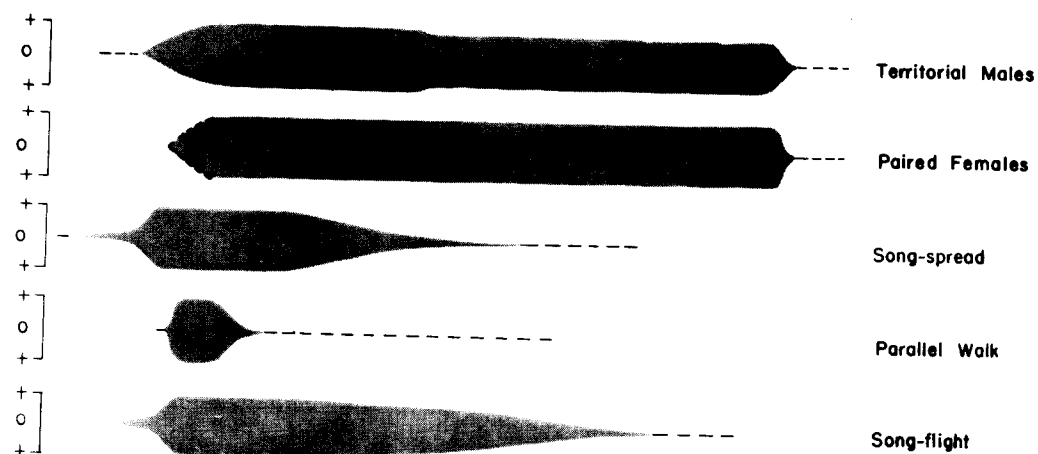
Figure 5. Chronology of events throughout the breeding season. For each date the vertical component of a horizontal time bar represents the relative frequency of occurrence of that particular category listed to the right of the bar. Broken lines indicate that occurrence was too infrequent to be quantified.

Figure 5. Chronology of events throughout the breeding season. For each date the vertical component of a horizontal time bar represents the relative frequency of occurrence of that particular category listed to the right of the bar. Broken lines indicate that occurrence was too infrequent to be quantified.



KEY

+ } 100% Relative Frequency
 0 } 0% Relative Frequency
 + }



remained through June, the sixteenth disappeared between 1 and 2 June. Although a few transients were noted occasionally throughout the breeding season none were known to remain for more than one day; however, the absence of clear identification marks makes it impossible to be sure that replacements did not occur. In 1967 two known instances of such replacements were recorded among 15 resident males.

The arrival of Bobolinks on Wiens' study area was spread over a longer period of time in 1966, and a few territories were not established until late May (pers. comm.). However, his grazed upland pasture offered relatively sparse habitat and nesting cover, and these late male arrivals may have been drifters unable to establish territories elsewhere.

Females

On 7 May the first female, individually recognizable by her bright yellow caste, was seen for a short while on the meadow; on 8 May it was gone and a darker female was present. Two females were seen on 10 May. By 14 May the majority of the resident female population had arrived and most were associating with territorial males. Inclement weather prevented ascertaining whether the increase between 10 May and 14 May was gradual or abrupt and whether resident females arrived individually or in groups, but in 1967 females arrived suddenly in large numbers, with residents among the first arrivals.

Kingsbury (1933) remarked that in New York female Bobolinks appeared singly, over a period of several days, unlike males which arrived in flocks. Bent (1958) noted that females often followed arrival of males by as much as a week; Kingsbury found an interval of nine days, and in my study a period of seven days elapsed between observations of the first male and female. In 1965 Wiens (pers. comm.) observed the first female on his study area 12 days after arrival of the first male. Upton (1918) reported that mixed flocks of migrating Bobolinks stopped in Georgia, arriving about 20 April. The "flock" remained in the region two weeks or more, but a continuous change of individuals occurred; females, initially in the minority, in time out-numbered the males, as the first of the latter departed as early as two weeks ahead of the females, which left gradually. Kingsbury thought that transient females arrived six days or more prior to resident females in Massachusetts.

Territory

Definition

Bobolink territories are vigorously defended by males against conspecific male intrusion: the areal components are both horizontal and vertical, for defending males do not tolerate other males flying low over their territories. Pair formation, courtship, nesting and the majority of foragings occur within the territory; thus, in the terminology of

Hinde (1956) the Bobolink maintains a modified type A territory. The entire area of the territory is utilized for foraging and display, but the male shows periodic preferences for certain portions of his territory during courtship, depending upon the location of the courted female. Courtship demands occasionally concentrate the male's activities within certain restricted regions, allowing adjacent males to encroach on other parts of the territory. Once the female initiates nesting, however, the male is usually successful in driving all intruders beyond the territory boundaries. Thereafter, intensity of maintenance by a male varies with the stages of breeding progress of his female. After young fledge, males are less persistent at territorial defense and usually tolerate other males well within their boundaries.

Previous authors have contended that Bobolinks are non-territorial. Kendeigh (1941) stated: "Notable in this species was the lack of territorial defense by either the adult male or female." His observations were made fairly late in the nesting season, when the mechanism for territorial advertisement had shifted from localized aggressive displays to group Song-flights involving many neighboring males. These group flights lack aggressive components and their connection with territorialism is easily overlooked. Kingsbury (1933) remarked that males are relatively non-aggressive and that often birds do not drive away males perched close by. She is reluctant to suggest that males defend specific areas, yet

she speaks of territorial behavior and describes violent attacks on mounted males. Karr (1964) was unclear as to the extent of Bobolink territorial behavior, but his study began too late in the season for observation of the aggressive encounters involved in territorial establishment.

Contrary to these reports, the Bobolinks on Wiens' (1966) study area "established territories shortly after their arrival and defended them vigorously well into the nesting season."

Territory Size

The multiple-flush technique (Wiens, 1966) was used for mapping territories. After flushing a bird I recorded on standard map forms the bird's initial position, its line of flight and its settling point. The bird was then reflushed and the information for the second flight was added to the map. A series of twenty to twenty-five consecutive flushes per male was usually sufficient to outline the boundaries of the home area. When these records were compared with data on the locations of observed aggressive interactions between rival males the two independent sets of records coincided closely. A composite map of all territories so compiled on the study area had a mosaic pattern of contiguous areas.

The flush procedure was conducted for each male on both 22 May and 5 June (see Fig. 6), and for some males on three consecutive days immediately after territory establishment. The method proved to be ineffective for females.

Figure 6. Bobolink territory configuration on 5 June, 1966. Territories are numbered and nest locations are indicated by underscored numerals. Also depicted are the positions of the three communal foraging regions.

LEGEND

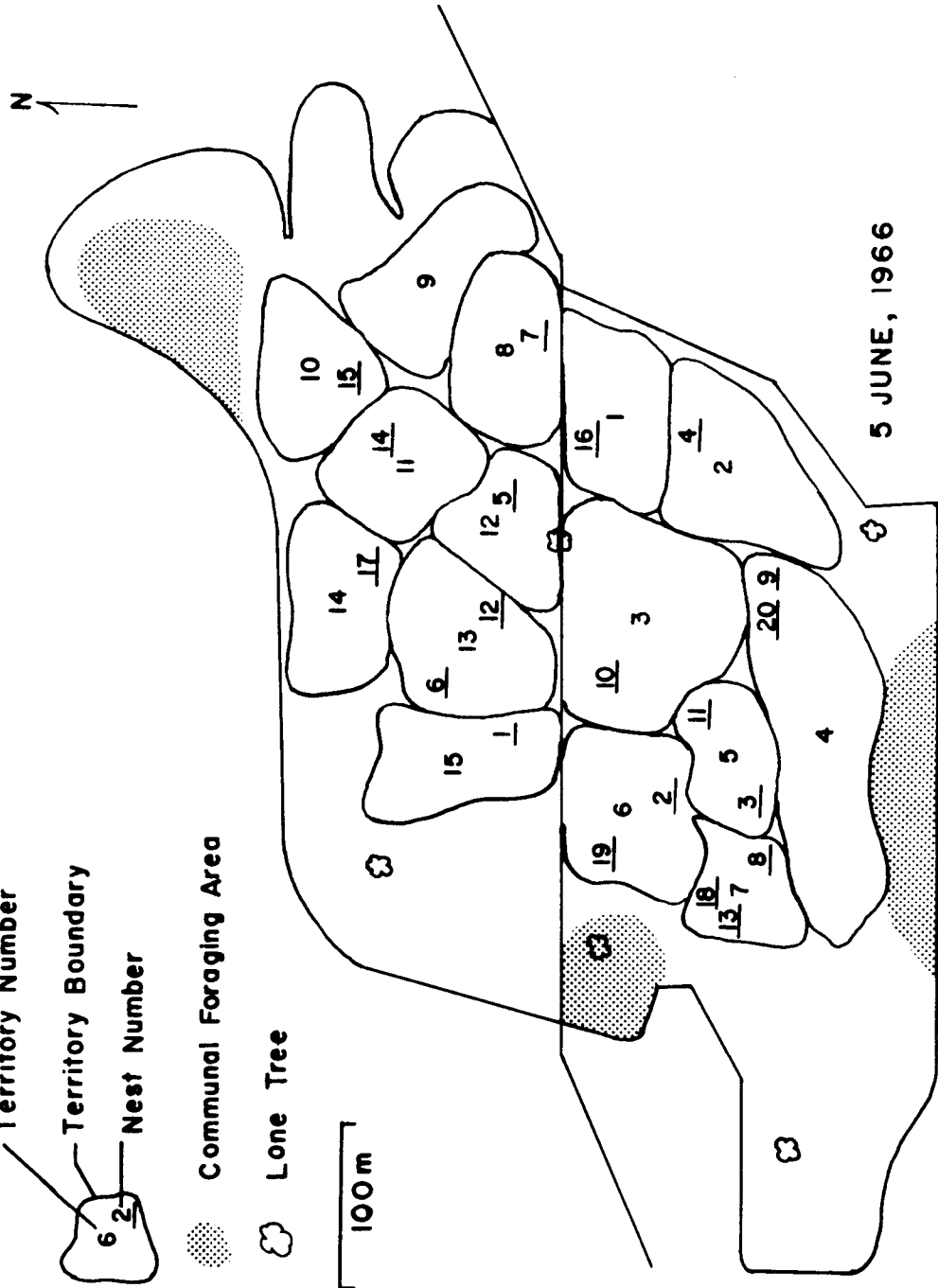
Territory Number

Territory Boundary

Nest Number

Communal Foraging Area

Lone Tree



Once established, territory positions were stable although exact boundary lines shifted slightly during the breeding season. Boundary fluctuations apparently occurred without reference to song perches, natural or artificial, for certain of these were included in one territory at one time and in another later. Bryant's (1943) modified acreage grid procedure was used to convert the 5 June map representation to a quantitative assessment of territory size. Table 1 gives territory sizes for the fifteen males present on that date. The average size of territories was 1.1 acres.

Table 1.

Territory size (acres) of male Bobolinks, 5 June, 1966

<u>Male</u>	<u>Acres</u>	<u>Male</u>	<u>Acres</u>	<u>Male</u>	<u>Acres</u>
1	1.0	6	1.1	11	0.8
2	1.3	7	0.7	12	0.8
3	1.7	8	0.8	13	1.6
4	1.3	9	0.9	14	1.4
5	0.8	10	0.8	15	1.4

Using the same methods, Wiens (1966) determined average Bobolink territory sizes of 9.2 acres (1964), 5.9 acres (1965), and 4.9 acres (1966) (a three-year average of 6.3 acres) on a dry, more sparsely vegetated grazed upland field

which had a substantially smaller Bobolink population.

Female Territoriality

Fautin (1940), Willson (1966), and Nero (1956b) have described female territorial defense in the Yellow-headed Blackbird and Red-winged Blackbird. The general pattern is one in which each female shares the territory of its mate, yet defends a region within that territory against intrusion by conspecific females. Prior to nest building a fairly large area is defended, but by initiation of egg laying female aggression subsides except in the area close to the nest. Although in these species female territories are not as bitterly contested as male territories, the same means of defense are employed by both sexes. Red-wing females direct well-developed Song-spread (see Visual Agonistic Displays) and Bill-tilting displays toward other females; and like males, females attack and chase intruding females.

Unlike the species described above, female Bobolinks show little aggressiveness toward one another and apparently lack high-intensity counterparts of male displays. This low level of female-female interactions in the Bobolink is correlated with a relatively low incidence of polygamy and a smaller number of females per male territory as compared to the Yellow-head and Red-wing. Nevertheless, in territory 7, the only one in which I discovered three females nesting simultaneously, five aggressive attack-chases between females

were observed between 24 to 28 May. Of these, three were instigated when one female alighted above another in a Meadow Rue, ruffed its nape feathers, and then pounced upon the other. In the other two instances a perched female turned to face another and performed a brief wing-spread just prior to diving at the other bird. A swift short flight ensued in each case, terminating as the pursued bird dove into the vegetation. On one occasion the aggressor dove twice again onto the pursued female after the latter had dropped into cover.

Aside from these five conflicts, no female-female aggression was observed on this male's territory, which was the smallest on the meadow. More females were located on this territory than on any of the larger ones and this density may account for the conflicts. No agonistic female encounters were observed other than Bill-flipping on those territories containing two females. It thus appears that in the usual relatively uncrowded circumstances of monogamous pairings, female Bobolinks are non-territorial.

Interspecific Responses

Bobolink males were very aggressive toward most other species during early phases of the breeding cycle, and frequently drove such individuals off song perches located on Bobolink territories. Aggression usually consisted of a short dive or swoop, either from the air or a perch, followed

by a displacement from the perch or by a chase of from one to over one hundred meters. Seven attacks were observed against flying individuals. In most cases no physical contact was actually made, the subordinate bird departing as the aggressor approached; less frequently, however, there was momentary contact and in these situations the ensuing chases usually were of longer duration and involved more intense and persistent behavior. On one occasion a Bobolink male dove directly onto a foraging Savannah Sparrow, and the two tumbled about on the ground for six to eight seconds before the Savannah Sparrow escaped. A lengthy chase followed. In no case was any display observed to precede these engagements, and in each of the 56 observed interspecific skirmishes the attacked individual fled.

Table 2 analyses the 56 interactions. Although the Bobolink was the aggressor species in 68 per cent of the encounters, male Red-winged Blackbirds dominated both Bobolink sexes in 15 of 16 conflicts. Excluding the Red-wing, Bobolinks dominated in 94 per cent of the interspecific exchanges. Of interactions initiated by the Bobolink, 66 per cent involved Savannah Sparrows and 88 per cent of these resulted in displacement of the sparrow from a song perch. Not infrequently, Bobolinks initiated a second and third chase once the Savannah Sparrow had alighted elsewhere.

The peak of interspecific aggression occurred between 13 May and 6 June, the period of maximum territoriality,

Table 2. Circumstances and Results of 56 Interspecific Encounters

Involving Bobolinks

Aggressor Aggressee	* No. of Encounters	Position of Subject		Method of Attack			Response of Subject	
		Ground	Song Air Perch	Slow Approach	Dive Dive from Flight Perch	**Immediate	Delayed	
<u>Bobolink ♂ to:</u>								
Tralll's	1		1			1		
Flycatcher	1		1			1		
Red-wing ♂	8		6	3	2	6	2	
Red-wing ♀	1				1	1		
Cowbird ♀	24	1	21		16	23	1	
Savannah Sp.	2	1	2		8	2		
Song Sp.		2			2			
<u>Bobolink ♀ to:</u>								
Savannah Sp.	1		1		1	1		
<u>E. Meadowlark to:</u>								
Bobolink ♀	1	1		1			1	
<u>Red-wing ♂ to:</u>								
Bobolink ♂	14		2			11	3	
Bobolink ♀	1		1	3	4 1	1 1		
<u>Red-wing ♀ to:</u>								
Bobolink ♂	1		1		1	1		
<u>C. Grackle to:</u>								
Bobolink ♂	1		1		1	1		

* In every instance the initiator remained dominant through the encounter

** Immediate response indicates a rapid departure upon approach or arrival of aggressor

courtship, nest building and incubation, with a gradual decrease during the nestling stage until 16 June, after which no interspecific activities were observed. A similar temporal trend was reported by Karr (1964), who indicated that the Bobolinks' tendency toward aggressiveness decreased so markedly following the nesting season that the Dickcissel (Spiza americana), until then subordinate to the Bobolink in every encounter, became the dominant species, and "was often seen bluffing the Bobolinks into leaving the area."

Wiens (1966) described a dominance hierarchy system operating in interspecific skirmishes between grassland bird species which had the following characteristics:

- (1) aggressors usually won.
- (2) the aggression was rarely contested.
- (3) the response of the attacked individual was usually immediate departure.
- (4) the outcomes indicated a roughly linear order of dominance between the species.

Furthermore, he suggested the dominance hierarchy might function in preventing lengthy, severe conflicts over song perches, for 85 per cent of his interactions involved song perch-based clashes; in my study 78 per cent were contested over song perches.

Wiens observed 66 encounters involving Bobolinks and in none was the Bobolink subordinate. However, Red-winged

Blackbirds were sporadic in occurrence on his study area and he observed no interactions between Bobolinks and Red-wings. Consequently, he was unable to assign Red-wings a position in the hierarchy. It is apparent from 15 encounters between males of these species on my meadow that the Bobolink was clearly subordinate to the male Red-wing, although in eight of nine encounters female Red-wings were dominated by male Bobolinks (Table 2). Karr (op. cit.) observed that whenever a Red-wing approached a perched Bobolink the latter took flight, and that in all skirmishes the Red-wing was the aggressor; he did not distinguish between Red-wing sexes. This aggressiveness of the Red-wing is probably an important factor in the recent wide-spread invasion of upland grass habitats by this species.

Despite their aggressive dominance, Red-wings did not supplant Bobolinks and other grassland birds on my study area; territories of the various species regularly overlapped, nest locations seemed unaffected and song perches were only sporadically contested. One interesting exception occurred during the afternoon of 6 June when a Red-wing male repeatedly perched on Bobolink nest stake11, dropping down out of sight on three occasions into the heavy cover near the Bobolink's nest. Eventually, a male Bobolink successfully chased the Red-wing off the perch, and neither returned to the nest site before observations were terminated. That evening when I investigated the nest contents, four eggs

were absent and the other lay in the nest, broken. That the Red-wing was responsible could not be positively ascertained, but the preceding activities of the bird were strongly suggestive.

Although the Eastern Meadowlark won the only observed encounter with a Bobolink on my study area, this does not verify its dominance (the Bobolink was a female, very near a meadowlark nest), for Wiens observed three engagements, all won by Bobolinks. Karr observed no Bobolink-meadowlark contests.

Although few hawks appeared above the meadow, Red-shouldered Hawks (Buteo lineatus), Cooper's Hawks (Accipiter cooperii), Sharp-shinned Hawks (Accipiter striatus) and Harriers (Circus cyaneus) were occasionally seen in the vicinity. The Red-shouldered Hawk was the commonest hunter over the field, but it and the accipitrine hawks never elicited an overt response in Bobolinks even though neighboring Red-wings frequently became aroused and gave alarm whistles or dropped into cover in the presence of these hawks. On two occasions when a Harrier was seen flying over the meadow a single male Bobolink (different bird in each case) rose in flight 15 to 25 meters above the hawk and circled over it in Song-flight for up to two minutes; simultaneously a group of male Red-winged Blackbirds harassed one of the Harriers. Nero (pers. comm.) observed a "hawk alarm vocalization" by a Bobolink as two Ospreys (Pandion haliaetus)

appeared at a considerable distance. The vocalization was similar to the high pitched whistle given by Red-wings. I never detected this call. Karr concluded that Bobolinks do not respond visibly to hawks or Turkey Vultures (Cathartes aura).

Mating System

Some authors (eg. Buttrick, 1909, Kingsbury, 1933, Kendeigh, 1941 Karr, 1964) have considered the Bobolinks to be polygamous, in the sense that one male is simultaneously paired with two or more mates. None of the above authors observed multiple copulations or saw a presumably polygamous male feeding young of two different broods. Polygamy was surmised only because of a seemingly unbalanced sex ratio on nesting fields, favoring females.

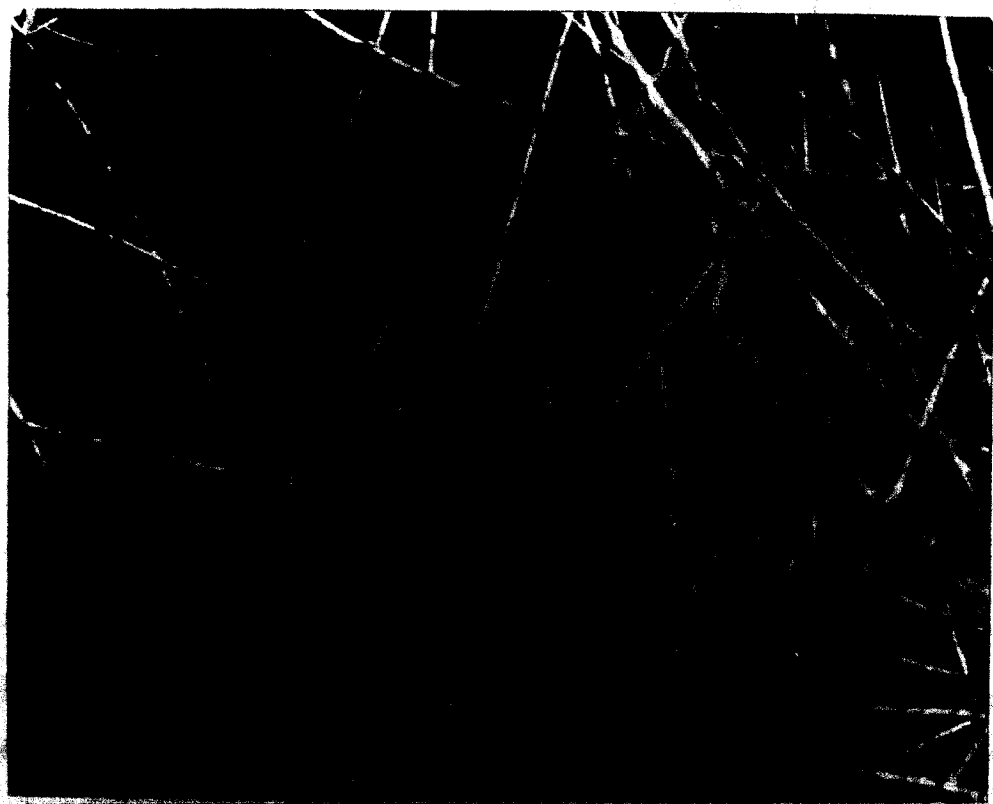
In 1966 I found two females nesting simultaneously on each of two male territories and on another territory the nesting cycles of three females coincided. However, since I observed few copulations and because most females were not individually recognizable, I was unable to determine which males serviced the females. On one territory both nests were destroyed; on another the male fed young at both nests. The male with three nests on his area fed fledglings of one but despite his performing Wing and Tail-flicking (see Visual Agonistic Displays) when intrusion occurred near the other nests he was never observed tending young.

In 1967 observations of color banded Bobolinks proved that polygamy indeed exists. I observed marked males copulate with as many as three marked females; of 13 permanent males eight had multiple matings, including two that mated with three females. Therefore, it is likely that the 1966 observations do represent polygamous matings. In 1966 five captures of widely scattered immatures included only three banded birds; obviously, all nests were not discovered. But in 1967 a total of 35 nests were discovered. It is likely that the actual number of nests in 1966 approximated the 1967 total, thus suggesting a higher incidence of polygamy than the three suspected cases.

Nest Construction and Description of Nest Site

Bobolink nests are built on the ground among the bases of forbs or within dense clumps of grass and sedge and consist of a thin lining of fine sedge stems, surrounded on the sides and bottom by coarser grass and sedge leaves (Fig. 7a). Of 20 nests investigated, 18 were completely open from above; coarse blades of dead sedge closed over the other two. One had a narrow slit-like entrance above the nest, the other had a wider side entrance (Fig. 7b). The litter from neither nest was positioned by the Bobolinks. Sometimes the outer shell of the nest appears to consist partly of living vegetation, but close examination indicates that living stems have grown up through the nest strands after nest con-

Figure 7. (a) A nest beneath a cluster of Meadow Rue (vegetation was parted to facilitate photography), open from above. The picture illustrates well the difference between the coarse vegetation composing the nest walls, and the fine lining; (b) a side view of a nest arched over by coarse sedge litter which completely conceals the nest from above. The dark left-central region of the photograph is occupied by nestlings. Foreground vegetation normally stands upright, concealing the nest entrance; (c) a female Bobolink carrying nesting material.

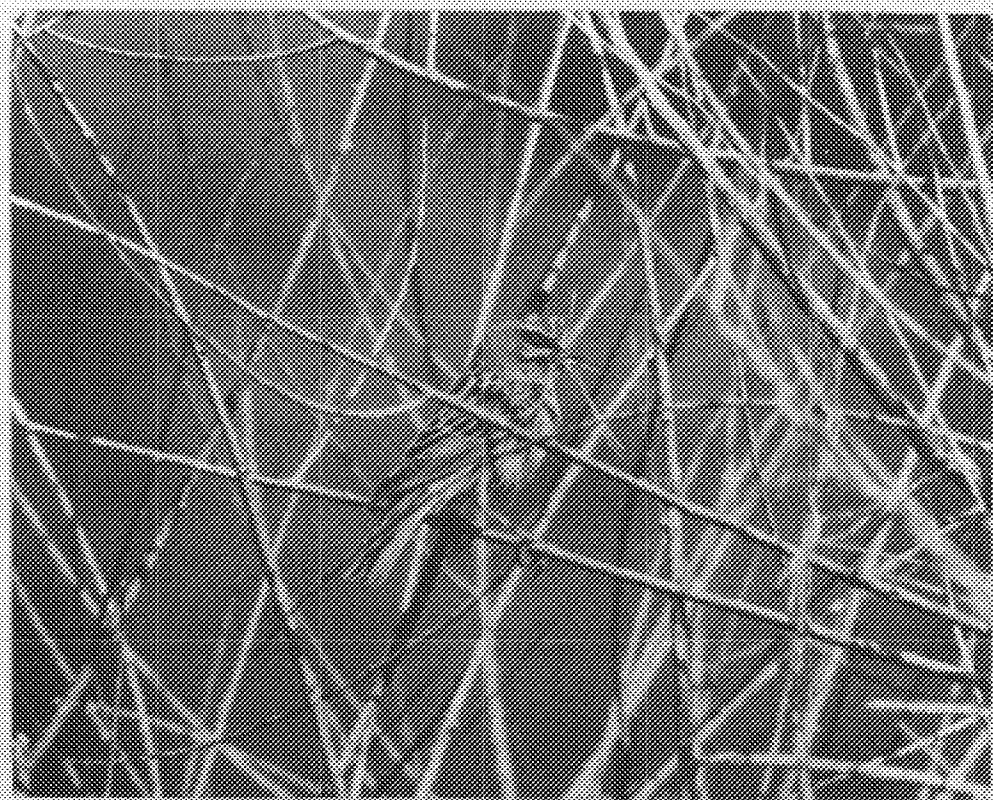
**A****B****C**



A



B



C

struction, and lend very little structural support. Kingsbury (1933) related dimensions and characteristics of ten Bobolink nests.

Only the female constructed the nest, and two individuals I observed constructing nests worked about two days from initiation to completion. Kingsbury (op. cit.) and Karr (1964) suggested that all nesting material was obtained from the immediate nest site vicinity, for despite their extended observations of birds at nesting meadows during the period of nest construction, only one female was actually seen carrying nesting material. Kingsbury concluded that this instance of a female bringing "straws" to the nest from a distance was atypical, although this was the only nest she saw under construction. However, in the two cases of nest building I watched for a total of 195 minutes, the females gathered many grass and sedge stems from the mate's territory or from non-occupied regions at distances up to 80 meters from the nest site. Indeed, it appears usual for females to secure nest components from distant areas, for the only three females observed actually carrying material (one by Kingsbury, two in the present study) were all noted obtaining it from a distance. The preponderance of sedge stems in nests located 10 or more meters from sedge growths also indicate a distant origin of nesting material. The fact that more females carrying nest materials have not been observed can no doubt be attributed to the manner in which females return to

their nests in swift, low flight, making detection of nesting material difficult.

Few data were secured indicating frequency of material-gathering flights, but for seven observation periods where time information was available the range was 13 to 41 minutes between successive returns. During my observations it is unlikely that females gathered additional materials near the nest vicinity, for females left the nest in less than 30 to 40 seconds after arrival. Each of the two birds consistently went to separate but localized regions for collection of additional grass and sedge. At each approach to the nest the female perched on forbs or grasses temporarily before dropping to the ground within two meters of the site. As many as six grass stems were brought at a time (Fig. 7c).

Eleven of the twenty nests were located beneath dense clusters of Meadow Rue. Only two of these, however, were built within the thick central area of a clump; the others were located toward the periphery, yet were still well screened by the vegetation. Three nests were constructed toward the east-facing periphery, five toward the south, none toward the west and one toward the north. This preponderance of east and south-exposed nests may give added insolation to the eggs, allowing the female to forage for longer periods after the long night's incubation. Available information on attentiveness, however, is insufficient to support this speculation. Lanyon (1957) analysed

directional aspects of meadowlark nest apertures and found that they faced predominately toward the north and east. He related this to the effect of the prevailing winds in depressing the grassy vegetation toward the north and east. Wiens (pers. comm.) found similar orientation in meadowlark and Grasshopper Sparrow nests on Lanyon's area. The openings of courting nests of the Long-billed Marsh Wren (Telmatodytes palustris) tended to have a west directional orientation while breeding nests opened to the northeast, but the biological significance of these orientations was uncertain (Verner, 1965).

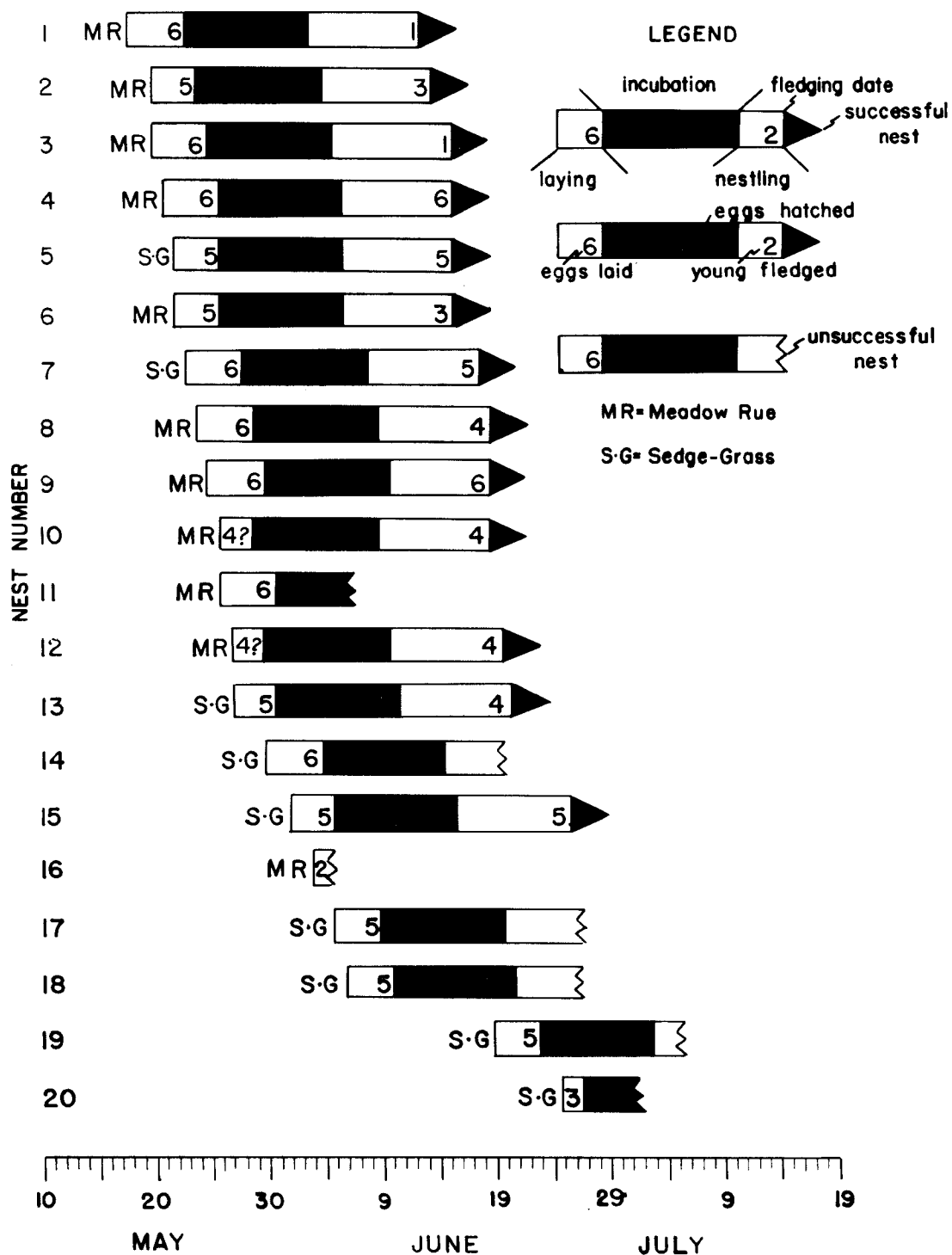
The remaining nine Bobolink nests were located in growths of blue grass and sedge and with one exception were carefully hidden in dense cover. This poorly concealed nest was built within two meters of a trail repeatedly showing mammalian use, and was eventually destroyed prior to the hatching of the chicks.

A study of habitat utilization of grassland birds by Wiens (1966) indicated the density and height of vegetation in the vicinity of Bobolink nests was greater than that in the rest of the male's territory. At 10 cm above the ground the average light intensity was 80.4 per cent of the open sky light over the territories as a whole but only 15 per cent at the nest sites. The dense vegetation about the nest allowed an average light penetration to the nest cup itself of only 12 per cent of the open sky light.

At the time nest building was initiated on my study area only Meadow Rue clumps had sufficient height and density to provide the shade and concealment requirements suggested by Wiens' study. The average date of nest completion for eleven nests located in Meadow Rue was 22 May (range 16 May to 1 June). For the nine nests located in grass and sedge, which did not develop dense cover until early June, the comparable date was 2 June (range 19 May to 23 June). The two earliest nests constructed in grass and sedge were those arched over by sedge, which gave additional concealment and shade. If these exceptional nests are omitted, the seven open nests located in grass-sedge were completed on an average of 5 June (range 25 May to 23 June).

Fig. 8 shows breeding chronologies at the 20 nests, and indicates the vegetation type in which each nest was built. Because the timing of certain events represented in the chronologies was extrapolated (dates of initial laying for 18 of the nests were extrapolated from the two for which accurate observations were available) the illustration is not meant to convey absolutely accurate time intervals for all nests. However, it is probable that even questionable events are accurate to within one day, and the timing of last egg laying, hatching and fledging dates are in most instances accurate to within 12 hours. All numerical data are precisely known with exception of nests 10 and 12, which were discovered too late to verify the original clutch size.

Figure 8. Chronologies of 20 Bobolink nests. MR indicates a nest was constructed beneath Meadow Rue, and S.G, that a nest was positioned within grass and/or sedge. Nests 5 and 7 were arched over by litter.



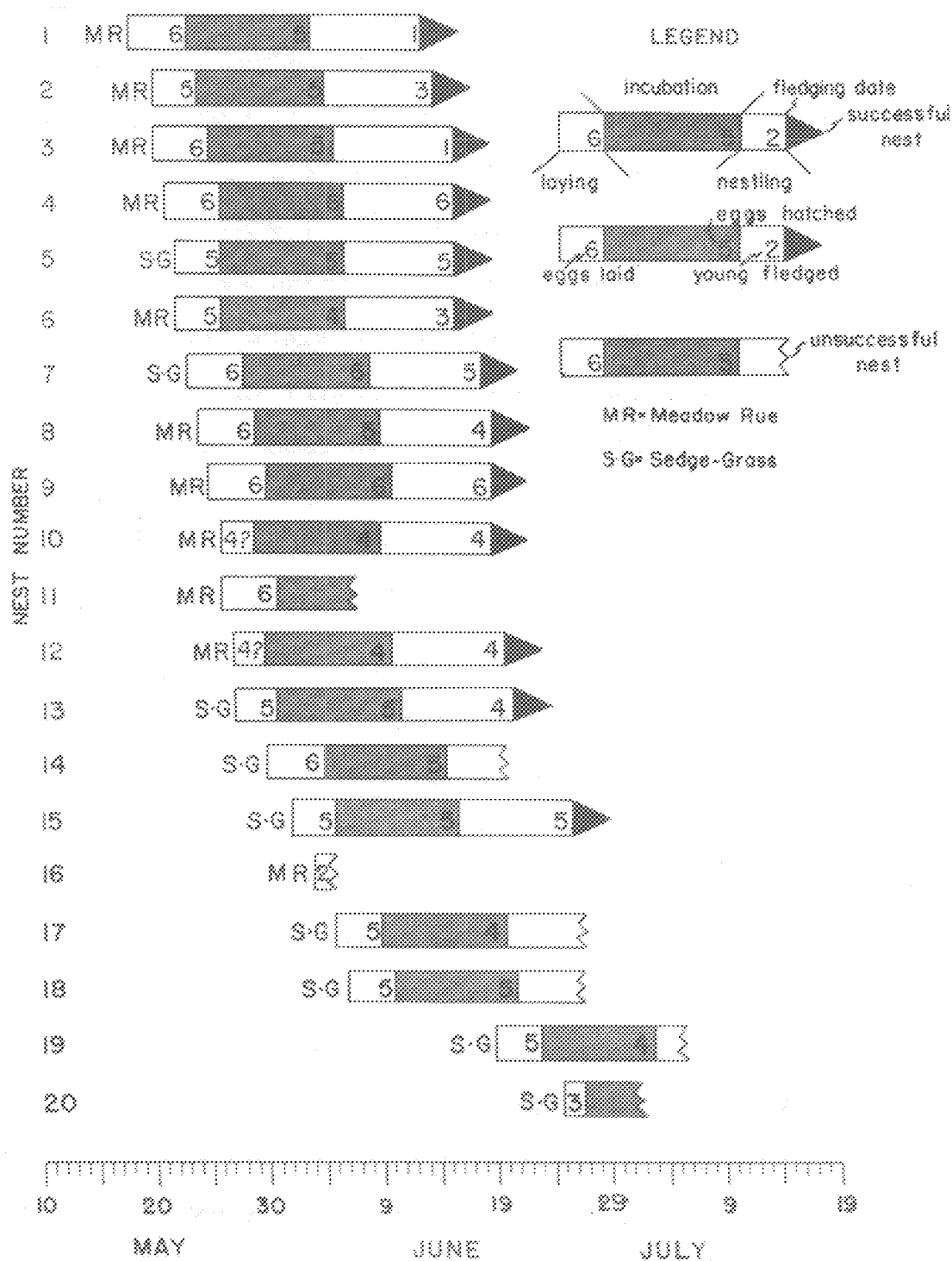


Fig. 8 illustrates that a degree of synchronization existed among female breeding cycles. During the week following egg laying in the first nest, nine females were laying and young in 11 of the 20 nests hatched within a week of one another. Similarly, of 13 nests successfully fledging young, 11 were fledged within an eight day interval. Such a curtailed breeding period is probably desirable for transequatorial migrants, to ensure time for immature birds to develop strong flight before the long migration, which in some locales Bobolinks begin as early as mid-July.

Egg Laying, Clutch Size

Eggs were marked with ink spots for individual identification and nests were observed daily to determine hatching dates and changes in egg numbers. At certain nests more than one daily inspection was made during the hatching period. To diminish the likelihood of predators following a path of scent or matted vegetation to the nest site, I approached nests with care and from varying directions.

Egg-laying apparently always occurred before 0900 hours, at intervals of one per day until the clutch was complete. My data are few concerning the deposition of the first three or four eggs, for many nests remained undiscovered through the early laying period. However, in all nests including the two found before egg deposition, the pattern of one egg laid per day did not vary. The first egg was deposited

two days following the completion of the nest in the two nests discovered during construction.

Table 3 compares Bobolink clutch sizes from four studies. It is unknown what criteria were used in three of these studies for determination of a complete clutch, but I am assuming that no loss of eggs occurred before discovery of each nest. In the present study only incubated nests known with a high degree of certainty to contain completed clutches are included in the table. Therefore, three additional nests were precluded because of possible partial loss of nest contents prior to discovery, or because the nest was abandoned before onset of incubation, indicating that the full set was not yet laid (see beyond). Wiens (pers. comm.) found an average of 4.4 young per nest for seven nests (range 1-6) over a three year (1964-66) period, but undoubtedly some destruction of eggs or nestling mortality had occurred before discovery, so the data are not included in the table. 54 per cent of nests in Table 3 contained five eggs and 30 per cent contained six. In my study, the nest that contained only three eggs, and another with five eggs were probably renestings (see Renesting and Second Nesting), and if these are excluded, the average was 5.53 eggs per complete clutch.

As the season progressed average clutch size tended to decrease. Nests initiated in the first and second weeks of nesting averaged 5.67 eggs/complete set, while nests begun

Table 3. Bobolink Clutch-sizes

Study	Year	No. of Eggs per Clutch					Mean Clutch Size	n
		3	4	5	6	7		
Tabor (1890) (Meridan, New York)	1888	-	1	5	2	-	5.12	8
	1889	-	2	9	1	-	4.92	12
	1890	-	2	7	1	1	5.09	11
Kingsbury (1933) (Ithaca, New York)	1932	-	1	2	6	1	5.70	10
	1933	-	3	6	1	-	4.80	10
Karr (1964) (Lafayette, Indiana)	1964	-	-	2	3	-	5.60	5
Present Study (Dane Co., Wisconsin)	1966	1	-	8	8	-	5.35	17
Totals		1	9	39	22	2	5.21	73

in the third nesting week averaged 5.0 eggs/clutch and those started thereafter averaged 4.0 eggs/clutch. Reasons for clutch size decrease coinciding with seasonal progression are unknown, but a number of possibilities exist: late nests may represent renestings after unsuccessful first attempts, and renesting hens may be incapable of laying "full" clutches; first year females may be the latest resident arrivals and may tend to yield smaller egg sets; or a decreased clutch may be an adaptive response by females to a declining food supply late in the season. The problem warrants further investigation with color marked individuals.

Renesting and Second Nesting

I have found no reports in the literature of Bobolink second nesting (nests after a successful fledging) or re-nesting (nests after a failure), but dates of construction of two nests (19 and 20) on my study area indicate one or the other might occur. The first egg was deposited in these nests on 19 and 25 June, respectively, 13 and 19 days after deposition of the first egg in the latest of the other 18 nests. By the time the clutches were complete the young in all but two of the other nests had fledged. The extrapolated fledging dates, had nests 19 and 20 been successful, are 14 and 18 July, six and ten days respectively after departure of the last Bobolinks from the field.

Because adult birds were not marked, it is uncertain

whether the females attending these nests had previously nested. Nest 19 was located in territory 6, and was constructed just three days after young had fledged from nest 2, the only other known nest on this territory. Both females 2 and 19 were seen simultaneously, so if nest 19 represents a second nest or renesting, female 19 either came from another territory or she and her original nest had escaped notice. Nest 20 was occupied by a female possessing a heavy yellowish tinge very much like the female of nest 9 which was located on the same territory just 13 meters from nest 20; this was a rather distinctive coloration, although at least one additional female on the meadow was tinged similarly. The young in nest 9 fledged on 19 June, six days prior to deposition of the first egg in nest 20; thereafter, no more than one female was seen on the territory at once, so females 9 and 20 were probably the same individual, and nest 20 probably is an example of a second nesting.

Brown-headed Cowbird Parasitism

The Bobolink is listed by Friedmann (1963) as an infrequent host of the Brown-headed Cowbird, and he compiled 22 records of parasitism and two instances where Bobolinks actually raised cowbird young. Almost half (10) of these records came from Hicks' (1934) survey of parasitized species in Ohio, in which he reported on 184 Bobolink nests discovered over a span of sixteen years. Friedmann failed to indicate the number of the nonparasitized nests reported or ignored

by his collaborators (except Hicks), so it is impossible to assess the parasitism percentage re-presented by the additional 12 reports. Friedmann stated: "When we remember what a small percentage of bobolink nests are even found--secreted as they are in grassy meadows and invisible from above because of their semi-domed structure"--I have never before seen references to this type of Bobolink nest-structure--"it may not seem surprising that relatively few records are available. However, it does not follow that the observed incidence of parasitism would be affected by this rather meager sampling."

I suggest that the Bobolink is less often parasitized than Friedmann implied in the term infrequent (the fourth of six categories) and that the rarity of nests containing cowbird eggs makes a record of sufficient interest to be reported while non-parasitized nests remain unheralded, thus biasing the result. The following data attest to the rare occurrence of the Bobolink as a host species in certain areas: of twenty nests located on my study area, none contained cowbird eggs, despite parasitism of Eastern Meadowlark nests on the field (a species, incidentally, listed by Friedmann as an "uncommon host"). Wiens (pers. comm.) found that none of the seven Bobolink nests he discovered over a period of three years contained cowbird eggs, although meadowlarks on the same field were parasitized frequently and Savannah Sparrows and Grasshopper Sparrows in-

frequently. Karr found eight Bobolink nests, none parasitized, but cowbird activity in the region was slight (pers. comm.). Three years of nesting data reported by Kingsbury (1933) showed no parasitism in 28 nests in New York and Massachusetts. It is difficult to evaluate her data, for no information is tendered concerning utilization of the area by cowbirds. In summary, of the 63 Bobolink nests reported in the above studies (all of which focused concerted attention on the Bobolink rather than being casual observations) none hosted eggs of the cowbird, despite presence of cowbirds on at least three of the areas. The extreme concealment of the Bobolink nest and its placement in dense cover may be factors in reducing parasitism in areas of good habitat.

Incubation Period

Copulation apparently was infrequent, for in about 83 hours of field work during the courtship period only three successful mounting sequences were observed. One of these occurred while the female was in terminal stages of nest construction, and the process took place within eight meters of the nest site. Another was performed 10 meters above ground level on a tree limb, off the male's territory; immediately following the final mount the male chased the female and both landed within the territory. I was unable to determine with which nest this female was associated. The third observed

copulation occurred on a territory 25 meters from the nest on approximately the first day of egg laying.

Incubation was apparently performed solely by the females; males were never observed at the nest proper until chicks were hatched. One male was seen brooding first-day young on 6 June while an egg remained unhatched; this was the only instance when a male was known to settle over an egg.

Data available for three nests where the exact length of the incubation interval (period from laying the last egg to hatching of the last egg) is known, all indicate a period of 12 days. Various authors have given data on incubation periods for the Bobolink, but none of these indicate what interval is measured, or if marked eggs were used for these determinations: Wheelock (1904), gave thirteen days; Eaton (1914), eleven days; Burns (1915), ten days; Kingsbury (1933), ten to thirteen days (this spread may represent the extremes she found in the literature). Burns' ten-day period is suspect, for according to Nice (1953), authenticated records of incubation periods of less than eleven days are rare for any species, and "most of these have something uncertain about them, usually some assumption as to the start or finish of incubation." Burns failed to provide the necessary details.

In my study, all but the last-laid egg of a clutch hatched in the order of laying over a period of from five to 11 hours; the last-laid egg opened about 22 to 36 hours

after the first egg hatched. This hatching schedule suggests that incubation is initiated following the laying of the penultimate egg; my visual observations on female attentiveness support this deduction.

In many species the young tend to hatch at times distributed throughout the day and night, while those of other species are apparently triggered by some daily rhythm or are influenced solely by the hour of laying and the incubation period, and accordingly hatch during a particular segment of the day (Skutch, 1952). Preliminary observations show no strongly marked tendency for Bobolink eggs to hatch during any specific part of the day, but more investigation is required.

A motion picture camera equipped with a single-frame regulator set to expose one frame every six seconds was positioned near a series of incubated Bobolink nests on 1-3 June; a total of 12 hours of attentiveness data were recorded in this manner. Unfortunately, the film was lost at the processing laboratory, so attentiveness-inattentiveness information is meager. The following data, summarized from Karr (1964), represent the only information available on Bobolink incubation rhythms: of eight attentive-inattentive periods the female averaged 22.0 (12-30) minutes on the nest and 12.3 (10-15) minutes off the nest.

During inattentive periods females foraged, usually within the male's territory, alone or accompanied by the mate.

On several occasions males initiated the break in attentiveness by flying low over the nest site, and swooping toward the attending female. Ordinarily the two birds foraged together following this sequence, and less frequently females accompanied their mates to distant foraging regions (see beyond); in these instances the birds returned to the territory together.

Ten of the males paid little or no attention to human intrusion near the nest during the incubation interval. The other five males sometimes reacted to humans in the nest vicinity by hovering in Song-flight or with the see yew vocalization (see chapter on Breeding Behavior) as close as four to five meters overhead. The intensity and frequency of this behavior increased once eggs were hatched, when all males except two occasionally performed in this manner.

Three classes of activities occupied the male during the incubation phase:

- (1) maintenance of pair bond(s) with his female(s)
- (2) maintenance of territory
- (3) foraging

Approximately 70 per cent of foraging was performed in vegetation within the territory or at one of three communal foraging regions on the meadow (Fig. 5), where males and females foraged together peacefully. As many as three males were seen simultaneously at one of these localities during the incubation period. Once young were in the nest these

areas received increased utilization, and as many as five males and two females were noted on one region concurrently. Males did about 30 per cent of their foraging at areas distant from the meadow; exact localities for this activity were not determined, but flight direction of males indicated utilization of an upland field about a kilometer away and a cattail marsh 0.5 kilometer distant. On a few occasions males returned to the study area in groups of two or three, dropping onto their individual territories.

I noted no males feeding incubating females, but Karr (1964) observed a male that flew to a nest vicinity with a food item and disappeared into the vegetation, reappearing a few moments later with no food. It was unknown whether this bird actually fed the female, but it was certain that the nest did not contain nestlings. Lack (1940b) reported that as of 1939 feeding of the incubating females by the male is unknown in the Icteridae; subsequently Williams (1952) noted that it occasionally occurred in the Brewer's Blackbird, and Nero (1956a) cited other possible instances within the family.

Nestling Period

Egg shell fragments were carried from the nest by females immediately after chicks were hatched. Brooding commenced immediately, continuing until the nestlings were at least four days old, and night brooding may have continued

after the fourth day. In some monogamous pairs both males and females shared in brooding duties but the females performed the greater share of the task. Males with multiple mates were never observed brooding young. Kingsbury (1933) thought that adults did not feed nestlings until their second day, but in many instances I observed females feeding within three or four hours after the first young was born. Nestlings two hours old gaped feebly to vibration caused by touching the nest rim. Older nestlings produced a barely perceptible buzz vocalization in conjunction with gaping. Males occasionally fed first-day nestlings; more commonly they commenced with feeding the morning following hatching. With one exception (described below) all males fed nestlings.

Young were hatched on two of three territories known to contain multiple nests. Male number 13 fed nestlings of his first mate approximately as frequently as did the hen. When chicks in the second nest hatched they received only slight male care, and were completely neglected by him after young were fledged from the first nest. Male number 7 possessed three mates. He was never observed feeding nestlings, but when the young fledged from his first nest he began feeding these fledglings.

Nestlings were apparently fed exclusively on animal material. Observation through a spotting scope indicate lepidopterous larvae made up the bulk of food. Other items included various species of dragon flies, darning needles,

spiders, grasshoppers, small adult lepidopterans, adult dipterans, harvestmen, cut worm larvae and small adult beetles. About 15 per cent of foraging for nestling food was done within the male's territory, and the majority of foragings occurred within communal foraging areas shown on Fig. 6. Additional foraging took place high in surrounding trees and apparently at distant fields and marshes previously mentioned. Returning adults perched temporarily on stakes or forbs before dropping to feed. Dragon flies were usually carried by the heads and larvae near one end. Commonly birds softened larvae by moving them rapidly from end to end through their beak.

Before the young were four days old adults brooded from two to 16 minutes after most feedings, the female tending to brood more frequently and for longer periods than the male. After the fourth day feeding adults remained at the nests for only brief periods of from eight to 20 seconds. In instances when fecal sacs were removed, the interval was sometimes increased to almost 30 seconds. Feces were removed by both sexes, and were usually dropped from flight 20 to 100 meters away. Fecal sacs were not observed being removed until chicks were three days old but prior to this age excreta may have been small and easily overlooked. It is unknown whether Bobolinks eat the fecal deposits of nestlings. Adults were efficient at nest sanitation, for in no instance did I find soiled nests when I

investigated after fledging. Dead nestlings were generally removed by adults. Unhatched infertile eggs, however, were left.

A few sample measures of rates of feeding are presented for five days of the nestling period in Table 4. These data were obtained from different nests for each nestling age category, and although they are not sufficient to show major trends they do demonstrate two points borne out by non-quantitative observations:

(1) At most nests males and females shared approximately equally in the amount of feeding.

(2) Females receiving no male help fed more frequently than did aided females. The five-day nestling sample which was obtained at nest 8 in the territory of polygamous male number 7 demonstrates this. The fledging date was not delayed at this nest, and young at the fledgling stage appeared to be as well-developed as those from nests being tended by both adults.

Table 4 illustrates no evidence for increased number of feeding trips correlated with progress of the nestling period, but here again enough data were not obtained to adequately determine if an increase did indeed exist. My subjective feeling is that after the second or third day the number of feeding trips per hour did not significantly increase regardless of nestling age. Many studies of passerines have reported a positive correlation between

Table 4. Role of Sexes in Feeding

Age of Nestlings (days)*	Observation Period (seconds)	<u>Trips/Nestling/Hour</u>		
		male	female	total
2	3600	1.67	2.00	3.67
4	5975	1.81	0.60	2.41
5	825	0.00	3.49	3.49
6	4740	4.05	2.28	6.33
7	2050	1.76	1.46	3.22

* Age of oldest young accurate to ± 12 hours

increase in rate of feeding with age of young (Willson, 1966 demonstrated this nicely for the Yellow-headed Blackbird); few have reported no increase (but see Power, 1966 for the Mountain Bluebird (Sialia sialis)). In the Bobolink, despite apparent constancy of feeding trips, a conspicuous increase in biomass transport was evident as a result of increased number of items brought per trip and of larger size of the items. Day-old chicks were presented one to two quite small adult insects or larvae per trip and as they became older food size and quantity increased to the point where males characteristically collected four to six large succulent-appearing larvae on almost every foraging trip; females usually brought one or two items less per carry. In this manner at least eight to ten times the volume of food was carried to nine-day chicks per trip than to two-day chicks. Future experiments using the pipe-cleaner food collection technique developed by Willson and Orians (1963) and further perfected by Snelling (1966) are planned in order to quantify and correlate increase in biomass utilization per hour with nestling age.

Fledging and Postbreeding Periods

In the presence of human disturbance at or near a nest, nestlings may leave prematurely (Skutch, 1945). Consequently, it is difficult to assign accurately a "natural" fledging date for a species. My banding activities undoubtedly caused

premature fledging from some nests. The mean fledging age was 9.7 days (range 8-11) for 27 young in eight disturbed nests. At three other nests where I banded the chicks before they showed crouch or fear reaction, and thereafter carefully avoided approaching closer than five meters the fledging time was about 11 days as determined by observations of parental activity from a distance.

At most closely watched nests all members of the brood fledged within a one to six hour period but this may have been a result of disturbance. In two nests the smallest bird failed to fledge on the day its siblings departed and one of these subsequently died of parental neglect. This instance suggests that concurrent fledging of all chicks may be advantageous and that once some young have left the nest a loudly begging fledgling tends to stimulate adults more than does a feebly begging nestling.

Fledglings tended to scatter by walking and running almost immediately on leaving the nest, and began their begging note within five or six minutes. This loud note differed from the weak buzzes given by nestlings (see Vocalizations). It appears that the adults divided the labor of feeding the brood, each parent concentrating on feeding specific fledglings. It is unclear, however, if this tendency persisted after the first day or two.

Fledglings did not remain near the nest, for banded birds were found over 70 meters from their fledging site less

than 24 hours after departing. Although incapable of flight at eleven days' age, young thirteen days old flew after adult birds, begging. By 16 days of age immatures were capable of sustained flight over the entire meadow, and they were frequently seen pursuing one adult after another with begging notes. As mentioned previously, ten nests fledged young in less than a one week interval. Within six days these fledglings and the associated adults began congregating in a "nursery" flock, and remained in this group until departure from the field. This flock increased in size as immatures from additional nests joined about their sixth day after fledging, until the flock numbered over 50 individuals on 5 and 6 July. It is unclear whether adult birds can distinguish their own young within these flocks but immatures appeared to beg from almost any adult. Observations on color-marked individuals in 1967 show that adult birds fed immatures for at least 21 days after young in their nests had fledged. Two recaptured immatures were fed by their own parents seven days after they had fledged, but no information of this sort was obtained for succeeding days.

By 28 June most adults within the flock were giving the pink call when in flight, and by 1 July many immatures were also emitting this vocalization. By this date the flock was mobile and generally moved as a unit; all birds flushed together when approached, and landed in some distant area of the meadow. Between noon on 6 July and the morning of 7 July

the flock departed, not to be seen again, and the four or five adults that remained on the field were gone by evening on 8 July.

Breeding Success

Of 20 Bobolink nests on my study area 13 (65 per cent) were successful in fledging at least one young. Comparable percentages for other studies are: La Rivers (1944)--Brewer's Blackbird, 107 nests, 49.5 per cent; Petersen^{and Young} (1950)--Common Grackle, 62 nests, 54.8; Lanyon (1957)--Eastern Meadowlark, 60 nests, 33, and Western Meadowlark, 62 nests, 35; Young (1963)--Red-winged Blackbird, 518 nests, 29, and Yellow-headed Blackbird, 116 nests, 30; Karr (1964)--Bobolink, 8 nests, 12.5; Kingsbury (1933)--Bobolink, 28 nests, 67.8. Two of these three Bobolink studies show a higher nesting success than is reported for the other icterids. Karr's low success rate is undoubtedly due in part to excessive disturbance associated with the daily weighing of the young in each nest. Nice (1957) gave 49 per cent nesting success for 7,788 nests of open-nesting altricial birds, and about 45 per cent success for open-nesting passerines.

Table 5 shows the fate of 101 Bobolink eggs from nests on my study area. Predation amounted to a minimum of 18.8 per cent of egg losses. Fledging success (percentage of eggs fledging young) was slightly higher (50.5 per cent) than that given by Nice (op. cit.) for open-nesting altricial

Table 5. Fate of 101 Bobolink Eggs

Fate	No.	Per Cent
Infertile (failed to hatch)	6	5.9
Deserted	4	4.0
Accidentally broken in marking	1	1.0
Probable Red-winged Blackbird Predation	6	5.9
Predation by "large" mammal (cat or fox)	8	8.0
Predation by "small" mammal (mouse)	5	4.9
Died in nest (crowding, starvation, unknown causes)	4	4.0
Died from exposure (one sibling survived)	5	4.9
Unknown (empty nests, no clues)	11	11.0
Fledged young	51	50.5

birds (46 per cent). Young (op. cit.) found a 23 per cent fledging success in the Red-wing and 30 per cent in the Yellow-head. Of 88 eggs Kingsbury (op. cit.) had 34 per cent fledging success in her Bobolinks.

In my study nesting success was directly related to time of nest-building (see Table 6 for numerical analysis and Fig. 8 for a graphic illustration of this correlation). Nests built early in the season had much higher success than later nests. This was due in part to larger clutches and in part to greater survival of the eggs and nestlings; both are relationships which support the idea previously presented that early nesting and synchronization of nesting are important to Bobolink production of fledglings.

Table 6. Nesting Success Related to Time of Deposition
of First Egg

Week of first egg	n*	Eggs/nest**	% Hatching	% Fledging***	% Nests Fledging young
18-24 May	(45/8)	5.63	91.1	62.2	100
25-31 May	(23/4)	5.75	69.5	43.5	50
1-7 June	(17/4)	4.25	82.3	29.4	25
post-7 June	(8/2)	4.00	50.0	0	0
Means	(93/18)	5.17	80.6	46.2	55

* (/) indicates the total number of eggs eventually deposited (above slash) in the nests (number below slash) in which the first egg was laid in that time interval.

** Eggs laid per nest does not necessarily correspond to clutch size, for desertions before completion of the egg set are included in this table. Two nests are omitted because of uncertainty of original clutch size. Both nests fledged young.

*** % fledging refers to per cent of eggs producing fledged young.

V. BREEDING BEHAVIOR

Vocalizations

Bobolink vocalizations are numerous and complex. Intensive study will be required before all can be adequately described and placed in functional relationships to displays. Not only are certain songs indescribable in terms of human symbolism, suggesting necessity for a sound spectrographic analysis, but the most characteristic full song is also fragmented, the segments being employed in various contexts as separate songs. The vocalizations described here are performed with activities discussed in the sections on "Visual Agonistic Displays" and "Courtship".

Male Song:

(1) The complex warble song usually began with three to five fairly distinct short whistled notes followed by a three to five second series of ascending warbles. This was the common male song given both in Song-spread and Song-flight displays. The warble series in flight was usually longer than in perched song. The difficulty of describing the warble segments in words is unsurmountable, and as Bent (1958) colorfully stated: "It is unique among bird songs, the despair of the recorder or the imitator...It is a bubbling delirium of ecstatic music that flows from the gifted throat of the bird like sparkling champagne."

Among the large repertory of note patterns preceding the warble phase, two were most frequent. One, used primarily in flight and to a lesser extent in perched song, consisted of three notes, each climbing in pitch, with the last extended directly into the warble. Each throaty note sounded like whaa. The other sequence was typical of most perched song; the first and third notes were at approximately the same pitch while the second and fourth notes were both lower. The first and second notes were distinct and rapid; the third and fourth were slurred on a downward gradient. The notes formed a fast series of pings and the warble began at a pitch higher than any of these four preceding notes.

(2) When engaged in courtship, males directed brief snatches of song toward females. This partial song normally consisted of from two to eight notes, most commonly about four to five, of similar composition to the ping introductory sequence of the warble song.

Notes

(1) A series of from three to 10 penetrating evenly-spaced zeep notes, all on the same pitch, were emitted by females during pre-nesting and while engaged in conflicts with other females. In the latter case the zeep appeared to be slightly higher in pitch.

(2) A rasping buzz was given by alighting males when circle-flight displaying to females. The buzz was short and was often repeated up to three times in quick succession at

from me, only to discover the sound arising 15 meters away.

(8) During late June and until they left the nesting area adults and immatures took short flights over the meadow, giving a metallic pink vocalization, which is also the note characteristic of migration.

Visual Agonistic Displays

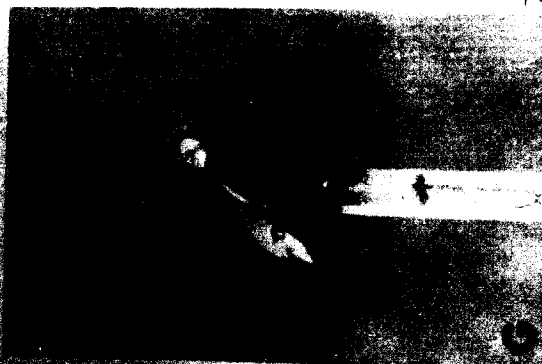
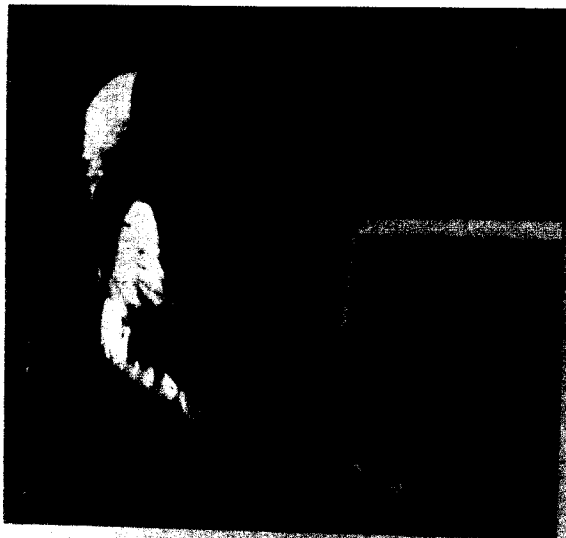
The following displays and movements are performed by Bobolinks during establishment, defense and maintenance of territories. "Displays" are defined by reference to Moynihan (1955): "i.e. those peculiarly standardized and often exaggerated performances, including all vocalizations and many movements and postures, which have become specialized and modified as social signals or releasers."

Song-spread: Song-spread was the most frequently performed agonistic display, functioning both in territorial advertisement and as a mild threat when directed toward other males. In addition it secondarily functioned in female attraction. It was performed both from perches and from the ground. The complex warble vocalization described above was given simultaneously with the postural components. In the display's extreme form the neck was slightly stretched as the head was lowered in a nod as low as the feet or, more frequently, to a level where breast and head lay on a horizontal plane as the first of the introductory whistled song notes was given; by the fourth note the head had been raised

almost to non-display height where it was held through the rest of the song (see Fig. 9 for variations). As the head was nodded with the first song note the tail was thrust downward and fanned, the wings were spread outward and downward and the nape feathers, white scapulars, back feathers, upper tail coverts and throat feathers were sharply elevated, displaying the striking color pattern of the dorsal surface to fullest advantage. The buff-colored nape feathers were further emphasized by a concurrent sleeking of the black feathers anterior to them. At the low point of bowing the exaggerated nape was often fully exposed toward the opposing male. Plumage on the ventral surface was raised to a lesser extent. Certain individuals often hopped in a turning movement during Song-spread, circling 180 degrees during the display. At completion of the song the original position was normally assumed, but in certain cases the plumage remained ruffled for as long as six to eight seconds. Some males slowly folded their tail to the rest position during the warble phase of song. Frequently a male performed Song-spread as it faced an opponent and then quickly turned to face away and presented its back before initiating another Song-spread (Fig. 10a). A male perched above another in a tree usually stooped down so low in Song-spread that its head was below its feet.

The several components of Song-spread varied greatly in intensity. When used in most territorial advertisement Song-spread was not directed toward another individual, and little

Figure 9. Variations of male Song-spread display. A sequence is shown in a-d: (a) first note; (b, c) two stages of the bow; (d) position of body through the warble portion of the song. This particular display is only of medium intensity, with no tail fanning and little wing spread. However, tail depression is substantial, as is plumage erection; (e) a relatively low bow. Note the extreme fluffing of dorsal feathers; (f) Song-spread from a ground position; (g) side view showing tail and wing spreading.



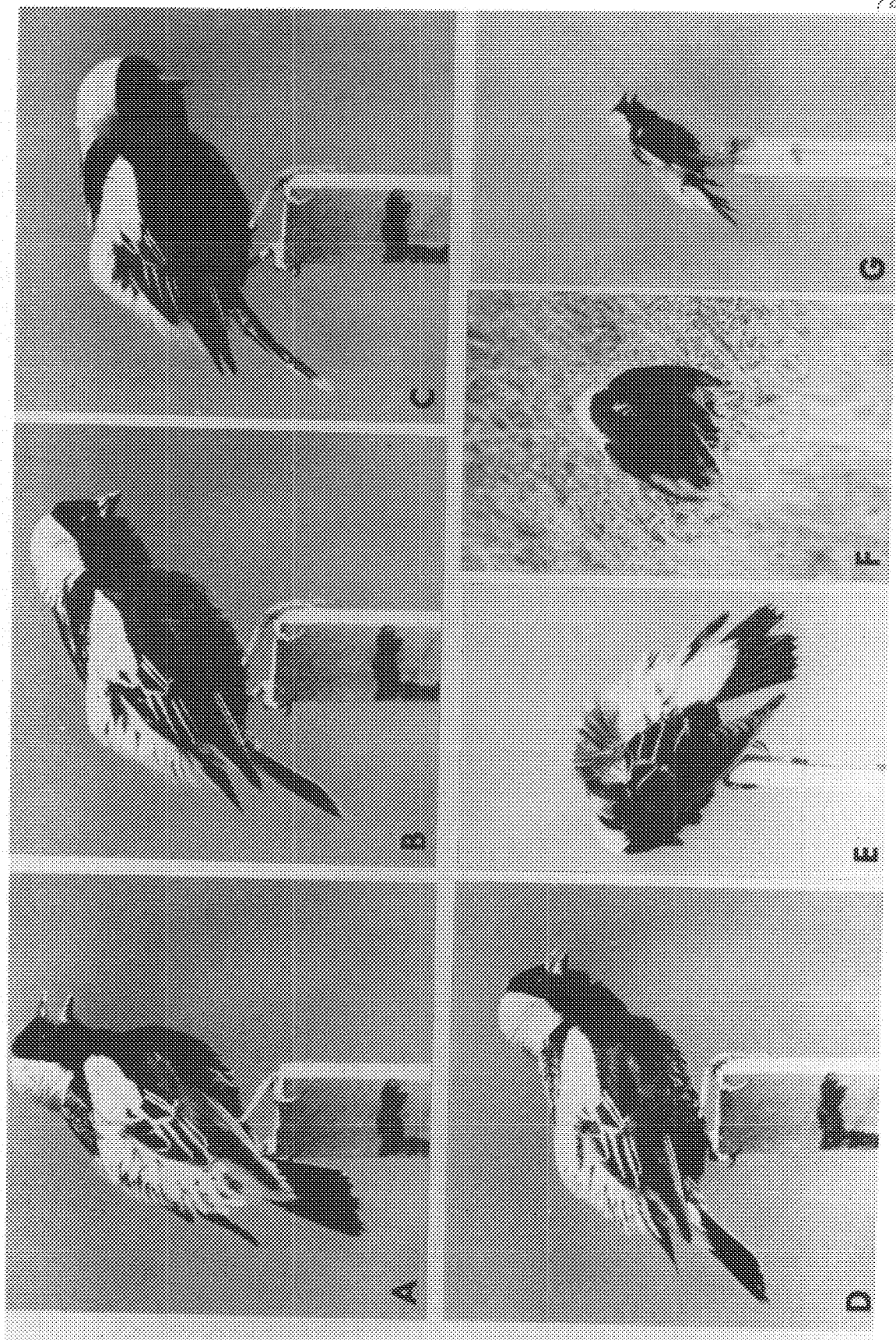


Figure 10. Variations of male Song-spread display. (a) A male giving Song-spread after orienting its back toward another male; (b, c) low intensity display used for territorial advertisement; (d, e) exaggerated Song-spread given as males or females pass overhead. Note the strong tail fan and lack of erected plumage; (f) an Elevated-wing threat display, usually not accompanied by song.

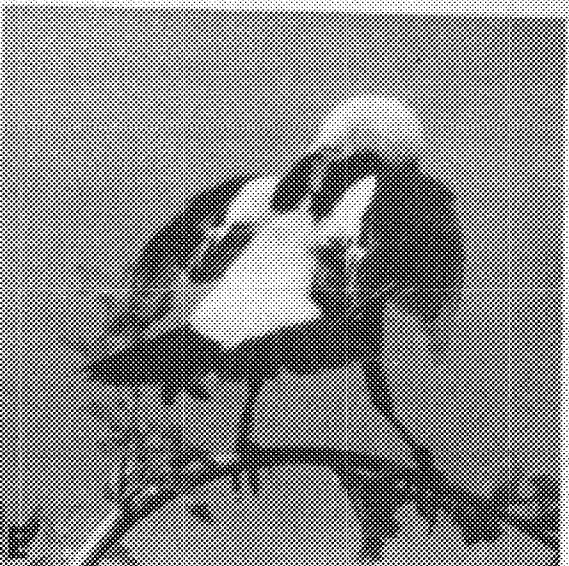
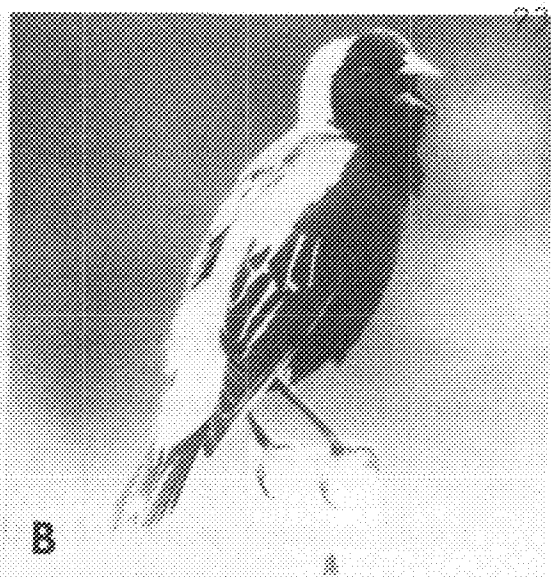


B



D





or no tail depression, tail fanning, wing spreading and body plumage ruffling occurred (Fig. 10b,c). But when males met at close quarters at the edges of their territories or when a perched male was confronted with an intruder the display was sometimes extreme. In these latter situations Song-spread was usually alternated with autochthonous, aggressive activities.

A modified Song-spread occurred when a female or an intruding male slowly flew over a perched male. On these occasions the perched bird sat upright and thrust its wings out perpendicularly, the tips held about seven or eight centimeters from the body. (Fig 10d,e). Little plumage erection accompanied this display but the tail was often widely spread; the posture was sometimes maintained for 20-30 seconds following closure of song if the bird did not take chase after the intruder or female. Nero (1964) observed intense Song-spreads under similar circumstances in the Red-wing and Yellow-headed Blackbirds and postulated that the "challenging" effect of birds flying overhead may serve to elicit the exaggerated display.

Another form of male display was occasionally given by a male when another male flew overhead. In this display the performer, while peering upward, threw his wings upward and out (Fig. 10f) and remained rigidly in this position for 10-15 seconds. Little or no vocalization accompanied this posture, which strongly resembles the Elevated-wing display

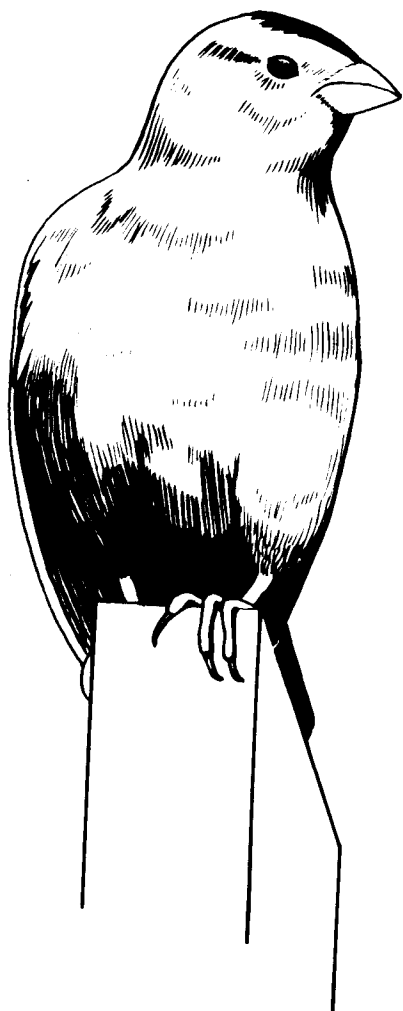
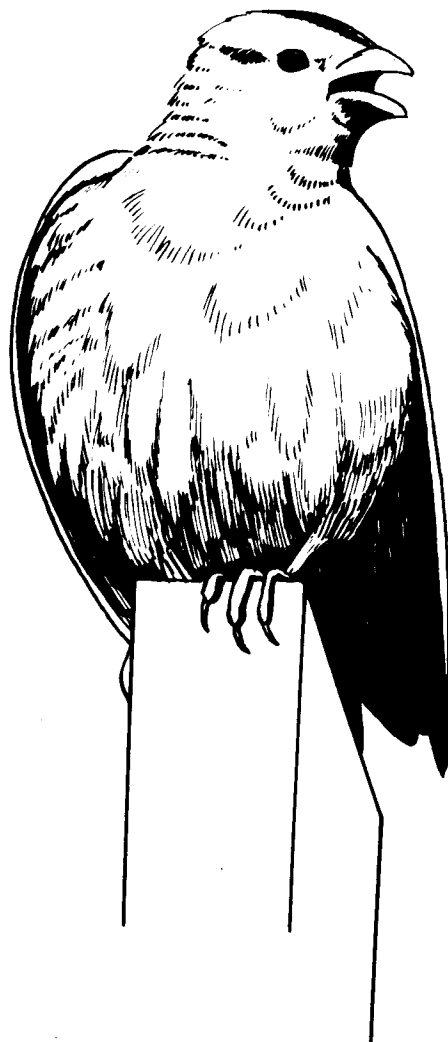
(see beyond) given to females in courtship.

Prior to territory establishment, Song-spread occurred infrequently and in a weak form lacking clear postural components. It quickly became the dominant display, however, between initiation of territoriality and pair formation. During this latter period Song-spread was elicited by intruding and neighboring males.

Male Song-spread displays appear to be homologous in many species of icterids. Nero (1956a) described a Red-wing display with quite similar components to, but which at high intensity is even more extreme than Bobolink Song-spread. A similar posture accompanied by song was described by Williams (1952) for the Brewer's Blackbird, and called the "Ruff-out", and Ficken (1963) labeled a comparable display in the Common Grackle the "Ruff-out Squeak". In the Yellow-head the display is asymmetrical, the right wing almost always held out to a greater extent than the left and the neck twisted as the bird sings over its left shoulder (Nero, 1964). Further examples were presented by Nero (op. cit.). In all species, the display serves a threat function as well as, secondarily, attraction of females to the displaying male.

Females apparently lack high-intensity counter parts of male Song-spread, although a weak form of Song-spread was occasionally given (Fig. 11). This display was brief, involved only slight erection of contour feathers, and contained only a trace of wing-spreading. Although the bill was

Figure 11. (a) A non-displaying female; (b) female posture during Song-spread. (Both were sketched from 16 mm. cine frames).

**A****B**

observed to open and close in the two instances when this behavior was seen (see Female Territoriality), no vocalizations were heard.

Song-flight: Territorial advertisement was effected through perched Song-spread and its aerial counterpart, Song-flight. Song-flight also had the supplementary function of female attraction, yet as in Song-spread the display was not directed specifically toward females--another flight form with different vocal components was given to females (see Courtship).

Song was not the only characteristic which differentiated Song-flight from regular songless flight, for the entire form of wing beat was altered when song commenced. In normal flight, the wings were brought substantially above and below the horizontal, appearing to almost touch at their highest level. Series of fast flaps were alternated with short glides. The wings in Song-flight were beaten in a hovering fashion, pointed downward; they barely attained the horizontal level at their peak height, and almost touched below the mid-ventral line at their low point. Beats were more rapid than in non-display, songless flight. Song-flight displays were flown at heights ranging from two to 40 meters and normally were performed over the territory. The vocalizations varied in length from two to eight seconds, and were sometimes continued as perched song, following alighting. A long series of song was sometimes given in a single flight

with only short interruptions. The notes preceding the warble portion of the song were variable, but most frequently Song-flight was initiated with three whaa notes. During the period of territory stabilization song occurred each time a male took flight, regardless of the distance to other males or the cause of flight (e.g., if a male were flushed by a human intruder Song-flight was given). Song was given by the pursuer in more than 50 per cent of male-male chases, but usually in this situation a normal flapping flight pattern was assumed rather than the hovering form of flight.

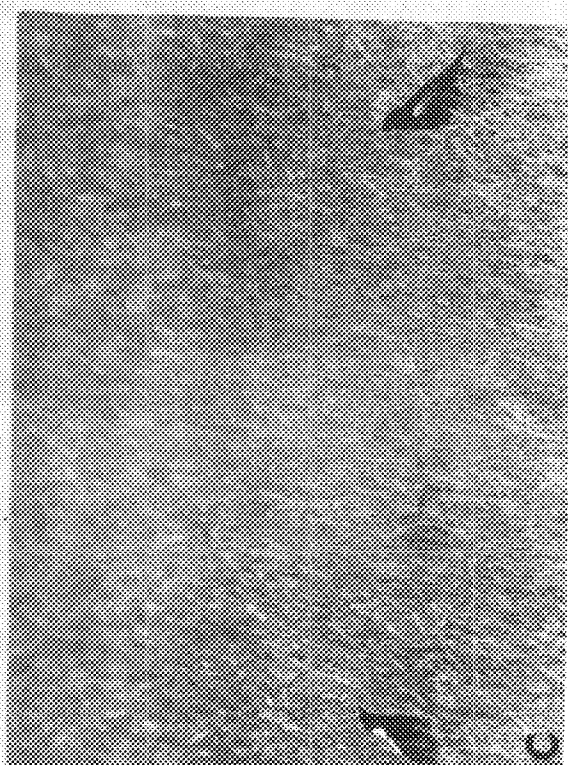
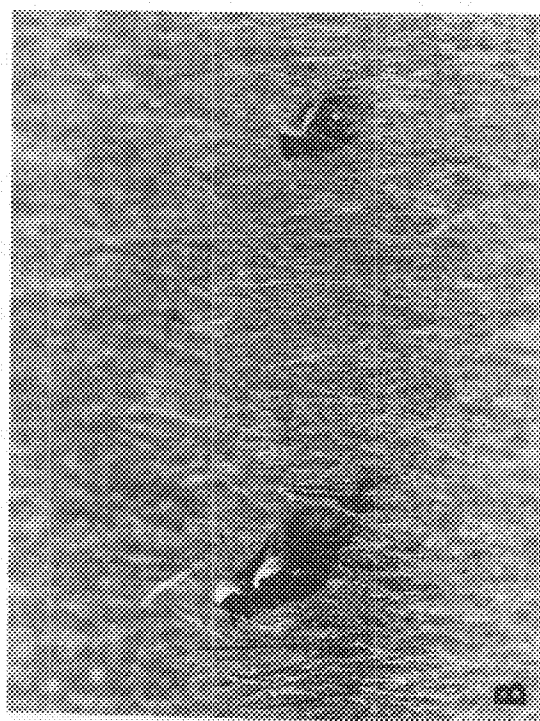
After a majority of the resident females were incubating, males performed group Song-flights which often involved as many as six to nine birds. In this group display all participating males rose into the air within a few seconds of one another, ascended 25 to 35 meters singing continuously for 10 to 15 seconds and then, suddenly, descended again to their territories. I have been unable to discover what initiates the synchronism of the flight, but have observed foraging males raise their heads as other males ascend, and then quickly fly up to join the flight.

Chase: Males chased intruding resident and migrant males from their territories throughout the breeding season, but the drives were most frequent and intense during the first week of territoriality. Most chases originating on the ground were initiated by swooping dives toward the intruder by the occupant. The length and intensity of the ensuing flight

were related to the season or stage of the breeding cycle. Those early in the territorial establishment sequence were long in duration (30 seconds to over one minute) and involved a great deal of song as the birds sometimes rose to heights of 40 meters. The speed was high and the pursuer generally followed within one to five meters, occasionally swooping and striking at the fleeing bird. Once territories were firmly established Chases were less frequent, of shorter duration (3 to 10 seconds), involved less Song-flight and were rarely performed at greater than 10 meter heights. Occasionally the pursuer became the pursued when it chased the fleeing male well into the latter's territory. The vocalization associated with Chases is that typical of Song-flight.

Parallel Walk: A series of ground displays occurred along territorial boundaries during territory establishment. These activities included Bill-flipping, Display-preening, Thrust-flight, Back-presentation, Aerial Contest, Direct-run, Head-flagging and Nodding, all described below, and were integrated by the Parallel Walk. In this activity two males slowly hopped and walked along 15 cm to one meter apart, with heads directed forward (Fig. 12a,b). Frequently a variation occurred as a bird lowered its head and slowly ran forward parallel to the other bird for 0.5 to one meter. High-intensity Song-spread was frequently given during Parallel Walks as a bird faced toward or away from his

Figure 12. Agonistic male ground displays: (a) Parallel Walk; (b) Song-spread within a Parallel Walk series; (c) Bill-flipping; (d) Direct-run posture.



opponent, often hopping onto a stem prior to singing. Males occasionally foraged for brief periods during the walk.

Parallel Walks were among the first indications of territory establishment. Two males commonly engaged in the behavior almost continuously for one to three hours, working slowly along their territorial boundary lines. After an interruption the birds quickly returned and continued the Parallel Walk or one of the associated ground displays. Prior to a high male population, two birds sometimes contested in Parallel Walks during portions of two or three consecutive days. As additional males arrived and surrounded a territory the defender alternated Parallel Walks with all adjacent males. After about three days of Parallel Walks neighboring males substituted frequent localized Face-offs for the mobile Parallel Walks. Face-offs possessed identical elements to Parallel Walks, except no "boundary patrolling" occurred. Frequency of Face-offs declined gradually and they were rare by incubation time.

Song-flights occasionally assumed a similar boundary patrol pattern as two males from adjacent territories approached their common territorial boundary, turned and flew parallel to one another in Song-flight for 10 to 30 meters, and then diverged to alight on their respective territories.

Bill-flipping: A ritualized display found in many species of icterids has as its primary components the stretching of the neck upward and holding of the bill at some angle

(variable) above the horizontal. The function of this display is to maintain a minimum distance between individuals. In a few species it additionally has a courtship function. Williams (1952), called it the "Head-up" display in the Brewer's Blackbird, Ficken (1963) the "Head Held Up" in the Common Grackle and Laskey (1950) "Bill-pointing" in the Brown-headed Cowbird. Nero (1956a, 1964), termed the posture "Bill-tilting", in the Red-winged and Yellow-headed Blackbirds, due to the prominence of the raised bill. In all of these species except the Yellow-head, where the tilting is most frequently given during flight, the bird is perched and the posture is rigidly maintained, in some instances for a number of seconds. It occurs only in the presence of another individual.

In the Bobolink a display with similar components was characterized by a flipping of the bill upward to a position of from 40 to 70 degrees above the horizontal (Fig. 12c), with the posture normally held fixed for less than a second. The flipping was often repeated two or three times in quick succession. Rarely, a male held the pose for as long as two seconds. In addition to the neck stretching and the upward bill movement, the most conspicuous feature of Bill-flipping was the simultaneous compression of contour feathers during the movement. The tail was not fanned but was generally slightly lowered.

This display was given only when two males were within

one to three meters of each other, either during a Parallel Walk or when perching. On one occasion Bill-flipping was performed four times by a male as it flew nearly vertically one meter, with dangling legs, neck continuously lengthened and bill pointed upward at approximately a 75 degree angle. This display was very similar to the "Jump-Flight" in meadowlarks as described by Lanyon (1957). It occurred at a territorial boundary, within one meter of a male giving high intensity Song-spread. The latter male chased the former for a short distance, both returning to their original positions where the first bird resumed Bill-flipping from the ground. Nero (1964) reported that Flight Bill-tilt is the most common form of Bill-tilting in the Yellow-headed Blackbird, and is performed frequently by the Brown-headed Cowbird, but is unusual in other icterids. The single observation from this study from among several hundred observations of ground and perched displays attests to its rarity in the Bobolink.

Female Bill-flipping was noted four times, each in a perched situation. In one case a female perching on a Meadow Rue gave a brief but clear Bill-flip with compressed contour feathers at the instant another female landed at her level 20 centimeters away. Both birds then remained quietly perched for over one minute, giving no further displays, before they flew in different directions. It was not determined if these females were mated to the same male. The other three observations of Bill-flipping occurred within the

willow patch, and all were performed in alternation with the female zeep vocalization; in two of the three cases both females participated, yet only one vocalized. The birds flipped their bill once or twice per sequence remaining perched for 15 to 45 seconds before repeating the flipping action. Four to six zeeps were given in some of these intervals. In two instances I inadvertently flushed the birds while positioning for photography; in the third case the females quickly ceased this activity soon after I noted it and began moving away through the willows. All female Bill-flipping occurred before the onset of the maximum egg laying period.

Bill-flipping appears to have a greater threat function than Song-spread in the Bobolink; this seems to be true in most other icterids as well.

Display-preening: Male Bobolinks frequently alternated a ritualized preening with other displays when contesting territory edges. With quick preening movements areas of the upper breast, sides of neck and shoulders were touched. A significant characteristic of most Display-preening was an orientation of raised nape feathers toward the opponent. The feathers most frequently preened were those of the white scapular area of the shoulder, which the male flicked upward with its bill; this was a very conspicuous action, and was almost always performed on the shoulder closest to the opposing male. Aside from raised nape feathers no ruffling of

body feathers was apparent. Preening movements normally lasted no longer than eight to 10 seconds before another activity was initiated.

Thrust-flight: Short quick one to two meter flights directly at another male were of uncommon occurrence in Parallel Walk series. Occasionally these aggressive thrusts took place following Bill-flipping or Song-spread. The bill was usually partly open but no audible vocalization was emitted. Thrust-flights often elicited a Chase or an Aerial Contest (see below). These Thrust-flights did not appear in a standardized form, and are not considered to be displays.

Direct-run: A common activity during Parallel Walks was the Direct-run, occurring when two males were spaced about 0.5 meter apart, and one lowered its head, pointed it straight ahead as the neck was lengthened, and ran swiftly toward the other male, often with bill slightly open (Fig. 12d). Except for slight erection of upper tail coverts, contour plumage was usually sleeked. The wings were pressed tightly against the body, the tail was lowered and no audible vocalization was given. Only rarely was contact made, for the submissive bird quickly reacted by running or flying a short distance. Quite frequently, however, an Aerial Contest or Chase arose from a Direct-run as the attacked bird flew upward at the last moment.

Ficken (1963) treated attack movements of this nature as unritualized activities, but the constancy of posture in

Bobolink Direct-runs suggests ritualization of these particular components into a standard display.

Aerial Contest: The most aggressive encounter involving Bobolink males was the Aerial Contest. This was almost always initiated as a male flew at or made a Direct-run or Thrust-flight toward another male that was on the ground; immediately the two rose vertically, facing one another with outstretched feet, flapping their wings, and maintaining a distance of less than 10 to 15 cm from one another. Throughout the flight the birds clutched at one another's feet and continuously struck at each other with their bills; it was not unusual for two males to interlock feet at the high point of flight and fall to the ground, where they occasionally continued grasping and striking one another as they thrashed wildly about for six or seven seconds. Flights to 20 meter heights occurred, but three to five meter Aerial Contests were most frequent. Despite the rapidity of wing beat, the flights proceeded upward in "slow motion," and occasionally lasted 10 to 15 seconds. In no instance was vocalization heard accompanying these flurries. In over half the observed Aerial Contests two or three successive flights occurred, the last ones tending to be shorter and attaining lower heights. On one occasion following an Aerial Contest the males alighted less than 50 cm apart and simultaneously performed a series of six or seven one meter high jumps, making contact with either feet or bills on

every jump.

These Aerial Contests occurred in almost all Face-off or Parallel Walk situations. On two occasions a male flew from a song perch directly into a perched male, knocking the latter from its perch; both then rose in vicious combat. After most Aerial Contests arising from Parallel Walks, the males resumed their display activities, but occasionally one male departed after the flight, or a short chase ensued.

The only account of this behavior I have encountered in other icterids is a description by Williams (1952) for the Brewer's Blackbird. Whereas the Bobolink Aerial Contests invariably arose in a situation of territorial establishment or defense, the activity in the Brewer's Blackbirds apparently occurs as an intruder makes sexual advances toward an already-paired female and is met but not repulsed by displays of the mate. Ficken's (1963) "Fly-up" described for the Common Grackle in agonistic encounters may be a related behavior. Although I have not seen a description of such activity for the Red-winged Blackbird, I have seen upland Red-wings engaged in a series of similar flights. However, I was unable to determine if they were associated with territorial defense or guarding of a mate.

Nodding: A Male engaged in territorial disputes from time to time faced the opponent and directed a sharp exaggerated bow toward him. Occasionally these movements dipped so low that the bill was depressed below perch level, but

they were never held for more than one second. No vocalization accompanied these Nods, which were reinforced by ruffling of nape and back feathers and slight spreading of wings. Nodding was interjected within many Parallel Walk series; however, the display was more frequently performed from perches.

Nero (1964) described a "deliberate downward movement of the head which often appears in agonistic situations" in the Yellow-headed Blackbird, but he suggested it was of unusual occurrence in other icterids except, perhaps, the Bobolink. He commented: "It seems possible that Nodding is a well-developed display in the Bobolink, although this needs to be verified, and that the conspicuous nape feathers are related to this particular display." In my study Nodding was a conspicuous and common display for only the short period immediately following territorial establishment. Some males Nodded frequently while with others it was a rare display; this may be a reflection of a tendency for Nodding to be more frequent in perched than in ground interactions, for few territory boundaries had bushes where males regularly engaged in perched defense. Nodding is ritualized in the Bobolink, as Nero suggested, and two elements are characteristic: the exposure to the opposing male of the raised nape feathers may have a threat function, but simultaneously the bill is brought low and hidden from the other male's view. This visual "cut-off" of the bill (c. f. Chance,

1962) may have a suppressing function of even greater significance than the threat element of nape exposure. In no case immediately succeeding Nodding did contact, fleeing or a chase result.

Head-flagging: A fairly common display given during Parallel Walks was Head-flagging. In this activity, performed as two birds walked beside one another, a male suddenly turned his face away from the other bird exposing his nape, and as in Nodding, completely hiding the bill. I suspect the latter may be the more significant of the two effects, and that the visual "cut-off" of bill-hiding functions in reducing the overall level of stimulation developed by the aggressive displays of the Parallel Walk.

Back-presentation: A Bobolink posture having a threat function was a mere orientation of the entire back toward a male opponent, the body held upright. In some instances the white dorsal body feathers and the nape plumage were slightly raised but just as often they remained unfluffed. In either case, the posture presented the conspicuous white and black dorsal surface to the opponent. This movement was frequently given during boundary disputes in Parallel Walks, or by two perched contestants. It was also frequently performed by a lone male on a song perch when another male flew near or landed close by in a neighboring territory. The display was commonly alternated with Song-spread and lacked vocal components. The high frequency of the Back-presentation

posture in boundary disputes is evidence that the movement is more than a casual activity having no communicatory function.

Tail and Wing-flicking: Although not patterns associated with territorial defense, Tail and Wing-flicking are described here because they are related to situations of anxiety and to intrusion of foreign objects into territories or close to fledglings. Perched male and female Bobolinks perform rapid flicking of the tail and wings when disturbed by intruders. In most instances both the wings and tail are simultaneously flicked in one quick movement; the tail is depressed and widely spread, then brought up as the rectrices fold. At the same instant both wings remaining folded at the wrist joint are flicked upward until they appear almost to touch above the body's mid-dorsal line, then are drawn down to rest position against the body. Aside from the nape feathers, body plumage is unraised. The male emits the tchenk vocalization during each movement while the female gives the quipt sound. Wing-flicking movements are so rapid in both sexes (approximately 0.1 second for the complete action as determined by cinephotography) that the wings can rarely be observed as they move, except as they reach the zenith. Similarly, in Tail-flicking it is difficult to detect exactly when the tail is fanned. In some cases the tail is lowered and raised without horizontal fanning. The most striking feature of the male's Wing-flicking is the

alternate exposure and concealment of the white rump patch as the wings flash up to expose and down to partially hide the rump feathers. Often the male orients his body at an oblique angle to the opponent or intruder further emphasizing the pattern.

The display is given predominantly toward intruders near the nest, and occurs most frequently at fledging time. In such instances I have recorded 144 complete Tail and Wing-flicks per minute in males and 54 per minute in females. I have noted females make rapid preening movements between the flicks. Prior to fledging of the young, Tail and Wing-flicking are less frequent and less intense. Hence, the displays serve as good indicators of fledging.

Tail-flicking not accompanied by Wing-flicking is performed by subordinate males while in the presence of a male directing Song-spread toward the Tail-flicking individual. This was observed only during early stages of territorial establishment, and in three observed instances the subordinate bird took flight soon thereafter.

Tail-flicking is a common icterid display, but Wing-flicking is rare in the family. Nero (pers. comm.) advised me that a similar "Anxiety Wing-flicking" occurs in the Rusty Blackbird. Red-wing females "wing-flick", but the movement is slight and often asymmetrical, is directed toward males, has no vocal accompaniment (Nero, 1956a), and is probably unrelated to Bobolink Wing-flicking.

Establishment, Maintenance and Dissolution of Territories

The five males exhibiting territorial behavior on 7 May quickly localized on separate areas and began giving Song-spread advertisement from perches dispersed over the territory. This low intensity Song-spread was not directed toward individuals except in cases where a neighbor flew or landed close by. The perched male then performed directed high intensity Song-spread. In the Common Grackle a lone male giving "Ruff-out squeak" shows low intensity components with every display. When another male is present 95 per cent of displays are high intensity and 84 per cent of these are directed toward the other male (Ficken, 1963). Aside from chases of transient males, aggressive interactions were uncommon, presumably because of the dispersal of the few territory defenders. However, these birds were kept employed Chasing trespassing transients from the as yet poorly-defined territories. Pursuing males in these early chases tended to remain below and on the territory side of the intruders, and although individual Chases were not long their frequency was such as to keep the defenders in the air for as long as 15 minutes at a time.

Until females arrived in fair numbers territorial males did not remain on their territories throughout the day; territorial activities were most intense in the early morning until about 0830 to 0930 hours, after which males frequently departed toward the east for periods ranging from

five to 25 minutes. Upon returning they dropped immediately onto their territories. During an individual's absence, the neighboring residents observed territorial boundaries to a degree, although considerable trespassing occurred.

Two patterns of territorial development were evidenced: (1) shrinkage of original large territories due to population pressure by incoming birds; and (2) expansion of the occupied sections of the field by peripheral annexation. The fate of a territory occupied on 7 and 8 May by a male north of the ditch offers an extreme example of territorial shrinkage. Most other males at this time were vying for territories on the south section of the field leaving this male relatively undisturbed. Early on 10 May, however, I observed this bird flying helter-skelter over the entire 10 acre extent of his original area, attempting to evict newly-arrived males. Within a few hours he had narrowed his defense to an area of less than three acres, and by 15 May his territory had shrunk to just over one acre. Similar but less drastic reductions in territory size occurred for most early resident males.

In other cases incoming males tended to establish moderate sized territories adjacent to previously occupied areas rather than settle on large tracts at a distance. This pattern was followed on the south half of the field where three territories were first established along the ditch despite availability of much uninhabited space of

similar vegetation further south. The next resident males "filled in" the space south of and adjacent to the first territories, producing only a slight alteration of the boundaries of previously established territories, but still not extending the new territories as far as the field permitted. The stimulation derived from territorial conflicts may be an important element in providing readiness for courtship upon arrival of females, and consequently may be a factor in the tendency for males to establish contiguous territories in a pattern conducive to intense territorial activity.

By 8 May prolonged Parallel Walks between adjacent rival males were taking place. Parallel Walks were extremely frequent from this date until courtship activities commenced about six days later, and were the most common means by which minor territorial boundary adjustments were effected. New potential resident males attempted to usurp portions of established territories by a technique similar to that observed by Nero (1956b) in Red-wings. In this sequence of events a male flew two to three meters high over the boundary line of another's territory and was chased back, both giving Song-flight. The defender, who quickly returned after driving the trespasser a short distance, was usually unable to alight before the intruder again advanced inviting further chase. If, after repeated invasions of this sort, the resident failed to give Chase the intruder landed two or

three meters from him, usually precipitating an immediate Chase. When faced with a persistent intruder an occupant eventually retired to a favorite song perch, where the trespasser initiated a series of flights less than 0.5 meter over his head. This stimulated further Chases. A few persistent males slowly gained access to portions of occupied territory, but more frequently they failed, and after a series of such performances left the meadow.

After all territories were firmly established it was an easy matter to identify new males on the field, for wherever they alighted they were quickly chased by residents. It was not uncommon about 20 May to observe a non-territorial male buffeted over the entire meadow as it attempted to land here and there without success. In each case the intruder remained on the field for only short periods. However, in 1967 a male being dealt with in this manner by residents was captured and color marked. He was observed on the meadow for over two hours after banding, being evicted from one territory after another before disappearing. Four days later he returned and successfully occupied a territory that had been vacated by a male the previous day. These observations demonstrate that a drifting population of Bobolink males existed, unable to establish territories except under special circumstances of male disappearance.

By early June when females were incubating eggs males spent much of their time foraging in deep grass. Song

became so infrequent that five to seven minutes occasionally elapsed without a sound from the territorial males, giving the impression of vacant or undefended territories. However, territorial advertisement was now performed almost entirely by group Song-flights involving as many as nine of the fifteen males simultaneously. Initiated by one male taking flight above his own territory in song, and joined quickly by the others, these flights were intraterritorial. Dives and chases still occurred when an intruder alighted within an occupied area or flew at less than three or four meters overhead. Birds from adjacent territories occasionally met at localized Face-off positions but ritualized displays became increasingly uncommon. Brief renewal of territorial defense arose when apparently unpaired late-arriving females appeared on the field. It is probable that certain of these females were not actually late-arrivals but were resuming courtship activities with their mate after destruction of their first nest.

When chicks were hatched all males with exception of male number 7 tended young, and accordingly participated even less in territorial activities, though renewed defense spontaneously arose from time to time. Song became mere fragments of its original extent and was given less and less frequently; by late June hours sometimes passed without a fragmentary song given. Male 7 guarded his territory longer and more persistently than any of the others, not

allowing trespass until young had fledged from his first mate's nest. As noted before, there was a high degree of coincidence in fledging of young from many nests. The young from any nest often quickly scattered over a number of territories, the attending adults followed and the last remnants of territorial behavior dissolved. This suggests another advantage of synchronization of nesting progress.

Sexual Behavior

Pair Formation and the Pair Bond

A Bobolink male reacts to all females alighting on its territory by giving Song-spread and by chasing the female. The first two females observed on the study meadow on 7 and 8 May quickly fled the field under the onslaught of male chases; but on 10 May two females repeatedly returned at the termination of every chase, each to a specific male territory. It appears that pair formation occurs when a female enters and remains on a male's territory.

Once the pair bonds had been formed on my area the members of pairs remained together until the time of departure from the field. Polygamous males, however, essentially broke pairing relationships with all but their initial female once young were fledged from her nest, the other females becoming independent. In 1967 color-banded pair members usually foraged in immediate proximity to one

another when on communal feeding grounds and in the post-breeding flock. The pair bond probably persists only during the breeding season, for males and females arrive separately during spring migration and are segregated during at least part of the non-breeding season.

Courtship

Nero (1964) described a sequence of male courtship displays common to a number of icterids and probably occurring in, but not yet described for many others. He called it "Symbolic-nesting," a term derived from certain nest-building movements that terminate the sequence. The displays occur from the time of pairing until pre-copulatory behavior is initiated. In the Red-winged and Yellow-headed Blackbirds (Nero, 1956a, op. cit.) the seven individual displays which comprise the sequence are: Elevated-wings, Flapping-flight, Dropping, Bowing, Crawling, Pecking and Building, usually occurring in this order. Many variations in completeness of individual displays occur, and often only portions of the sequence, usually Elevated-wings and Flapping-flight are given. A brief summary of the usual pattern in the Redwing and Yellowhead as described by Nero follows: a courting male addresses a female with wing tips elevated above its back, often giving Song-spread. He then flies to a "potential" nest site with slow, labored flight and drops into or onto vegetation giving a buzzing note and keeping the wings elevated for several seconds. The male

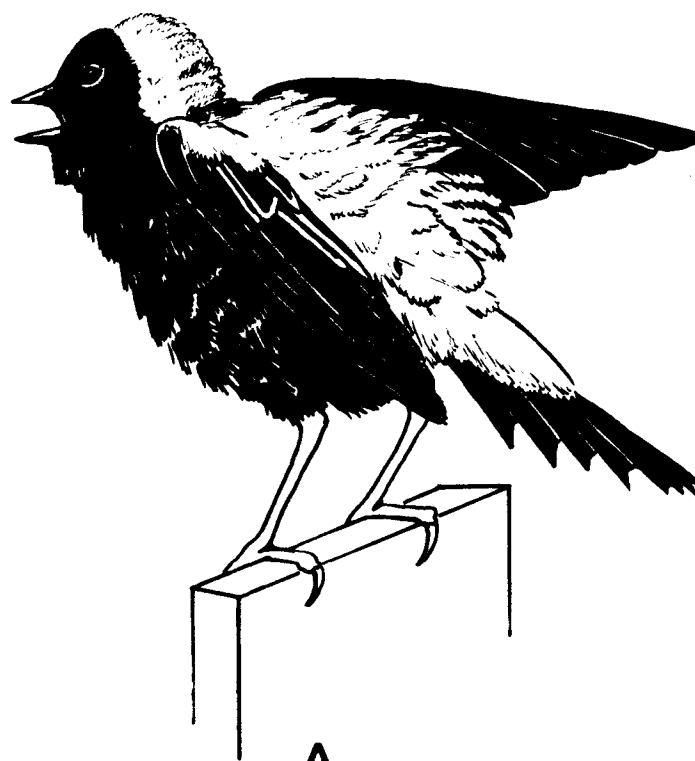
then Crawls through the vegetation while retaining partially up-right wings and suddenly bows, and bites or pecks at nearby plants. Usually the sequence proceeds no further, but rarely nesting material is manipulated in movements suggestive of nest-building. The sequence may be repeated a number of times and sometimes the female follows the male as he crawls.

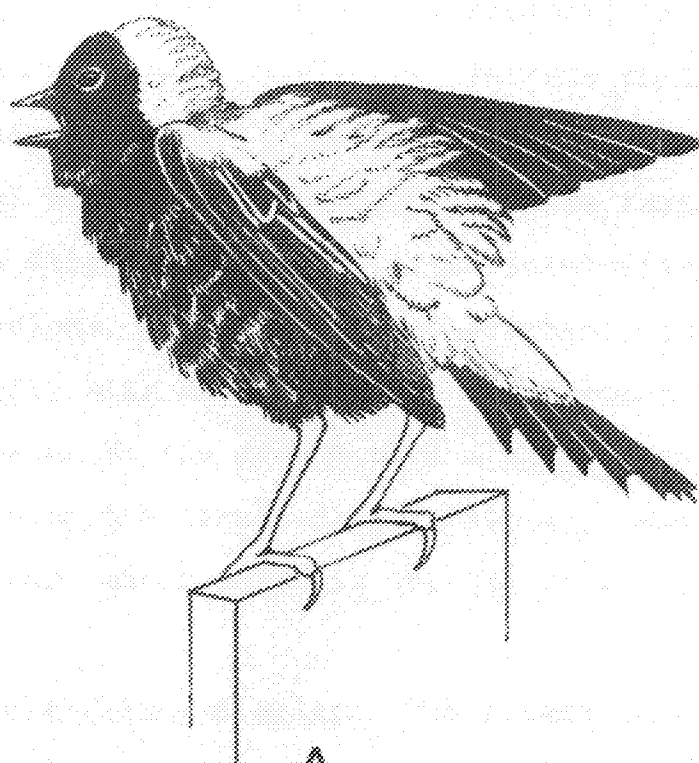
Certain displays of Bobolink courtship are strikingly similar to elements of the above sequence, but in this species the series usually terminates after the Bowing or Crawling stage.

(1) Elevated-wing display (Fig. 13a): This display was given both in Symbolic-nesting sequences or independently when followed by no other visible display. The latter usually occurred when a mate or new female flew overhead, and the display had little or no vocal accompaniment and generally was rigidly maintained for five to 10 seconds. A similar display was described on page 73 as a variant of Bobolink Song-spread. I have been unable to discover consistent postural differences between Elevated-wings given in agonistic and courtship situations; however, plumage erection and song appear to be more common in courtship Elevated-wings (Compare Fig. 13a and Fig. 10f).

When the Elevated-wing display was performed as a part of courtship the male was usually oriented away from or at an oblique to a female five to 20 meters away and the

Figure 13. (a) Courtship Elevated-wing display. The tail is extremely fanned and body plumage is fluffed. (Sketched from a 16 mm cine frame); (b) posture accompanying courtship partial song directed toward females. This male has a missing rectrice, allowing the investigator to make confident individual recognition; (c) orientation of male's dorsal surface toward a female between mounts. Vegetation conceals a fanned tail. Frequently, the male turns his head toward the female while he maintains this posture.

**A****B****C**



A



B



C

Elevated-wing display was usually accompanied by prominent ruffling of body plumage except for feathers on the forehead. The tail was almost always widely spread and partial song was given with most displays. In these instances the male took flight immediately after terminating song. On a few occasions, as a female flew overhead, the male postured briefly with Elevated-wings and Dropped immediately from the perch to the ground with a buzzing rasp (see beyond), omitting the Circle-flight display. Nero (1964) reported similar "short cuts" in the Yellowhead and Red-wing sequence.

(2) Circle-flight display: The flight in this display usually followed a circular route, sometimes terminating near its origin. The pattern of flight closely resembled the hovering of Song-flight, but was usually slower and always occurred at less than a three meter height. A one to three second song was given during flight and the tail was spread. Accordingly, the Circle-flight of courtship was much different from the high Song-flight used for territorial advertisement. It was also noticeably different from the Flapping-flight of the Yellowhead described by Nero (1964) in which the wings are kept elevated. Although no song is reported to accompany the Yellowhead Flapping-flight, a rattling sound "possibly produced by the primary quills" may serve to emphasize the flight and may be a functional counterpart of the partial song of the Bobolink's flight.

(3) Dropping display: After completing its song the male Dropped with legs dangling and with wings held at a strong dihedral above its back to a forb perch or to the ground. As it Dropped, from one to three rasping buzz notes were given, the last being the most drawn-out and loud. Wings were often retained in the elevated position for three to five seconds after alighting, and occasionally the male tilted slightly forward (Bow). Often the courtship sequence terminated at this stage, but occasionally a male continued by walking through the vegetation (Crawling) with wings partially spread but not elevated. Frequently the dorsal surface was oriented toward the female during the Crawl. On at least five occasions a female trailed three or four meters behind the male while he Crawled. In over 200 observations of the courtship sequence only two sequences progressed to the Pecking stage. In both cases the male picked once or twice at grass stems.

During the period of most intense courtship a male commonly performed the entire sequence up to at least the Drop stage about every two minutes. Aside from the few times a female accompanied the male as he Crawled, the female's role during the courtship sequence was passive and she usually remained on a perch a few meters away or on the ground. However, short sexual chases were frequently activated by the female if she flew over the male or gave a series of zeep notes.

Frequently during the courtship period a male alighted near his mate and sang, facing her. This partial song was not directly related to the courtship sequence. Most dorsal feathers remained unraised during the song (Fig. 13b).

Sexual Chasing

Chases were numerous from the date of first female arrival until approximately the middle of the laying period. Males chased all females that landed on their territories and frequently joined in group chases of females paired to other males. In almost all instances sexual chases were initiated by males but females often stimulated their origin and lengthened them; prior to many chases females perched conspicuously, preening or giving zeep notes, or they flew to land near a male. Either of these female behaviors frequently resulted in a chase. Often females repeatedly turned and swooped in front of the male when he ceased his pursuit and retreated toward his territory. In these instances the flight was extended for as long as four to six minutes. On two occasions I saw a perched female fail to take flight as a male swooped at her and in both cases the two rose five to six meters in a vigorous Aerial Contest; it was not determined if these birds were paired.

Most of these two-bird sexual chases were centered over the territory. The female's flight was rapid and elusive and the pursuing male often dove directly at the female, but in only three instances in over 150 chases noted

in detail did I observe brief contact. Song was commonly given by the male during the chases.

Sex chases were longest in the period just following pair formation. It was at this time, also, that a maximum of group-chasing occurred. As many as six males participated in such performances but more commonly three or four. In group chases the female's mate usually showed the most aggressive pursuit and males gave more song than in chases involving a single male. Nero (1956a) pointed out that in the Red-wing, "...the great amount of song which occurs during the group chase is an indication of the mutual aggression of the males rather than a direct response to the female." This appears to be true for the Bobolink as well. By about 21 May most chases were short intra-territorial flights with little vocalization, involving only the pair. By this time many females were laying eggs.

Sexual flights are common in many passerines (c.f. Nero, 1956a for review), and Tinbergen (1939) felt that sexual unreadiness in the female causes her to flee the male's advance, thus generating the chase. In no instance following a Bobolink sex chase was a copulation observed, which lends credence to this idea. However, this explanation fails to explain the obvious persistence of the female in extending the flight. In addition, I have observed about 10 instances where a polygamous male's second mate perched zeeping while he was chasing his other female; the former

took flight, continuing to zeep, and swooped between the male and the pursued bird. In all cases the male altered course to briefly chase the second female before resuming the original chase. The tendency for females to prolong or to become involved in these chases suggests that sexual unreadiness is not the only cause of the flights.

Sexual chases may function in the mutual stimulation of the entire localized population. The peak number of group chases on my field occurred within the interval from pairing to conception of the majority of females, after which there was a sharp decline in frequency of sexual chases. This peak may be important in the synchronization of nesting cycles, which has been discussed above.

Precopulation and Copulation

Crouch: The frequency of courtship declined four or five days after pair-formation when males began directing the pre-copulatory Crouch display toward females. Male Crouches were given facing the female immediately after alighting on a low perch or on the ground within 0.5 meter of her; approximately half were accompanied by partial song. In the Crouch display (Fig. 14a, b, c) the wings were partially spread and the shoulders hunched; the tail was depressed and usually fully fanned. Feather erection was conspicuous on the nape, upper back, throat and breast, and the body was usually bowed forward, occasionally with the head lower than the feet. The bill was generally tilted downward

Figure 14. (a, b, c) Three intensities of the male's Crouch display; (d) female performing a head-thrust as a male approaches in an attempt to mount.



A



B



C



D

to a varying degree. Crouches were rigidly held for three to five seconds.

On the first day of Crouch display the male usually departed immediately after performing the behavior. By the second day, however, the male often attempted to mount with a direct short flight from the Crouch position, although the female never made solicitation movements. Occasionally these mounting attempts were successful as the female struck copulation posture (described below) just as the male mounted. But usually the female repulsed the approaching male by pecking toward him with open bill (Fig. 14d); in all of these latter cases the male quickly departed. A "spitting" note was often given in conjunction with the female's head-thrust.

About two or three days after initiation of male Crouching the female began giving Solicitation display. In this posture the female crouched on flexed tarsi with tail slightly elevated and with spread, rapidly quivering wings. The display was performed with or in alternation with long rapid series of zeep notes and was usually performed as the male flew overhead or was perched further than 10 meters away. In no instance was this posture noted during or following a male Crouch display. Usually a female terminated Solicitation prior to copulation, and gave a separate Reception posture an instant before the male mounted; but occasionally the Solicitation display progressed directly in-

to the Reception posture. In the Reception posture the female's head was held high, the neck slightly hunched and the bill was pointed upward. The entire body was tilted forward on flexed tarsi and the tail was raised upward and cocked to one side. The female apparently did not vocalize during copulation.

Mounting usually occurred directly following a flight from a perch or near-by ground position. Occasionally the male hopped directly onto the female from about a 15 centimeter distance. Mounting flights from the ground were invariably preceded by a slow walking variation of the Crouch display, in which the male approached in a stiff fairly upright posture with greatly arched wings and erect body plumage. The tail was lowered, spread and dragged on the ground, and occasionally partial song was given.

Copulation contact was brief, usually lasting less than one second as the male rapidly fluttered its wings and lowered its tail. Action was too fast to determine position of the male's feet. Dismounting was always by flight. As many as 17 consecutive mounts were noted, although eight to 10 were most frequent, spaced six to 40 seconds apart. On one occasion only two mounts occurred. Between mounts the male frequently perched or remained on the ground with his back oriented toward the female with prominent erection of nape and upper back feathers, wings slightly spread, and tail lowered and fanned (Fig. 13 c). This display differed

by its more upright posture and longer duration from the Crouch display. Partial song was often given once or twice and except for head movement the display was held rigid for as long as 10 seconds.

In intervals between mounts the female preened, scratched her head with her feet and fluffed her plumage. Sometimes the tail was fanned laterally from side to side for one to two seconds in extremely rapid movements, and wings were vigorously flipped asynchronously up and down. All of these motions increased the conspicuousness of the female. After the final mount females usually perched stiffly upright for 15 to 20 seconds, wing tips held rigidly below body level and neck stretched upward. This posture was succeeded by movements described above. Males never were seen engaging in post-copulatory activities, and frequently they departed abruptly after the last mount.

One copulation sequence observed in 1967 involving a polygamous male was of special interest. The male, engaged in a sexual pursuit with his mate A passed five meters over the head of his mate B, who responded by performing a high intensity Solicitation display complete with elevated bill and tail, and emitting a series of zeep calls. This occurred three times within 70 or 80 seconds, and on the third pass the male abruptly banked and landed two meters away from female B, arched his wings, fanned and lowered his tail and walked toward her in a fairly upright posture dragging his

tail in the grasses. When about 15 cm from her he jumped and mounted, then flew to a near-by stake and gave three, three-note pings before returning to the ground near her. After eleven mounts another female, presumably female A, appeared and dove between the pair inducing the male to follow in a twisting, rapid sex chase. Within two minutes after the male's departure female B flew to a perch with four or five stems of nesting material in her bill.

Diversiory Behavior

With an aim of gaining clearer insights into functional aspects, Gramza (1967) urged extended observations of "Distraction display," or "Diversiory behavior," those types of responses of brooding adult birds tending to increase their conspicuousness and enabling them to lead or divert intruders from the nest vicinity. Among icterids Diversiory Behavior is apparently rare, having been reported in only Bobolinks and Eastern Meadowlarks (Nero, 1956a). Nero (1955) related a single observation he made of a female Bobolink performing as she "...alternately ran and flew along the ground in the pasture with slightly spread and shaking wings." Diversiory Behavior was frequent in Bobolinks on my study area and both sexes engaged in it when flushed from eggs or young. Diversiory Behavior was exhibited in 38 of 103 occasions when an adult was flushed directly from the nest; 10 were performed by males, 28 by females.

Some individuals never gave Diversionary Behavior, and either flushed while I was 15 to 20 meters away or flew directly from the nest with straight swift flight for 20 or more meters. A few females were especially adept at sighting my approach and left inconspicuously long before my actual arrival. Others sat until I was close to them and then frequently gave diversionary activities as they left. In most instances after three or four daily flushings even these birds moved off the nest long before my arrival. Consequently, the greatest amount of Diversionary Behavior at a particular nest was evidenced in the first two or three days after its discovery. Another peak occurred during and just after hatching, when brooding adults often remained unflushed until I approached closely; only during this period of the nesting cycle did males show the behavior.

The forms of Diversionary Behavior were variable. A typical female pattern began with a one meter hop-flight directly from the nest; the bird then skimmed along above the vegetation for a meter or two and plummeted with outspread wings into the vegetation. She then ran in a weaving, "rodent-run" fashion for two or three meters lurching from side to side, alternately exposing right and left outstretched wings. The body was kept "hunched" throughout the run. Another hop-flight was then performed, commonly with rapid fluttering, wings beating hard against the vegetation or with one or both wings held back and downward.

The tail was usually fanned. Never did a female vocalize during this series of activities until I left, when she usually initiated chunk notes. If I followed a female engaging in diversionary activities, she remained two or three meters ahead of me, alternating the lurching runs with the fluttering hop-flights and occasionally turning her head toward me. In this manner I was sometimes "led" as far as 80 meters from the nest; and when I returned to determine nest contents during the early nestling period, males were sometimes already on the nest brooding young. On one occasion within a 15 minute interval I was "led" from a nest five consecutive times, with male and female alternating in brooding as I followed one or the other.

Some females performed more conspicuously than others; one bird when flushed on two consecutive days ran for 10 meters dragging her left wing behind on the vegetation but keeping her right wing against her body. On both occasions she then perched on a Meadow Rue and drooped a wing conspicuously downward for more than 30 seconds. Certain other females consistently remained so tenaciously on the nest that my hand came within 5 centimeters of them before they flushed. On one occasion a female slowly crawled from the nest, flapping weakly as she moved through the vegetation. I was convinced she was injured and actually picked her up! But immediately upon releasing my grasp she flew 10 meters and perched, scolding with chunk notes.

Three times as I moved toward nests, females approached and landed near me from a non-nest direction, then moved away from the nest with diversionary movements. Twice as females I had flushed from nests were performing hop-flights, their mates landed close by and exhibited similar behavior.

In contrast to the silent performances of females all males engaged in diversionary activities gave the warble song almost continuously from time of flushing until I turned away when they began perched tchenk notes. They usually gave more conspicuous diversionary movements than did females, including more elaborate wing dragging and sideways lurching; even when not trailing wings behind both wings were held low, prominently exposing the white rump feathers.

SUMMARY

During the 1966 breeding season the ecology and behavior of the Bobolink were studied on a lowland meadow near Madison, Wisconsin with the purpose of providing more precise information on aspects of breeding ecology than is currently available, and of elucidating in detail the agonistic and courtship displays of the species. Observations of displays obtained in 1967 are included to complement the 1966 data.

A discussion is given of certain possible environmental factors which may be important in the "micro-distribution" of Bobolinks over a relatively homogeneous grassland habitat.

Contrary to previous reports Bobolink males were found to vigorously defend territories from time of their arrival until after young hatched. Pair formation, courtship and foraging occurred within the territory, which averaged 1.1 acre in size for the 15 males on the study field. Unlike some female icterids, Bobolink females exhibited only slight antagonism toward one another. During interspecific interactions, Bobolink males proved dominant over most other species, displacing them from song perches or chasing them. An important exception was the male Red-winged Blackbird, which strongly dominated Bobolinks. Nest locations and territorial boundaries seemed unaffected by these interspecific skirmishes. No hawk alarm vocalizations were detected.

At least three Bobolink males were polygynous, but monogamy was the most common mating type. Nests were built solely by females, and were located on the ground in the more thickly covered parts of the male's territory. Nest materials were obtained at distances ranging up to 80 meters from the nest, and construction took about two days. One egg was laid per day until the set was complete. Clutch size averaged 5.35 but tended to decrease in size as the season progressed. There was evidence that at least two females initiated a second nest following failure of, or successful fledging of young from, their first nest. No cowbird parasitism was recorded from 20 nests. The incubation period was approximately 12 days, the female alone performing the duty. Incubation was initiated following laying of the penultimate egg. No males were observed feeding their incubating females.

Monogamous males and their mates alternated between brooding and feeding chicks. Brooding ceased when nestlings were four to five days old. Polygynous males were not observed brooding young, but usually fed chicks or fledglings of their first female; young from second or third nests of polygynous males were usually attended by only the female. Feeding commenced within three hours after hatching; nestlings were fed animal food gathered both on the territory and at communal foraging areas on the field. At most nests males and females shared equally in nest sanitation and in care of the young. After the third day of feeding the number of

trips per young per hour remained relatively constant, but there was a significant increase in the biomass of incoming food.

Chicks not disturbed by humans fledged at 11 days of age, while chicks at disturbed nests fledged on an average of 9.7 days. Fledglings scattered almost immediately upon leaving the nest and were capable of flight by 13 days of age. About six days after young fledged, immatures and associated adults from a number of nests grouped into a flock which remained together until the Bobolinks departed from the field. Adults were observed feeding immatures for at least 21 days after young in their nest had fledged. Immatures begged toward all adults, but it was unclear whether parents fed only young of their brood.

Bobolink nesting success was higher than that reported for other icterids, and fledging success was higher than the average for open-nesting altricial birds. Early nests had higher success than those initiated later. Advantages of synchronization of the nesting cycle of Bobolink females are discussed in relation to an abbreviated breeding season known for some transequatorial migrant species.

Ten of the more frequently given vocalizations are described, and displays and activities are analysed in detail. The more important displays were Song-spread, Song-flight and a series of ground displays (Parallel Walk). Within the Parallel Walk series, Bill-flipping, Display-

preening, Direct-runs, Aerial Contests and Head-flagging were the most frequently performed activities. Similarities of Bobolink displays to those of other icterids are discussed.

Pair formation occurred if a female appeared and remained on a male's territory, and the pair bond apparently persisted for only the breeding season. Courtship consisted of a sequence of displays similar to that described for certain other icterids, and termed "Symbolic-nesting." Sex chases were frequent throughout the courtship period, and they may function to stimulate synchronization of mating and nesting. Males began performing the precopulatory Crouch display within a week after the arrival of the first resident females. Successful copulations occasionally followed male precopulatory displays, but more frequently females attracted their non-displaying mates with a vocalization accompanying the Solicitation posture, which closely resembled the Reception posture taken at mounting. Mounting was brief and occurred as many as 17 times consecutively. Female post-copulatory movements are described, but males apparently lacked a post-copulatory display.

The form of Bobolink Diversionary Behavior is described and the occurrence of Diversionary Behavior in the icterids is reviewed. Both males and females participated in diversionary activities.

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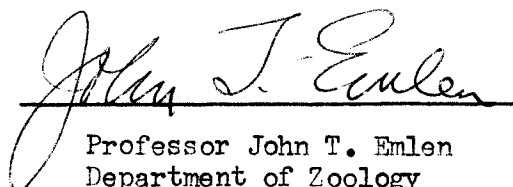
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Approved

A handwritten signature in cursive script, reading "John T. Emlen", written over a horizontal line.

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August 9, 1967