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Abstract approved: \_\_\_\_\_  
John A. Wiens

The adaptiveness of polygyny in passerines poses a particularly intriguing problem. The altricial young of this group require extended parental care, but young of polygynous pairings generally lack the undivided attention of the male which young of monogamous pairings receive. Polygynous offspring may thus be undernourished and experience greater mortality. Hence, the selection for polygyny in populations where unmated males are available suggests that an uneven distribution of ecological factors affecting breeding success permits females settling in excellent habitat to raise more offspring unassisted by a polygynous male than can be produced with full male cooperation in a less suitable area. This study's central objective was to determine if male Bobolink (Dolichonyx oryzivorus) pairing success was correlated with specific ecological factors within their territories, and if territory to territory differences in quality were sufficient to

account for the selection of this mating pattern. In addition, I examined those adaptive modifications of breeding biology and parental behavior which served to minimize reproductive failure at nests not attended by males.

Measures of various structural features of the vegetation were made at 1921 randomly-located sample points within an 11.3 ha sedge-grass meadow in south central Wisconsin. The data from sample points falling within bachelor-occupied territories were grouped and statistically compared with values from territories of other mating classes, and with values from 388 sample points which surrounded nest cups. In addition, the breeding biology of a large number of color-banded individuals was intensively studied over five breeding seasons. These observations included carefully standardized recordings of adult time-budgetings.

Morphological and behavioral differences between males and inter-territorial differences in food abundance were of minor importance in female mate choice compared to the enormous habitat disparities between different territory classes. Areas defended by bachelors, monogamists, bigamists and trigamists differed significantly in the density of large forbs which provided the only satisfactory nest concealment at the time nesting commenced. Furthermore, significant ( $P < 0.01$ ) discrepancies existed between these territories in the distribution and abundance of almost all habitat features characterizing nesting areas (per cent coverage of grasses, sedges and forbs, shading

properties of the vegetation, and the vegetative foliage height profile). Bachelor territories were deficient in features important in female nest site selection and were thus unsatisfactory for breeding. The quality of monogamous and bigamous territories was improved over that in bachelor holdings, and trigamists occupied the most satisfactory habitat. Thus, when some males are forced into habitats too marginal for successful breeding, this polygynous system grants each female an opportunity to nest in a satisfactory location.

Bobolink males generally assisted only their first (primary) female in feeding and brooding nestlings. A number of interrelated adaptations (the adaptive complex) functioned to circumvent heavy reproductive failure at secondary nests, where males did not aid. Secondary clutch sizes were significantly smaller than primary egg sets. This, combined with asynchronous hatching which promoted rapid brood reduction, brought brood size into correspondence with food transfer capabilities of secondary females. Moreover, male flexibility in feeding unusually large secondary broods and in caring for secondary nestlings late in the season increased secondary nesting success. Two of a series of other adaptive patterns were: (1) an optimization of the food delivery tempo of primary pairs, which probably extended breeding longevity; (2) a postponement of energy expenditure by yearling males in territorial and sexual advertisement behavior until special circumstances permitted opportunistic establishment in good habitat. This decreased unnecessary competition with older, experienced males.

Polygyny in the Bobolink: Habitat Quality and  
the Adaptive Complex

by

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## TABLE OF CONTENTS

<u>Chapter</u>		<u>Page</u>
1	INTRODUCTION	1
	Hypotheses of the Adaptiveness of Polygyny	6
	The Sex Ratio Hypothesis	6
	The Population Regulation Hypothesis	8
	The Habitat Quality Hypothesis	10
	The Natural Selection Model	14
2	DESCRIPTION OF THE STUDY AREA	22
	The Riverbottom Site	22
	Secondary Study Site	32
3	PROCEDURES	35
	Banding Program	36
	Grid System	38
	Behavioral Observations	39
	Breeding Biology	40
	Analysis of Vegetation Structure and Territories	41
	Light Penetration	43
	Vertical Density	43
	Percentage Cover	44
	Litter Characteristics	44
	Forb Density	44
	Time Budgets	47
4	A BRIEF LIFE HISTORY ACCOUNT OF THE BOBOLINK	51
	Migration	52
	Breeding Habitat	53
	Arrival and Territoriality	54
	The Question of Drifting Males	60
	Sex Ratios and Mating Levels	64
	Pair Formation and Courtship	66
	Copulation and Nest Construction	70
	Egg Laying, Incubation and Nestling Period	71
	Fledging, Post-fledging Period, and Breeding Success	73



<u>Chapter</u>		<u>Page</u>
5	TERRITORIAL QUALITY AND MATING STRUCTURE	76
	Territory Dimensions and Pairing Success	76
	Food Abundance	86
	Vegetative Structure Surrounding Nest Sites	88
	Vegetative Structure of the Territories	99
	Bachelor Territories	103
	Monogamous Territories	105
	Bigamous Territories	107
	Trigamous Territories	108
	Effects of Habitat Manipulation on Pairing Success	112
6	DISCUSSION: DIFFERENTIAL BREEDING SUCCESS, THE ADAPTIVE COMPLEX, AND BEHAVIORAL ASPECTS OF POLYGyny	117
	Differential Breeding Success	118
	Factors Influencing Differential Breeding Success	122
	Minimization of Secondary Reproductive Failure	135
	Clutch Size Differences	136
	Asynchronous Hatching	139
	Flexibility in Male Feeding Attention	142
	The Relation of Male Age and Behavior to Mating Status	146
	A Reexamination of the Drifting Class	152
	Effects of Polygyny on Time Apportionment	159
7	CONCLUSIONS	163
	LITERATURE CITED	172

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Comparisons of features of Bobolink breeding biology at the riverbottom meadow, 1966-70.	58
2 Sex ratios of adult Bobolinks, 1967-70.	65
3 Comparison of mating levels of territorial males, 1967-70.	67
4 Territory size and mating status, 1967-70.	85
5 Vegetative substrate of 127 nests.	89
6 Characteristics of vegetative structure surrounding nest sites, compared with values from random samples in the entire meadow.	90
7 Per cent coverage of physiognomic types according to territory class.	99
8 Density and height of major forbs according to territory class.	100
9 Total vertical density and depth of accumulated litter according to territory class.	101
10 Shading properties of vegetation in different territory classes.	102
11 Correlation coefficients (r) between various features of habitat structure and male pairing level.	111
12 Comparative breeding success of primary and secondary female Bobolinks, 1966-70.	119
13 Comparative breeding success of monogamous, bigamous and trigamous male Bobolinks, 1967-70.	122
14 Mean number of occurrences of selected male activities per five minute interval, in different stages of the reproductive cycle.	160

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	A modification of the general model of Orians (1969), illustrating the alternatives open to females by two systems of mating.	16
2	Map of the riverbottom study area.	23
3	A view of a low ridge in mid May; a view of a similar ridge in early July.	25
4	Two photographs of sedge swales in July.	26
5	Scattered large forbs along ridge - swale interfaces.	27
6	As the meadow appeared in flood (June 1968, 1969).	31
7	Summary of banding and return data on male Bobolinks at the riverbottom meadow.	56
8	Territorial configurations and ownership in late May, 1966-69.	77
9	Territorial configurations in late May, 1970.	78
10	Locations of 127 nests found from 1966-70.	92
11	Vertical profiles of vegetation density.	95
12	Differences between primary pairs and secondary females in the number of food carries per nestling per hour as related to nestling age.	124
13	Differences between primary pairs and secondary females in the total number of food carries to the nest per hour.	125
14	Differential growth of primary and secondary young.	131

# POLYGyny IN THE BOBOLINK: HABITAT QUALITY AND THE ADAPTIVE COMPLEX

## CHAPTER 1

### INTRODUCTION

Polygynous mating systems<sup>1</sup> are relatively rare among birds. Probably less than one per cent of the roughly 8600 species of birds of the world are truly polygynous, and these are scattered through widely divergent phyletic lines. In passerine birds, where the male can make a direct and substantial contribution to the care and survival of the altricial young, the evolution of polygyny poses a particularly intriguing adaptive enigma. The simultaneous attachment to more than one female and nest limits the time a male may devote to each female and her young. Prolonged male advertisement for additional females further limits allocation of time to hens during the crucial nestling period. Thus, a female that pairs polygynously when bachelors are available risks a substantial loss of male attention and assistance in tending young relative to that which she would derive in a monogamous relationship. This could have a direct bearing on

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<sup>1</sup>As used here, polygyny refers to a male's simultaneous maintenance of pair bonds with more than one female (the male form of polygamy, with bi- and tri- indicating the number of mates). Application of the term to successive pairings which do not overlap in time (von Haartman, 1951) is not correct.

the growth and survival of her young, and thus on her ultimate reproductive success. Yet for multiple-pairing to be favored by natural selection in instances where unmated males are present and actively advertising, females making this seemingly imprudent choice must realize a higher reproductive output than that which they would have attained had they paired with bachelors that could have more capably assisted them. This suggests that more satisfactory conditions for potential breeding success must exist in the territory of the selected male.

This problem has prompted considerable recent generalization and speculation on the possible adaptive significance of polygynous mating systems (Armstrong, 1955; Brown, 1969a; Crook, 1962, 1963, 1965; Downhower and Armitage, MS; von Haartman, 1969; Haigh, 1968; Lack, 1968; Orians, 1961, 1969; Selander, 1965; Verner, 1963, 1964; Verner and Willson, 1966; Willson, 1966; Wynne-Edwards, 1962). Despite this widespread interest, few investigations have examined in any quantitative depth the physical and structural parameters of avian territories suggested to be crucial in maintaining polygyny as an effective mating strategy. Zimmerman (1966), Verner (1963), and Verner and Engelsen (1970) have distinguished quantitatively certain ecological factors which are correlated with the ability of males to attract multiple mates in the Dickcissel (Spiza americana) and the Long-billed Marsh Wren (Telmatodytes palustris),

respectively. However, more detailed work on these and on other polygynous birds is essential to provide a framework for understanding the nature of the environmental circumstances governing the development and maintenance of a polygynous strategy. Because of the rarity of this mating system in passerines (Verner and Willson, 1969, reported that only 14 of the 291 North American passerines are regularly polygynous) it is particularly instructive to search for underlying ecological factors which contribute to the adaptiveness of polygyny to these few species. Moreover, the behavioral and breeding biology factors and processes which have evolved to adaptively reinforce polygyny have been by and large ignored.

The present investigation was directed toward determining if significant correlations exist between mating statuses of male Bobolinks (Dolichonyx oryzivorus) and various structural habitat features in territories defended by bachelor, monogamous and polygynous males. A further goal was to ascertain if differences in reproductive success existed between males and between females engaged in these various levels of mating. If relationships between territorial quality, social structure and breeding success could indeed be established, I hoped to examine carefully the relative importance of a number of territorial parameters which might play a significant role in maintaining the Bobolink's polygynous system. In addition, if it could be demonstrated that a male's ability to pair with females was

related to certain fine-grained (MacArthur and Levins, 1964; MacArthur and Pianka, 1966; Levins, 1968) differences in territorial habitat structure which influenced reproductive success, a posteriori speculations could be made as to the evolution of this mating convention in the Bobolink and perhaps in other passerines as well. A final objective was to discover and evaluate adaptive themes of breeding biology, behavioral propensities and time budgeting of adult activities, which served to maximize the reproductive output of a polygynous strategy.

This species is a particularly suitable subject for a study of this nature. The family Icteridae, to which it belongs, is probably the most exhaustively studied group of North American passerines, both ecologically and behaviorally. Consequently, this reservoir of precise and extensive literature enhances and complements the results of this study. Furthermore, polygynous themes are deeply entrenched in the evolution of icterid social organizations: Verner and Willson (1969) reported that icterids comprise seven of the 14 North American polygynous passerines and that nine of the 18 North American icterine species are either polygynous or promiscuous. The broad spectrum of adaptive radiation in icterid social organization is of added interest in illustrating the striking variation created by differing selective forces. This range extends from the nest parasitic cowbirds (Friedmann, 1929, 1963) through routine territoriality in a majority of the

species to compact coloniality in the Tricolored Blackbird (Agelaius tricolor), as described by Lack and Emlen (1939), Orians (1960, 1961) and Orians and Collier (1963). The various species holding close phylogenetic affinities with the Bobolink, therefore, exhibit a diversity of mating and social systems which provide interesting source material for possible comparative purposes.

An additional advantage of investigating the evolution of polygyny in the Bobolink is the ease of observation in its rather low, two-dimensional grassland breeding habitat. Because of certain ecological features characteristic of grassland and marsh communities that will be discussed later, these habitats theoretically provide exceptional opportunities for the maintenance of a polygynous mating organization in birds (Verner and Willson, 1966; Orians, 1969). Indeed, 12 of the 14 North American polygynous passerines breed in these two habitats (Verner and Willson, op. cit.).

The one disadvantage of working with the Bobolink is a paucity of any more than fragmentary accounts of its life history, ecology and behavior. This unusual species has been virtually ignored by the mainstream of precise, quantitative icterine investigation. This limitation was overcome by a thorough examination of the Bobolink's behavioral ecology as a substudy of the present research.



### Hypotheses of the Adaptiveness of Polygyny

A plausible explanation for the evolution of polygyny should, I feel, provide for an increased mean reproductive output of individuals engaging in this practice, over those pairing monogamously, when environmental circumstances favor multiple mate acquisition. Or, as Selander (1965:138) succinctly stated, a "complete understanding of the evolution of mating systems in birds will require study of the nature of environmental situations which select for loss of monogamy."

From the numerous discussions relating to the adaptiveness of mating systems, three conflicting hypotheses have been advanced to account for the development and maintenance of polygyny in passerines. To provide a framework within which to judge the significance of the results from this investigation, I will here briefly restate the salient features of these hypotheses and consider the merits of each, in view of results of contemporary field studies.

#### The Sex Ratio Hypothesis

It has long been widely held that polygyny is a byproduct of a skewed or unbalanced sex ratio favoring females (Chapman, 1928; Skutch, 1935; Mayr, 1939; Armstrong, 1947; Williams, 1952). Proponents of this opinion have argued that to prevent wasted reproductive potential of surplus females, some males must obviously service

more than one hen. Hence, a polygynous system develops.

When this hypothesis is applied to polygynous passerines, two difficulties emerge: first, among many well-studied species, size-able populations of sexually mature bachelor males are conspicuously present and advertising for females at the time of multiple mate acquisition by another male of the population. In fact, in the Bobolink (this study), Prairie Warbler (Dendroica discolor)(Nolan, 1963), Long-billed Marsh Wren (Verner, 1964) and the Red-winged Blackbird (Agelaius phoeniceus)(Orians, 1961) for example, bachelor males occupied territories abutting extensively with those maintained by polygynists. Further, in many species, populations of mature drifting males are also present. Clearly, polygynously pairing females made a free choice, and were not forced into accepting a previously mated male simply from want of unmated prospects.

Second, in many polygynous and promiscuous passerines whose breeding biologies have been carefully investigated, the sex ratio of immatures when they become independent of adults approaches equity (Williams, 1940; Lack, 1954; Selander, 1960, 1961; Orians, 1969). Moreover, theoretical considerations suggest that equalization of parental expenditure on the two sexes is the best evolutionary strategy for maximizing production of young (Fisher, 1958; Kolman, 1960; Willson and Pianka, 1963; Verner, 1965a; Emlen, 1968). In certain polygynous species (e.g., Red-winged Blackbird) greater

mortality rates on the large, conspicuous male combined with delayed maturation of the male skew the tertiary sex ratio in favor of females. But even here the presence of sexually mature bachelors coupled with conspicuous populations of mature, drifting males (Orians, 1961), discounts the need for employing a skewed sex ratio explanation for polygyny. Indeed, it is highly possible, as Selander (1965:134) and Orians (1969:601) contended, that a polygynous system might be the selective cause of, rather than the consequence of, delayed maturation of males and inequality of sexes, as will be discussed later. Despite these disparities between fact and hypothesis, the idea that mating systems have invariably evolved simply to maximize reproductive output when sex ratios are unequal has until recently been widely accepted, leading Verner (1964) to suggest that this point of view has led to a stagnation of thought on the subject.

### The Population Regulation Hypothesis

Wynne-Edwards (1962:216, 515) hypothesized that polygyny and other systems of social organization evolved through group selection as a means of effectively providing feedback on density to members of the population. The purpose of this feedback was to keep individuals well informed of density vacillations so that compensatory population control measures could ensue when density threatened to exceed the habitat carrying capacity. Continuous interactions resulting from the

greatly intensified intra-male competition for females and territories by polygynous males was assumed to allow males to gauge one another's successful sexual exploits more precisely than could monogamous species. This afforded each male an accurate tabulation of the fertilizations resulting from the group's mating activities. When the proper number of inseminations had occurred (relative to population density and suitability of the habitat), Wynne-Edwards contended that males became sexually inert, or voluntarily refused service to soliciting females. Thus, he felt that polygyny had evolved as a means for regulating the reproductive output of populations through a collective reduction of fecundity.

This hypothesis is simply at variance with the facts, for in no instance has observation of well-studied polygynous species confirmed that males withhold coition from receptive females, regardless of population density (cf., Selander, 1965:135). Further, Wynne-Edwards' fundamental reliance on group selection as the mechanism for the evolution of polygyny, rather than on conventional evolutionary processes operating through selection on the individual, is highly questionable (Elton, 1963; Brown, 1964; Maynard-Smith, 1964; Selander, 1965; Wiens, 1966). Indeed, little enthusiasm has been garnered for his proposal.

### The Habitat Quality Hypothesis

The third approach relating to the evolution and maintenance of non-monogamous mating systems blends and combines considerations of the environment, population density, and behavior into a natural selection model. In brief, it is suggested that polygyny will be favored by selection whenever a range exists in the quality of territories occupied by males such that females can rear more young in a polygynous relationship with males in superior habitats over that which they would produce by pairing with bachelors holding marginal habitats. It has drawn the support and substantiation of a variety of recent workers and studies, especially Crook (1962, 1963); Verner (1964); Verner and Willson (1966); Willson (1966); Zimmerman (1966); Lack (1968); von Haartman (1969); and Orians (1969). The most concise statement and summary of this viewpoint is found in Verner and Willson (1966) and in Orians (1969). The hypothesis makes three basic assumptions, all seemingly valid when applied to passerines:

(a) The female is the sex which makes the choice of mating partner. There are several adaptive reasons why the female should make this discrimination, all adequately reviewed by Orians (op. cit.). In contrast to the severely limited egg production of females, the physiological capability of males to manufacture gametes is virtually unlimited. Accordingly, so long as males engaging in multiple mating

can contribute more progeny, on the average, than can monogamous males, polygynous tendencies by males should always be favored. Such tendencies are, of course, subject to counterselection by predation pressure. Thus, because polygyny is almost always advantageous to males, the occurrence of polygyny or monogamy in a species should depend primarily on the balance of the advantages and disadvantages to females; it is the female that loses heavily by an unwise choice of mating situation, for this is the sex that invests enormous time and energy in the futile nesting attempt. Field observations document the assumption of female choice. In the Bobolink, for instance, males actively advertise for and court any newly arriving female, but it is the latter sex that moves from location to location about the meadow before eventually pairing. Clearly, the choice is that of the female.

(b) Over any region, the habitat has a spatial heterogeneity, a variability, with respect to plant distribution and requisites that depend upon plant species or habitat structure, such as potential nest sites, abundance of food resources, and cover for protection from weather and predators. That is, a range of habitat quality exists. Plant ecologists have documented that the distribution of vegetation rarely takes a random or a strictly uniform pattern (Ashby, 1948:226, 230; Odum, 1959:213; Greig-Smith, 1964:85). In natural communities individuals of a plant species usually are grouped in contagious

patterns in response to localized soil type, topographic relief, toxins, or other environmental factors, or because of vegetative reproduction or poor seed dispersal mechanisms. Nest sites associated with specific physiognomic types hence mimic this non-random pattern. Moreover, insects, which provide food for adult birds and nestlings, exhibit strong behavioral preferences for specific plant substrates and likewise show a distribution dependent upon vegetative dispersion and pattern. Orians (1969:598) pointed out that a mosaic pattern of vegetation probably shows a very uneven distribution of associated insects, because some clumps of favorable vegetation go undetected by herbivorous insects while others are found and opportunistically exploited by insect concentrations. It follows that substantial differences in food abundance from territory to territory are likely to exist. Accordingly, a rather gross spatial patchiness involving a host of factors is usually associated with natural systems. In grasslands, especially, where productivity is confined to a narrow "two-dimensional" belt, this patchiness is expressed horizontally, resulting in distinct physiognomic zonations.

(c) There is a direct relationship between the quality of the territory a male holds and the mean reproductive success of females settling in that territory. Territories lacking suitable protective substrate for nest sites or those lacking satisfactory food reserves or any combination of requisites offer prospective occupants bleak

opportunity for high fledging success.

The habitat quality hypothesis depends on fulfillment of these three assumptions, and suggests that a polygynous strategy will be employed by species whenever some males are regularly forced, through high density, to occupy territories in marginal or unsuitable habitat. When these conditions are met, natural selection should favor those females making the choice of male and territory which, on the average, maximizes their progeny production, irrespective of whether or not the selected male has previously paired.

Obviously in a choice situation such as this, selection places a premium on a female's ability to perceive and choose those key indicators of ultimate breeding success. Three types of factors can be of potential importance in the female's selection: (1) morphological and behavioral characteristics of the male; (2) the distribution and abundance of food resources in different territories; (3) the patterning and structure of the vegetation in different territories. As will be shown later, the indicators or recognition stimuli which guide the female Bobolink's choice of the best composite situation are probably for the most part unrelated to qualities of the male per se (other than indirectly, as gauged by the male's ability to perceptually choose, establish in, and adequately defend the territory of choicest quality). The likely proximate cues of ultimate reproductive success are physiognomic features, the gross structural properties and patterning of



the vegetation found in the various territories the female evaluates. The importance of physiognomic factors in guiding the general selection of habitats by birds is well established (Lack, 1933, 1937; Beecher, 1942; Hildén, 1965; Wiens, 1969), and such structural cues are probably equally important to females of polygynous species making the more refined selection of one territory from among all those available.

Linsdale (1938:140) was perhaps the first ecologist to clearly recognize the relationship between the habitat suitability of bird territories and the number of females nesting in the territories. Referring to Red-winged Blackbirds he stated:

The success of a male in obtaining females in its territory seemed to depend almost entirely upon the suitability of the habitat for nest locations. A male with a thickly grown stand of strong, upright cattail stems would have as many as 6 females all actively nesting. Another in a less suitable part of the same marsh might have only 1 female. At least 1 male kept a territory throughout a season where the sites for nesting were few, there being no tall vegetation, and not a single female settled there.

Verner (1964), Willson (1966), Zimmerman (1966) and Haigh (1968) have shown qualitatively that this relationship holds in certain other species as well.

### The Natural Selection Model

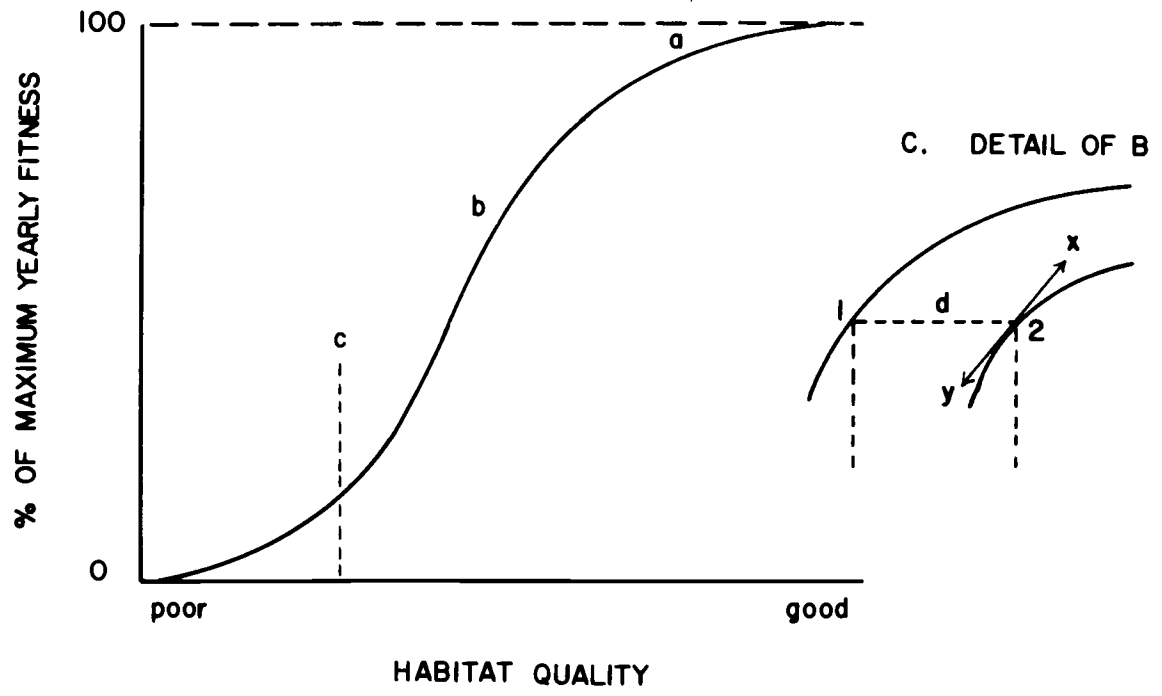
Using ideas developed by Orians (1961) and by Verner and Willson (1966) and others, Orians (1969) presented a model depicting

the relationship between the ability of females to raise progeny which live to reproduce and the environmental quality of territories (Figure 1). In the form given by Orians, the model plotted "fitness" against quality. The concept of female fitness, however, should consider the total number of offspring living to reproduce which are raised by a female in her lifetime, rather than in a single breeding season. For this and other reasons of clarity, several changes have been incorporated in my presentation of the model here. The biological constraints over the shape of the curves relating reproductive success in any season to habitat quality require that they be asymptotic (the maximum success is determined by the species' intrinsic rate of natural increase--the physiological capacity of the female to manufacture complete, viable eggs, or her ability to evenly incubate a maximum area of egg surface, etc.) and that the slope be everywhere positive (a form imposed by the assumption of a positive correlation between habitat quality and reproductive success). Environmental quality is ordered linearly, a realistic arrangement in natural systems, where resource concentrations probably range along a continuum from poor in certain patches to exceptionally good in others.

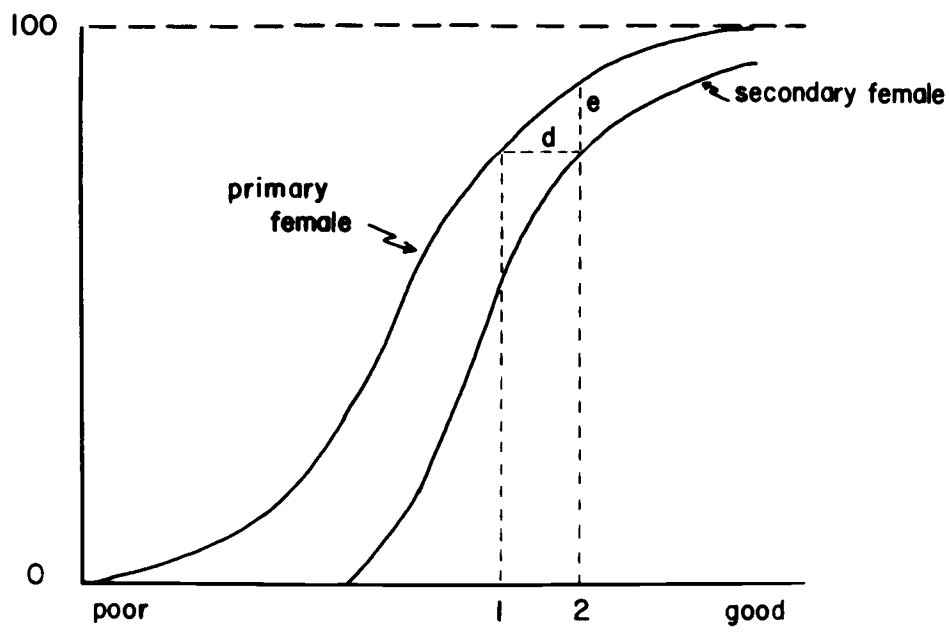
From the relationship depicted by the curve in Figure 1A, the best female strategy for maximizing reproductive success is to pair with the male defending the territory possessing the finest quality in the breeding habitat. Under a hypothetical system where a female

Figure 1. A modification of the general model of Orians (1969), which illustrates the alternatives open to females by two systems of mating. The relationship of reproductive success of females and the environmental quality of the territories where they settle is depicted. A primary female is the first female pairing with a male. All additional hens are secondary mates. (A) the situation prevailing in an impermissive system which requires females to pair only with unmated males. (B) Alternatives open to females when polygyny is permissible. (C) Detail of alternatives shown in (B). Refer to text for a full discussion and for the meaning of letters and numbers.

A. OBLIGATE MONOGAMY



B. POLYGYNY PERMISSIBLE



must pair with a bachelor (obligate monogamy) the first females to pair gain the advantage of nesting in sheltered and concealed locations in territories containing plentiful requisite resources (a in Figure 1A). Females that arrive later meet with poorer prospects for successful nesting (b). The situation becomes acute when each territory containing satisfactory habitat has a female nesting, so that all unpaired males hold territories possessing a quality below a "habitat suitability threshold" (c). Thus, additional hens are forced to attempt nesting in marginal regions which offer exceedingly remote opportunities for nesting success. Here, when faced with assured failure, it would be adaptive to simply forego breeding, rather than waste energy and risk predation; decreasing these unnecessary risks and stresses should on the average increase the hen's life span and her chances for breeding successfully in later years (cf., Lack, 1954: 63). Introducing the flexible alternative that pair formation be permitted between any male and female regardless of the male's mating status, natural selection would favor any female that increases her reproductive output by choosing a previously mated male with a territory sufficiently superior to that held by available bachelors so that more offspring are fledged. The minimum difference in the quality of habitats between territories in the same breeding region which is sufficient for natural selection to favor polygynous pairings by

females has been called the "polygyny threshold" by Verner and Willson (1966).

With this alternative, a second curve (the lower curve in Figure 1B) representing the breeding success-habitat quality relationship of polygynously mated females can be constructed. For most polygynous passerines this curve falls below the monogamy line for several reasons, primarily because individual females no longer derive the undivided time and attention of their male. For instance, Bobolink males share equally with their first female in feeding and brooding the young but virtually ignore the young of their second and third females (for convenience, I will hereafter denote a male's first female as its "primary" female and all others as its "secondary" females). As a result, on any territory the success of a secondary female is expected to be less than the primary female's (the distance e in Figure 1B) because she alone must provide sufficient food for her entire brood. Moreover, the increased tempo of food delivery required of a secondary female substantially alters her activity budget, diminishing the time she can devote to her own maintenance and health. Nevertheless, in situations where the territories differ so much in habitat quality that the polygyny threshold is exceeded, a female stands to increase her production of young by the appropriate selection of partner and habitat, for in any of the better territories she will raise more young unassisted by her mate than could two

adults working together in a territory possessing marginal habitat.

The location of the polygyny threshold (that difference in quality between territories necessary for polygyny to be an appropriate strategy, d) along the gradient of environmental quality depends for the most part on the decline in reproductive success (e) that is experienced by secondary females relative to primary females in the same habitat quality. When e is small (e.g., in an environment possessing a superabundance of food which allows the secondary female to satisfactorily feed an entire brood, or, in species where neither primary nor secondary females derive the assistance of their mate in tending young) the two curves are almost superimposed, and a relatively small difference in quality between two territories will be sufficient to favor polygyny. That is, the threshold will lie far to the right on the continuum of quality and a greater number of males will defend territories having habitat qualities falling to the left of the threshold. But under situations where e is large, the threshold will lie farther to the left along the quality gradient, requiring sizeable differences between territories in order for polygyny to be worthwhile. Regardless of the placement of the threshold, a secondary female at 2 (Figure 1C) will theoretically achieve the same success as does a primary female at 1, and can increase her average contribution (moving in the x direction) by settling in any territory with quality above 2. However, a choice toward y would be selected against.

Accordingly, with this view that polygyny is an adaptive strategy operated upon by selective processes, the advantage of polygyny to a female is that it allows her to increase her potential progeny production by having a free choice of all males and all territories.

Under the conceptual framework of this model, polygyny should evolve only when a species is frequently confronted during the breeding season with a habitat which is patchy in the spatial distribution of necessary commodities--that is, when differences exceeding the polygyny threshold are regularly found. Verner and Willson (1966) cited quantitative evidence which showed that the range of magnitude of the patchiness associated with primary productivity (and thus probably also with insect abundance and other features positively correlated with vegetative structure and distribution) is greater in marshes and other early successional communities such as grasslands, than it is in later successional stages. When male density is high in grasslands and marshes showing a mosaic patterning of vegetation, it is unlikely that all males can appropriate equally suitable territories, just the situation necessary for polygyny to be an adaptive system. As stated previously, of the 14 regularly polygynous species of North American passerines, the breeding habitats of 12 are limited to marshes, grasslands and savannahs (Verner and Willson, op. cit.). The mating systems of 70 species of African weavers (Ploceinae) show a similar direct correspondence to plant



community structure. Monogamy is the only mating form among forest dwelling weavers, while there is a high incidence of polygyny in species nesting in savannahs and grasslands (Crook, 1963, 1964).

Several aspects of this third hypothesis are subject to documentation by field tests, especially in these relatively simple grassland and marsh ecosystems. The approach developed here and the careful quantification of the variables studied in the present investigation, forge a strong foundation for viewing the evolutionary questions posed earlier; further, they potentially can substantiate or refute certain aspects of the hypotheses just discussed.

## CHAPTER 2

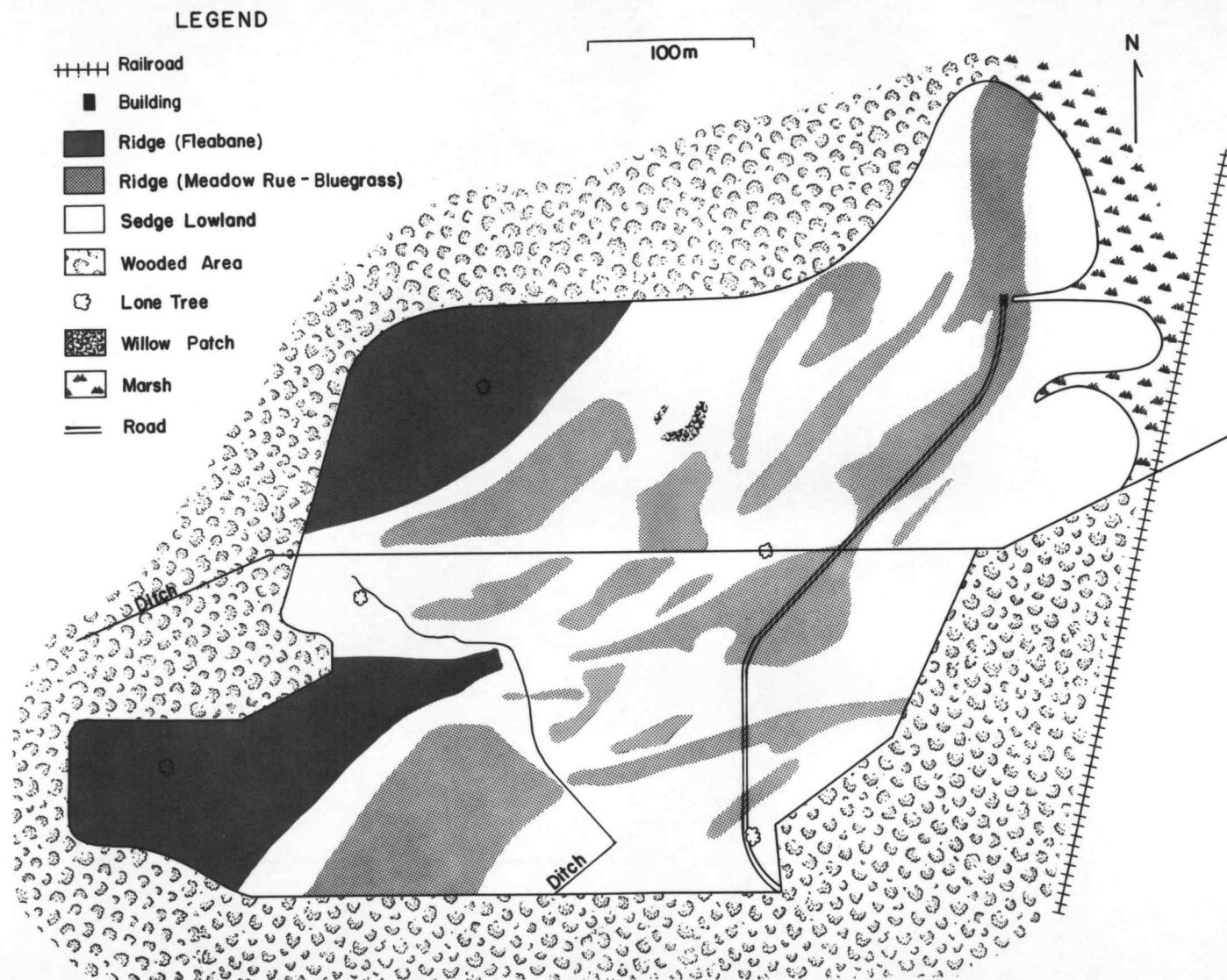
## DESCRIPTION OF THE STUDY AREA

The Riverbottom Site

An 11.3 ha mixed sedge-grass field located 3 km southwest of Sauk City, in Dane County, Wisconsin (T9N, R6E, Sec 13) was chosen as the primary site for this investigation. The meadow was situated in the floodplain of the Wisconsin River, 450 m from the river. It was bounded on three sides by a dense mesic forest characteristic of southwestern Wisconsin river bottomlands (Curtis, 1959), dominated by Silver Maple (Acer saccharinum), large River Birch (Betula nigra) and American Elm (Ulmus americana), with occasional groups of Cottonwood (Populus deltoides) interspersed within the forest. A dense stand of young Cottonwood and a small cattail (Typha) marsh comprised the remaining boundary of the meadow (Figure 2).

Two smaller (2.0 and 3.6 ha) lowland meadows of similar vegetative composition and surroundings were less than 2 km distant, while several upland pastures were located within 1 km of the site. With one exception when in 1970 a single male defended a territory in the larger wet meadow, no Bobolinks resided in these fields. However, occasionally in late May and early June single males were noted in the meadows giving territorial advertising songs. At times some

Figure 2. Map of the riverbottom study area depicting salient features and the general coverage of the major vegetation forms.



of these individuals (color banded) harassed territorial males at the riverbottom research site.

In general appearance the meadow seemed to be flat, but closer inspection revealed a pattern of microrelief resulting from floods that had swept over the region, depositing loads of fine sand and shaping these deposits into a repeating series of long narrow ridges (Figure 3A and B) with wider flat swales between the ridges. This relief varied at the most by 0.4-0.6 m, but the soils following the relief pattern (see beyond) exerted a profound impact on the distribution of vegetation in the meadow (Figure 2) resulting in a patchwork or mosaic of vegetative types. Sedge (Carex) covered the lower portions of the field (Figure 4A and B) with patches of a manna grass, (Glyceria), Marsh Marigold (Caltha palustris), Canada Anemone (Anemone canadensis) and Common Goldenrod (Solidago altissima) interspersed within the sedge growth. Numerous species of very small forbs that were too diminutive to provide cover for the birds but which were heavily utilized in foraging maneuvers were widely dispersed throughout the sedge areas. Vegetation on the elevations (Figures 3A and B, 4B, 5B), by contrast, was comprised of sparse Kentucky Bluegrass (Poa pratensis), Timothy (Phleum pratense) and Ticklegrass (Agrostis scabra), overtopped by dense irregular clumps of a forb, Meadow Rue (Thalictrum dasycarpum), and occasionally by Aster (Aster puniceus). Meadow Rue, like Golden Alexander (Zizia

Figure 3. (A) A view of a low ridge in mid May, showing a heavy concentration of Meadow Rue, which is already emerging as overstory cover to the shorter grasses. Two stakes of the grid system (see Chapter 3) are prominent. Sedge growth is seen in the upper right, and to the left of the closer stake.

(B) A view of a similar ridge in early July, demonstrating the two different strata. A sedge expanse is shown to the left.

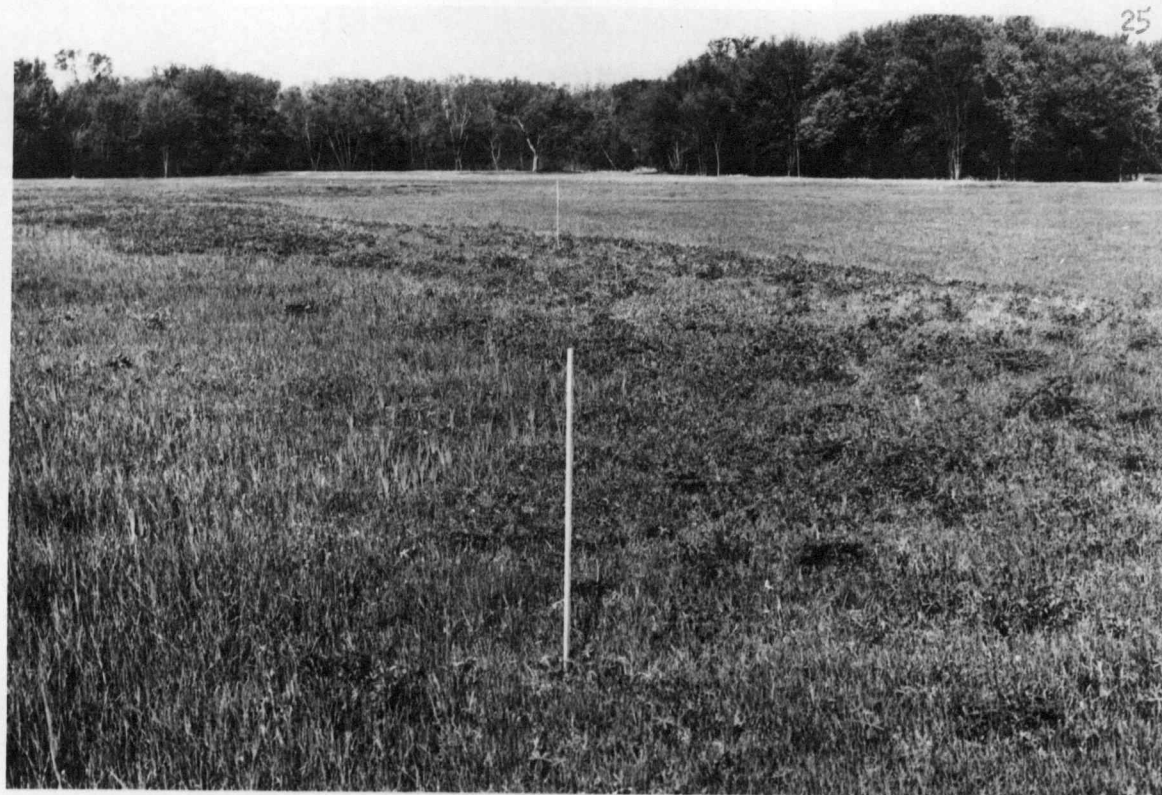
**A****B**

Figure 4. Two photographs of sedge swales in early to mid July. A slight ridge with tall scattered forbs occupies the background in A, and near the center of A a small Meadow Rue cluster rises above the rather homogeneous and dense sedge growth. Toward the right in B is a larger group of forbs. Also depicted in B is an elevation which is densely covered with tall forbs.



**A****B**

Figure 5. (A) A view west, showing the dry Fleabane-covered ridge (in white) in the southwest arm of the meadow, taken in early July. Until the Fleabane bloomed, vegetation on this ridge was low and open. In the foreground are tall scattered forbs growing on a slight elevation within a sedge flat. Here mesic conditions permitted fuller forb development than did the drier soils on the major ridges.

(B) Note the scattered nature of forbs in the region where a low ridge (to the right) merges into sedge cover. An observation tower is also shown.

**A****B**

aurea), was sporadically scattered on small knolls through the sedge swards as well. Fleabane (Erigeron pilosus) and bluegrass covered two large dry ridges along the field's western edge, where ground cover, shading and concealment were slight (Figure 5A).

Four basic physiognomic or structural forms of vegetation, therefore, dominated the meadow's plant community: (1) large forbs, providing an overstory stratum, were concentrated on slight elevations but were also scattered irregularly through the low moister areas; (2) small forbs grew profusely throughout the low areas but never overstoried the sedges; (3) dense sedge comprised the principle growth form in the low swales; (4) grass, generally short and providing poor concealment, grew on the dry ridges. The distinct spatial heterogeneity of these four structural components of the vegetation was exceedingly important in influencing almost all aspects of the Bobolink's utilization of the meadow, such as placement of territories, the sites selected for territorial advertisement, courtship, foraging, the locations of nest sites, the time budgets of males and their ability to attract multiple mates to their territories. In many respects, the horizontal patterning of vegetation over the surface of the meadow dictated the spatial organization of the avifaunal community.

The field was divided into two sections by an old dredged drainage ditch, arched at intervals by 3-5 m willows (Salix) and low

brambles (Rubus). Because the ditch served each year as a conspicuous natural boundary between adjacent Bobolink territories, these few willows received a disproportionately large use as display and dispute sites. Bordering the ditch on each side was a 1 m-wide strip of tall fallow vegetation, where females commonly gathered litter for use in nest construction. Additional shallow ditches traversed the southern portion of the meadow and provided for water run off. Within the field stood three widely-spaced American Elms and a River Birch, all about 25 m high, and a small patch of 5 m-high willows.

Soils underlying the meadow were of an undifferentiated alluvial composition. The ridges were composed of fine sand, becoming coarse at a depth of 1-1.5 m, overlain by 15-20 cm of black top soil. In the sedge areas a layer of oxidized muck graded into a deeper zone of peat which was very rich in partially decomposed organic material. At a depth of approximately 0.8 m a thin 8-10 cm layer of clay mixed with small amounts of fine sand was sandwiched between the rich peat and the coarser sand that apparently extended beneath the entire meadow. This coarse sand remained saturated with water throughout the summer. The thin basement zone of mixed clay-sand was an exceedingly sticky, plastic mixture which was relatively impermeable to water.

Under conditions of extended heavy rain or severe thunderstorms,

the consequences of this impermeable soil zone to the nesting avifauna were catastrophic: rain water filtered through the soil to this soil band where it was immediately arrested. Very quickly the overlying peat became saturated and pools of water collected in the lower parts of the meadow. If the storm were prolonged, up to 25 cm of water might collect in such depressions, chilling eggs, drowning nestlings and leading to nest desertion. In 1968 and 1969 fronts of violent thunderstorms swept over the region at the height of the nesting season, resulting in 10-15 cm of rainfall in brief periods; then, many of the elevated areas were subjected to heavy nest loss as well. A dam 6.4 km upstream served to control flooding from the river proper, yet in both 1968 and 1969 it was necessary to release water from the dam during these extended storm periods, resulting in further nest losses as the river overflowed its banks and swept across the breeding meadow (Figure 6). Most adult birds of all species vacated the region after the flooding damage. Since 1943, when modern flood control policies were established for the Wisconsin River, this meadow has not been inundated during the Bobolink's nesting period except in these two summers, attesting to the severity and rarity of these two June storms.

Prior to this study, the field was usually mowed in early July when the Meadow Rue was about 1.5 m tall and the sedges and grasses were 0.5 to 0.7 m high. Beginning in 1966, mowing was delayed each

Figure 6. As the meadow appeared in mid to late June in 1968 and 1969.







summer until my work was completed. Portions of the field were again mowed in October. When the Bobolinks arrived in early May new annual growth was only a few centimeters high and old growth stood as a coarse stubble about 10 cm tall over a loose mat of litter.

Species comprising the breeding avifauna in the meadow each year, in addition to the Bobolink, were three to five pairs of Short-billed Marsh Wrens (Cistothorus platensis); four to six pairs of Yellow-throats (Geothlypis trichas), which nested along the ditch; six to eight pairs of Eastern Meadowlarks (Sturnella magna); six to ten male Red-winged Blackbirds (Agelaius phoeniceus) and their harems; nine to fifteen pairs of Savannah Sparrows (Passerculus sandwichensis); and three to five pairs of Song Sparrows (Melospiza melodia). In 1968 two pairs of Henslow's Sparrows (Passerherbulus henslowii) nested in a small area of standing litter which had not been mowed the previous fall. Common Grackles (Quiscalus quiscula) and Robins (Turdus migratorius) were often observed foraging in the field, and Brown-headed Cowbirds (Molothrus ater) parasitized some nests in the meadow.

#### Secondary Study Site

One other study area received scant attention compared to the riverbottom site, but was occasionally visited because it differed strikingly in vegetative structure and composition while still

supporting a dense Bobolink population. This plot was at Faville Prairie (cf., Buss and Hawkins, 1939; Hawkins, 1940; Odum, 1959: 430-431), about 70 km east of the riverbottom meadow, and 8 km north of Lake Mills in Jefferson County, Wisconsin (T8N, R14E, Sec 19). The 14.2 ha prairie probably represents the last remaining tract of uncultivated virgin prairie in Wisconsin. It was dominated by tall prairie forbs such as the Compass Plant (Silphium laciniatum), and Prairie Dock (Silphium terebinthinaceum), standing above a thick carpet of lush sedge. Faville Prairie was burned every two or three years to prevent the establishment of woody invaders. The burning routine prevented accumulation of heavy litter mats or of numerous dead standing forb stalks. Contiguous with the prairie was a 10.1 ha fallow field that had gone untouched since 1960. Numerous weedy invaders dominated the vegetation, with Kentucky Bluegrass as the principle ground cover and Common Goldenrod as the dominant large forb. Deep, heavy litter and extensive patches of thin standing dead goldenrod stems were abundant in this field. Because the two adjacent fields contrasted so markedly in plant species composition and in the availability of litter and elevated perches, I intended to use this study plot to evaluate the results of artificial manipulation of habitat through controlled burning schedules to quantitatively assess the relationships between territorial quality and the ability of

males to attract and retain females. However, my observational schedule at the riverbottom meadow prevented more than qualitative evaluation of these relationships at Faville Prairie.

## CHAPTER 3

### PROCEDURES

The results reported here stem from records collected at the riverbottom meadow over four breeding seasons, from May 1966 through July 1969, totaling 283 days of field work. Limited data collected on 25 days in late May and early June 1970, are also included. In 1966 observations were concentrated in early morning and late afternoon while in 1967 many full days were spent collecting field data. In 1968 and 1969 virtually all daylight hours were occupied by research procedures from the early May arrival of males until a majority of individuals departed from the breeding meadow in mid to late July. During the last three full years of the investigation I was absent from this study area only three days during the Bobolink breeding season. Most 1966 observations focused on the species' behavioral repertoire and general breeding biology. Relatively little quantitative information on mating systems was obtained during 1966; accordingly, almost all accounts presented here are derived from the 1967-70 seasons.

Beginning in early June 1968, occasional observations were made at the Faville Prairie site. These supplementary studies, however, did not interfere with the daily standardized program at the

riverbottom area. The following specific methodologies and technical aids contributed to the goals of the study.

### Banding Program

Almost all adult Bobolinks resident in the riverbottom meadow from 1967-70 were banded with distinctive combinations of up to three celluloid colored leg bands as well as a standard Fish and Wildlife Service aluminum band. In addition, to facilitate individual recognition of birds at a distance, conspicuous dyes were applied to certain feather tracts of males and females using alcohol base dyes of picric acid (yellow), methyl green (blue) and rhodamine B (scarlet); felt tipped marking pens provided other color combinations. Most dye colors remained visible and useful for approximately four weeks, and had no apparent affects on the birds' behavior or on mating preferences.

Several mist netting methods were used to capture birds for banding. The most efficient technique involved flushing an incubating or brooding individual into two nets arranged in a "V" or tunnel configuration around the nest (Martin, 1969). When an incubating female was caught near the nest site she often decoyed her mate into the net. This V net procedure, however, became feasible only after the onset of incubation. Due to the importance of recognizing individuals during the earliest stages of pair formation, major efforts were taken to

band birds soon after their arrival using the more time-consuming and cumbersome method of placing numerous nets in irregular patterns over sections of the meadow so that a bird blundered into one net while attempting to avoid others. No attempts were made to band adults in 1966. From 1967 to 1970 a total of 75 females and 41 males were marked at the riverbottom field. During the five years of the study 257 nestlings were color banded. Similar color marking and banding operations were conducted at Faville Prairie, where 33 females, 22 males, and 98 nestlings were banded in 1968 and 1969. Most adults which evaded capture had distinctive morphological or vocal quirks which permitted reliable identification.

In a very real sense, the preciseness of the data gathered in this study depended upon the employment of a banding program of this scope. In many instances, my ability to identify distinctly-banded or dyed individuals allowed me to make accurate statements of fact rather than speculations. Recognizable individuals were followed through the season, despite some abrupt major shifts in the location of territories. Disappearances or aggressive replacements of males were noted as were numerous anomalies in aspects of life history. Having individually recognizable subjects permitted me to objectively record mate relations, and in most instances the actual existence of polygyny was verified by repeated observations of copulations by one male with two or more colorbanded females. In the few cases where I

failed to observe coitions, observations of characteristic behaviors which invariably coincided with the copulatory stage attested to the status of a pair. Furthermore, because of the high incidence of site tenacity in male Bobolinks, I was able to observe year to year changes in social structure, mating structure, territorial locations and individual behavior. It was also possible to note alterations in the territorial behavior and social status of first year males as they returned to the study area in subsequent years.

### Grid System

Beginning in 1967 numbered meter-high stakes were positioned in a square grid system at 30.5 m intervals over the entire field. These stakes, placed in the meadow in late April prior to the arrival of Bobolinks, served as guide marks which permitted me to accurately plot on field maps locations of territorial boundaries, sites of territorial confrontations and activity concentrations, copulations, nests, and foraging regions. Males often perched on these stakes while engaging in territorial advertisement and courtship sequences, and thus were readily visible for photography and detailed display observations. It is unlikely that the availability of these artificial perches increased the field's attractiveness to male Bobolinks, or, more importantly, permitted an increased density, for as many males were resident in 1966, when a grid was not established, as in other years.

### Behavioral Observations

A careful analysis of mating systems necessitates a detailed understanding of basic behavioral activities and patternings, for two reasons. First, it is crucial that the investigator follow each male's temporal relationships with each of its females through their entire reproductive cycles. If the order of a male's pairings and subsequent coitions are known, confident statements regarding differences in the reproductive success of the various females, in terms of their order of pairing, can be made. In the Bobolink, changes in postures and in the timing of behavioral sequences and activities of a pair accurately signal the stage of the breeding cycle. Second, subtle differences in the manners in which males apportion their time among the constellation of activities necessary for their survival and successful reproduction (territorial defense, advertisement, courtship, attending young, foraging, and body maintenance behaviors) probably bear directly on their ability to defend territories of appropriate quality and to attract females. Obtaining standardized time budgets of males provides a means of assessing differences in time allocated to these activities by bachelor, monogamous and polygynous males. Again, an extensive knowledge of the species' behavioral action patterns is prerequisite for conducting time budget studies: without a fairly sophisticated ethogram of a species one is unable to anticipate the



types of activities and sequences to be involved in activity budgets. Furthermore, precise descriptions of behavior are required for speculations on the functional significance of activities.

To provide a repository of information on breeding behavior, the spring of 1966 was devoted to descriptive ethology. Observations were made from elevated vantages (haywagon, cartop, tree crotches) and from ground level with the aid of 7X35 binoculars and a 20X spotting scope. In 1968 two 4.3 m towers (see Figure 5B) were erected at strategic locations in the riverbottom field and thereafter most observations were made from these structures. Throughout the early phase of behavioral description a small battery-operated tape recorder was used for dictating descriptions of displays and sequences and other pertinent activities requiring the observer's undivided attention. Each evening all recordings were transcribed verbatim to a notebook. Both cine and still photography were employed to obtain detailed records of display postures, and vocalizations were taped and subsequently analysed spectrographically.

### Breeding Biology

Assessments of the average reproductive success of males and females of different mating statuses were predicated on careful studies of pertinent aspects of breeding biology. Most nests were discovered during their construction or early in egg deposition. I noted changes

in nest contents daily at a standardized time. Eggs were marked with dots of nail polish in the order of laying and newly hatched young were distinctively spotted with dyes on the ventral surface. Each day between 1800-2000 (CDT) I weighed nestlings on an Ohaus Cent-o-Gram field balance. Records were kept of egg and nestling mortality at all nests, but I was unable to determine post-fledging mortality.

To judge whether unassisted secondary hens could compensate in their rate of feeding for the lack of male assistance, recordings of the tempo of food deliveries at primary and secondary nests were taken. In all, 57 hours of feeding schedule observations were made. Birds were observed through a 20X spotting scope, using a stop watch for timing the various components of foraging trips. Foraging sites were also recorded. To minimize disturbance of adults, a majority of these observations were made from the towers. However, some were made at distances close enough to the nest to permit counting and rough identification of the taxa of the carried insects.

### Analysis of Vegetation Structure and Territories

A major objective of this investigation was to determine and appraise the ecological factors affecting the Bobolink which could contribute to the adaptiveness of polygyny in this species. Because structural features of the environment have been shown to be the major stimuli in governing a bird's selection of the proper habitat for

breeding (Lack, 1933, 1937; Odum, 1945; Hildén, 1965; Wiens, 1969), it can be argued that when a spatial patchiness exists in physiognomy such that different territories possess vegetation offering varying suitabilities for successful reproduction, then those territories providing the most favorable conditions should attract the most females and be settled in first.

My objective in measuring and analysing vegetative organization in the riverbottom study field was to determine if measurable differences in vegetative physiognomy did indeed exist between territories of bachelor, monogamist and polygynist Bobolinks. Obviously, a multitude of factors and combinations could contribute to providing important cues, but it is likely that natural selection has narrowed this array to a few of the more reliable and persistent indicators of ultimate resource availability. By exercising careful selection of those structural parameters I felt were most relevant to the Bobolink I settled on a descriptive format quite similar to that developed by Wiens (1969:14-25) for describing grassland habitats for birds. The general components selected for measurement were those found to be important in the distribution of grassland birds by Tester and Marshall (1961), Cody (1968), and Wiens (1969). My initial subjective evaluation of the vegetative characteristics surrounding Bobolink nests also contributed to my selection of properties to be measured.

Sampling positions were located by a stratified random design

(Southwood, 1966:21), which assured random placement of samples as well as equal sampling intensity over all sections of the meadow. Grid lines served as transects and a sample location, determined by pacing distances given by digits drawn from a table of random numbers, was positioned between every pair of stakes along each grid line (see Wiens, 1969:22, for an illustration of this location method).

At every sample location two 1 m stakes were crossed perpendicularly on the ground, the ends positioned in the principle compass directions. Extreme care was taken not to alter the natural lay of the vegetation. At each of the four ends (each end is a sample point) a series of vegetative measures and descriptions were made:

Light penetration--to evaluate the shading or concealment properties of the vegetation at the point, penetration of light through the vegetation was measured in foot candles using a sensitive photometer with a thin probe (cf., Wiens, 1967) which was inserted horizontally through the vegetation at ground level and at decimeter increments above the ground. Footcandle values were transformed to percent of unshaded skylight intensity above the sample point in order to make readings taken at all sample locations comparable. In all instances light readings were made on clear days between 1130-1430 (CDT), when the sun was most vertical.

Vertical density--foliage density was measured by inserting a sturdy 6.5 mm diameter metal rod vertically through the vegetation

to the ground. Counts were then made of the number of stems and leaves of all vegetative types intercepting the rod in each 10 cm interval above the ground. Such a measure describes a vegetation profile of the vertical layering of the vegetation, which in some communities, at least, appears to be important in influencing the diversity of breeding bird species (MacArthur and MacArthur, 1961; MacArthur, MacArthur and Preer, 1962; MacArthur, 1964). In grasslands, vertical density provides another index of concealment characteristics or of the denseness of cover above any point.

Per cent coverage--the per cent coverage (Goodall, 1952; Greig-Smith, 1964) of forb, gramoid (grasses and sedges), and woody vegetation was determined by recording the presence or absence of these physiognomic types contacting the metal rod anywhere along its length.

Litter characteristics--depth of litter was measured and per cent coverage and compactness of litter were estimated at a distance of 10 cm from each point (cf., Wiens, 1969:24).

Forb density--at each sampling location the two crossed stakes delineated four 90 degree sectors; by employing the point-centered quarter method (Cottam and Curtis, 1956; Dix, 1961) the distance from the intersection of the stakes to the nearest Meadow Rue or Golden Alexander in each quadrant was measured, allowing computation of the densities of these forbs. The application of this method

to grasslands, where species tend to be strongly aggregated, has been criticized by Greig-Smith (1964) and by Risser and Zedler (1968). But here I used mean distance values for comparing forb abundance from area to area in the same meadow, rather than for determining actual density values, and hence this limitation of the procedure is not applicable.

The same sampling format was applied at many Bobolink nests found from 1967-70. At the nest site, values of per cent coverage, vertical stratification, light intensity and litter properties were obtained at the four standard sampling points and at a fifth point located 5 cm north of the nest cup.

All vegetative sampling data were collected during a four-day period in mid June at the peak of the nesting season. Light intensity readings at some nest sites constituted an exception to this sampling regime, for these measures were made 8-10 days after non-nest data were gathered, and accordingly are not strictly comparable. All other nest-site data were obtained during the mid June sampling period.

The configurations and sizes of Bobolink territories were determined by plotting the sites of observed aggressive encounters between rival neighboring males and from a multiple flush procedure, as described by Wiens (1969:20). In this method the location of a

male was marked on a field map, the bird was approached and flushed, and its line of flight and settling point were drawn on the map. The bird was reflushed and the same information was recorded. After 20-25 consecutive flushes the composite settling points and lines of flight delineated the shape and boundaries of the territory. These boundaries coincided well with those determined by the independent observations of confrontation sites between adjacent males. A pattern of contiguous, non-overlapping territories resulted. Bryan's (1943) modified grid was used to calculate the area of each territory.

The positions of vegetation sample locations were plotted on maps showing boundaries of male territories from 1967 to 1969. For all samples falling within bachelor, monogamous, bigamous and trigamous territories, separate mean values of data for forb distance, forb height, litter depth, per cent of open skylight, per cent coverage, and the vertical density were determined. Vegetative samples located within the territory of the only male holding simultaneous pair bonds with four females were included with samples from territories of trigamists. These mean values were subjected to t-test comparisons for tests of significance in all possible pair-wise combinations. Where appropriate, data were transformed to a  $\sqrt{X + \frac{1}{2}}$  and a log  $(X + 1)$  scale. In these instances values tabulated are the back-transformed means.

### Time Budgets

Despite the emphasis this report will place on the correlation between mating levels and certain structural features of territories, it is important to recognize that morphological and behavioral attributes of males may also influence their success at procuring simultaneous mates. A male's intensity and tenacity at advertisement and courtship activities should bear directly on its success in attracting females. Moreover, the male's expediency in carrying its first female to the copulatory stage in turn determines how rapidly it can initiate advertising for a second hen. Indirectly, the intensity and frequency of agonistic displays and aggressive confrontations while establishing and defending a territory should ultimately affect the male's breeding status: with the reasonable assumption that males can discriminate between good and poor habitats, the stronger, more aggressive males should be able to establish territories in more suitable areas of the meadow than should less aggressive birds, and should, therefore, be chosen by unpaired females. The results of carefully standardized time-activity budgets (Verbeek, 1964; Verner, 1963, 1965b) are useful in comparing how males of different mating levels differ in their partitioning of time among these agonistic and courtship behaviors. More than 200 hours of time budgets were obtained during this study. The bulk of these data are not yet



analysed and thus only limited attention will be given time budgets in the following text. Nonetheless, a description of the methods used in gathering time budget information is still profitable for the interpretation of later remarks on behavior.

The development of a suitable time budget format requires careful attention to several important methodological considerations. In general, I followed the suggestions and guidelines offered by Wiens, et al. (1970). A small battery-operated metronome which emitted periodic pulses through an earphone provided a time base for observations. With a pulse frequency of 10 seconds I could easily record sequentially on paper shorthand notations for all the activities and locations of a male as rapidly as they occurred, inserting a standard mark for each time signal that sounded, only rarely having to glance down at my written record. A standard observation period of 30 minutes was used.

The general format developed to systematically evaluate differing apportionments of time to various activities by birds of different mating statuses, and during different diurnal periods and reproductive stages, included arbitrarily dividing days into four intervals of approximately four hours each. Each day within each four-hour block, efforts were made to obtain two 30-minute time budgets of males. These observations were distributed on a rotating schedule among the four male mating classes every two days, equalizing observation

intensities for each class for all daily periods. Choice of the specific individuals to be observed within each four-hour interval was determined prior to my arrival at the meadow each morning, so I would not be influenced by the varying "interest" potential of the initial activities of the possible candidates (see comments by Wiens, 1969: 66, concerning the misleading results gained from opportunistic observations). When time permitted, more than two observations were made in each diurnal division. Five reproductive stages were also considered in the overall activity budget format: pre-pairing, pairing and courtship; copulation and nest-building; egg deposition and incubation; and nestling stage. The temporal settings for these stages are defined in the life history chapter.

Obviously, data collected in this manner are amenable to a variety of analyses, ranging from sophisticated methods of sequential analysis (e.g., Wiepkema, 1961; Nelson, 1964; Delius, 1969), through comparisons of seasonal or diurnal differences in frequencies of specific behaviors, to comparisons of how bachelors, monogamists and polygynists differ in their activity expenditures. Presumably the most important behavioral distinctions are those between bachelors and mated males, but because bachelor territories were too distant from observation towers, an inadequate number of budgets have been obtained of bachelors at this time to present a satisfactory comparison. Future plans include constructing towers in regions frequently

occupied by bachelors. Detailed time budget analysis must thus await collection of these additional data, when statistical tests of differences in times devoted to activities by males of different mating statuses will be made. In this report only tentative results will be discussed.

## CHAPTER 4

## A BRIEF LIFE HISTORY ACCOUNT OF THE BOBOLINK

A detailed knowledge of the basic life history of a species is prerequisite to understanding and describing the organization of its social and mating systems. Indeed, Verner and Willson (1969) chastized ecologists and ornithologists for their failure to report life history phenomena concisely and accurately, pointing out that despite voluminous avian life history publications, only four per cent of the North American passerine species have been adequately characterized even in terms of their breeding biology alone. Concerned primarily with the possible predictive inferences regarding the form and variability of mating systems that can be made from a knowledge of life history, they stated (p. 36):

The general inadequacy of our total knowledge of the life histories of passerine birds pointed up by this review, coupled with the all-too-often sloppy reporting of same, call for a more serious and systematic approach to these natural history studies. It will ultimately be essential for all aspects of the life histories of all species to be expressed in quantitative terms, which will permit analysis of individual and populational variability. Until we know what percentages of what members of what populations perform what behaviors how frequently and at what points in their lives, we cannot hope to generalize accurately about the difference of roles between males of monomorphic and dimorphic species and between males of monogamous and polygynous species.

The few life history reports on the Bobolink suffer from their

anecdotal nature and imprecision. The only previous substantial study of this species (Kingsbury, 1933) is unpublished and was concerned in great part with distribution. Some fragmentary aspects of life history were compiled and summarized by Bent (1958), but he found little systematically collected quantitative information to report on, although Skutch (in litt.) provided a few nesting details. Karr (1963) touched on general breeding biology and habitat utilization, while other naturalistic notes were presented by Bendire (1895), Buttrick (1909), Chapman (1909) and Kendeigh (1941). The following condensed account of Bobolink life history covers those aspects fundamental to an analysis of the adaptive significance of the Bobolink's mating system. A more complete and precise life history of this species is being prepared for publication. Many of the subtopics were developed more fully previously (Martin, 1967).

### Migration

Of North American passerines, the Bobolink surpasses all others in the distance of its yearly 19,000 km round trip transequatorial migration. The species slowly vacates breeding locales from mid July until late August, after a post-nuptial molt by both sexes. It normally flies gregariously by night although "a part of the migration is regularly performed by day" (Wetmore, 1927). Most of the birds breeding in eastern North America pass through Florida, Cuba

and Jamaica before setting off non-stop across the Caribbean directly to South America, where they over-winter in southern Brazil, Paraguay, Uruguay and northern Argentina. Pettingill (pers. comm.) reported that South American marshes and rice fields are extensively utilized by the species during this period, and Wetmore (1927) reported that the center of its winter distribution is a vast area of poorly drained swampy land with broad grass-grown savannahs. In contrast to its insectivorous feeding habits during the breeding season the Bobolink is granivorous throughout the winter and on both legs of its migration (Beal, 1900; Martin, Zim and Nelson, 1951) and in the past has caused locally heavy damage to grain crops grown along its migratory routes (McAtee, 1919; Meanley and Neff, 1953; Neff and Meanley, 1957). The route northward, after a pre-nuptial molt, seems less well defined. Chapman (1890) compiled summaries of Bobolink migration routes but it remained for later workers, especially Hamilton (1962a, 1962b), to correct some previously held misconceptions about these routes. Kingsbury (1933) cited dates and localities of seasonal migratory advances of the species within the United States.

#### Breeding Habitat

The breeding range of the Bobolink is limited to the northern part of the United States, primarily east of the Great Plains. Isolated

breeding colonies are scattered throughout the west and northwest, generally in association with naturally wet meadows. These probably represent, as Hamilton (1962b) suggested, relicts of a once more extensive distribution of the species. Over its range the species nests in open, moist meadows having lush vegetation, appearing to prefer those fields that have a stratum of large forbs which rises above the general ground cover layer. It is found more sparingly in dryer, upland habitats. A number of authors (Kingsbury, 1933; Good and Dambach, 1943; Graber and Graber, 1963) have associated Bobolink occupancy of certain meadow types with the general structure or appearance (openness, availability of elevated song perches, type of regions surrounding the fields) and size of the meadow; others (Beecher, 1942; Tester and Marshall, 1961; Martin, 1967; Cody, 1968; Wiens, 1969) have related its microdistribution more specifically with the phytosociology of the vegetation, its structure, patterning, density, and its suitability as substrate for the breeding routines and nesting requirements of the bird.

#### Arrival and Territoriality

The bulk of males arrived at the breeding meadow between 10-13 May. Most that had resided in the field in previous years exhibited ortstreue, that is, site faithfulness, returning to the same vicinity of the meadow. In Figure 7 I have graphically summarized

the complex nature of these return data. This complexity arises from the yearly addition of categories necessary to account for recruitment of returning yearlings and of foreign males. Furthermore, males holding territories must be distinguished from drifting (floating) males that were also banded, for certain of these latter males returned annually. These categories are essential in order to properly evaluate relationships between changes in male status and male maturation and origin. Hereafter, when referring to specific individuals listed in this figure, I will cite a year-male number. Hence, 69-36 refers to male 36 in 1969.

Of 13 banded males resident in 1967, five (38.5 per cent) returned as territorial males in 1968, in addition to two males hatched in the field in 1967. Four other yearlings returned as drifters. The returns in 1969 are difficult to summarize without careful reference to the figure, for territorial males that year included both residents and drifters from 1968. Of 13 banded males resident in 1968, eight (61.5 per cent) returned as territorial holders and one (7.8 per cent) returned as a drifter; of 10 drifters in 1968, four (40.0 per cent) returned as territorial males and one (10.0 per cent) as a drifter. In addition, 67-13, a past transient, reappeared as a drifter in 1969 and 1970. The 1970 returns show a similar consortium of classes. Many of the males holding territories in 1968 and 1969 (and probably in 1970 as well) that were unbanded when they



Figure 7. Summary of banding and return data on male Bobolinks at the riverbottom meadow. Numbers refer to individual males that were color banded, and U indicates an unbanded territorial male. For each year, males in the left column held territories; those in the right column were "drifters" or "transients." Transients appeared at the meadow in early to mid May, and remained only briefly. Drifters arrived late in May or in June and reappeared occasionally at the field over the remainder of the season. The number of drifting males was unknown because many were unbanded.

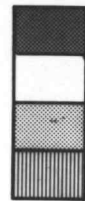
The following letters denote male status:

A--Bachelor	Q--Quadgamous
M--Monogamous	D--Drifter
B--Bigamous	E--Transient
T--Trigamous	

Key to Superscripts:

- <sup>a</sup> Drifter that eventually established a territory in approximately mid June.
- <sup>b</sup> Disappeared after servicing a female (territorial for 11 days (67-12) and at least 19 days (70-6)).
- <sup>c</sup> Became a drifter after approximately 15 days of unsuccessful advertising.
- <sup>d</sup> Became a drifter or disappeared (unbanded male) after approximately 15 days of unsuccessful advertising.
- <sup>e</sup> Disappeared after pairing with a female (no servicing).
- <sup>f</sup> Disappeared after a brief three day period of territoriality.
- <sup>g</sup> Defended a territory in the meadow 1.5 km south of the riverbottom field.

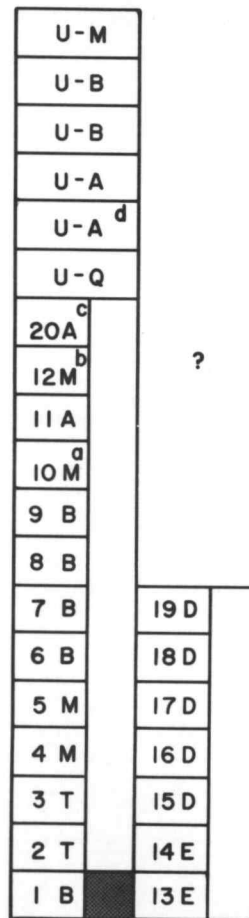
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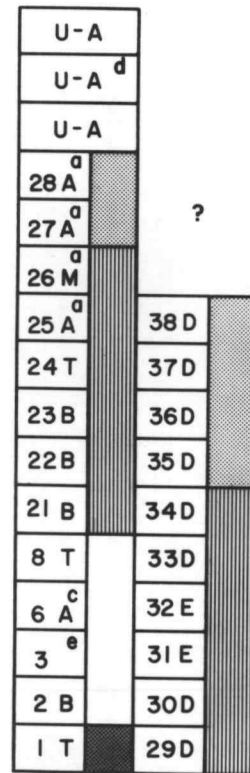
1966 NESTLING  
1967 ADULT  
1967 NESTLING  
1968 ADULT



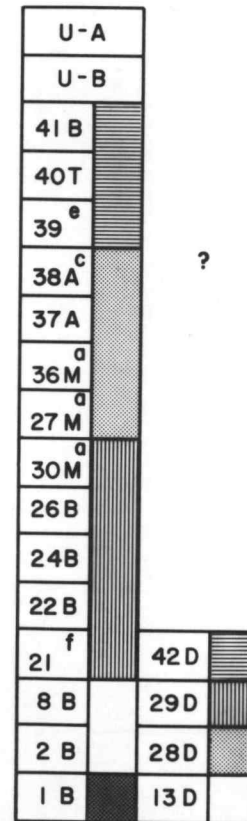
1969 ADULT  
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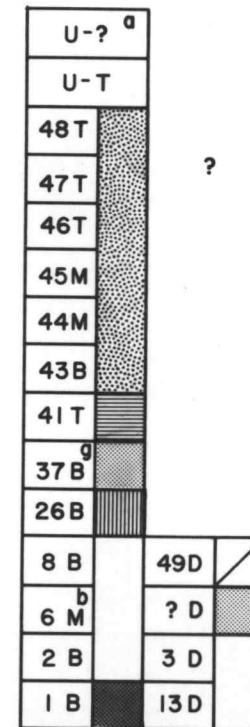
1967



1968



1969



1970

arrived at the field appeared concurrently or a few days after previously resident birds, and usually about 12-18 days before the bulk of drifters appeared. Because males of known age that returned this early were at least two years old, I suspect that these males were of similar ages, that their breeding fields of the previous year had been converted to other agricultural use, and as a result they settled at this location. Others in this class were probably past residents which had avoided my banding efforts.

Strong competition for territories ensued immediately upon the arrival of males; song, ritualized display, fighting and chases were employed in gaining and maintaining territories (cf., Martin, 1967: 67-97). Two patterns of territorial development were evidenced: (1) compression of original large territories in the more suitable regions of the meadow due to pressure of newly arriving males; and (2) expansion of occupancy of the meadow by peripheral annexation. By late May or early June most territorial males were established. Each spring Bobolinks defended a pattern of contiguous, non-overlapping territories (Figures 8, 9). Sizes of 78 territories averaged  $1.72 \pm 0.104$  acres ( $0.70 \pm 0.008$  ha) (Table 1).

Until females arrived, males were active in territorial behavior for about four hours each morning and again for a briefer period in the evening, occasionally leaving the meadow for 20-45 minutes during mid-day. Once females arrived, males rarely left their

TABLE 1. COMPARISONS OF FEATURES OF BOBOLINK BREEDING BIOLOGY AT THE RIVERBOTTOM MEADOW, 1966-70

	Year					
	1966	1967	1968	1969	1970	All Years
Territory:						
Number	17	19	13	16	13	78
Mean size in acres	1.65(0.874) <sup>a</sup>	1.60(0.125)	1.91(0.143)	1.81(0.143)	1.58(0.128)	1.72(0.057)
Range	0.92-2.43	0.76-2.78	1.09-2.92	0.99-3.01	0.81-2.48	0.76-3.01
Nests:						
Number <sup>b</sup>	20	35	20	23	27	125
Renestings	Unknown	3	0	3	0 <sup>c</sup>	6
Clutch:						
Number complete sets	17	30	19	21	27	114
Mean size	5.35(0.191)	5.13(0.164)	5.26(0.185)	4.95(0.223)	5.26(0.137)	5.18(0.079)
Range	3-6	3-7	4-6	3-7	4-7	3-7
Success:						
% nests fledging young	60.0	57.7	42.1	17.4	64.4	49.19
% eggs producing young	48.3	48.4	35.8	22.8	49.9	42.05
Mean fledglings/nest	2.50(0.526)	2.36(0.386)	1.68(0.536)	1.08(0.474)	2.59(0.414)	2.08(0.207)

<sup>a</sup>Standard error of mean in parentheses.

<sup>b</sup>Some nests went undetected in 1966. In subsequent years virtually all nests were located. Value includes the renestings.

<sup>c</sup>My early departure in 1970 precluded discovery of renestings that year.

territories except to chase away neighboring intruders or drifters. Territories were utilized for courtship, foraging and nesting, and were vigorously defended until the male began feeding nestlings. At this time frequent trips were made to more distant areas of the field in search of food for the nestlings.

The first wave of female residents arrived five to ten days after the first territories were established. Older females preceded yearlings by at least two weeks. Females were not as tenacious as males in returning to the same field. Those that did return usually paired with the male holding a territory encompassing the region of her nest site the previous year. Of 19 colorbanded females that nested in the meadow in 1967, only five (26.2 per cent) returned to breed in 1968; one (6.3 per cent) of the 16 banded females of 1968 returned the next year; and four (25.0 per cent) of the 16 banded females of 1969 returned in 1970, in addition to one that had nested in 1968 but had not appeared in 1969. Of 28 hens colorbanded during 1967, nine that were captured early in the season left the meadow. This suggests that female transients occasionally stop over in the field, or, alternatively, that prior to nesting females are not as strongly attached to the site where they settle as are males. Territorial males rarely departed after being banded. Once nest construction commenced the attachment of a female to the nest was considerable: only three of 47 females captured at nests from 1968-70 vacated the meadow after

banding. Before 1970, no females that had been unsuccessful in fledging at least one young in the preceding year returned to nest. In 1970 three such females returned.

### The Question of Drifting Males

The decline in the total number of banded floating males in 1969 and 1970 resulted from two causes: first, since many territorial males in these years had been colorbanded in previous springs, most banding efforts to capture the few unbanded males were confined to nest sites. This naturally precluded capture of non-territorial males that were chased about the meadow by residents. The massive effort to capture all territorial males in 1967 and 1968, by contrast, was rewarded by bonus captures of drifters. Second, a majority of drifters were yearlings; reproductive success in 1968 and 1969 was extremely low (Table 1) as a consequence of the floodings, so it is natural that fewer floating males were present the spring following each unsuccessful breeding season.

The behavior of floating males was particularly fascinating, and points up further inconsistencies concerning the already muddled views on the role of territorial behavior as an effective regulator of population density (cf., Brown, 1969a, for an excellent review of these conflicting opinions). According to Brown's (1969a, 1969b) classification, Bobolinks in this population are at density level 3,

because of the conspicuous presence of floating males. However, with a level 3 density, Brown assumes that all habitats where breeding can possibly occur are occupied by territorial holders, and that floaters are surplus individuals unable to breed.

For the Bobolink this generalization simply does not hold. Surrounding fields suitable for Bobolink breeding were continually ignored by these males. The 3.6 ha meadow 1.5 km south of the riverbottom site provides a case in point. This field differed very little in floristic and physiognomic structure or in per cent coverage of vegetative forms from the riverbottom field, and both were surrounded by similar brush and woodland communities. Yet prior to 1970 no male Bobolinks held territories in the southern meadow during the term of this study. Other species which nested in the riverbottom tract bred in similar densities at this other location, although at the southern field Red-winged Blackbirds were more numerous. The southern meadow, then, seemed suitable in all respects for nesting, and when in 1970 a single male (70-37) established a territory, subsequently becoming a bigamist, this assumption was verified. This male, hatched in the riverbottom meadow in 1967, had been a drifter in 1968 and a bachelor in 1969 at the major study area. In previous years other lone males were occasionally sighted in this and other meadows but they displayed only ephemeral evidences of territoriality and remained for only brief intervals.

From this evidence one must conclude that adequate breeding localities are available in the region close to the research meadow, and a species as mobile as the Bobolink has ready access to hundreds of suitable breeding areas in southern Wisconsin alone. Moreover, at least in 1970 there was a region along the southern edge of the riverbottom meadow which was ignored by drifting males but which in past years was held by males which had paired successfully.

Males in the drifting class which appeared at the field from time to time usually behaved in a similar fashion. Rather than settle in an undefended area, the intruder flew directly toward a territorial male and attempted to land near the displaying defender. It was then chased from the territory and usually met and chased by the adjacent male. If the neighboring male failed to respond to the approaching drifter the latter would again land, close to that owner; another chase would ensue. These males rarely harassed bachelor males, but directed their efforts at the males defending the most suitable sites in the meadow, as gauged by their pairing success. Orians (1961: 302) reported a similar strategy employed by drifting Tricolored Blackbirds that attempted to substitute themselves for territorial males rather than settle in peripheral areas.

After viewing this stereotyped pattern hundreds of times, I can only conclude that the drifters were not attempting to gain territories, or if they were, they were testing males occupying only the choicest



habitat available. Later in the breeding season when territorial males became occupied with feeding young, the behavior of many drifters changed abruptly. Indeed, they suddenly became aggressive and established territories vacated by the feeding males, usually in the better areas of the field. Certain of these males were successful at pairing (e.g., 67-10; 68-26; 69-27; 69-30). Male 68-26 successfully fledged young and returned among the earliest males in subsequent years, to the same territory.

A majority of drifters were yearling males. Figure 7 fails to portray this age structure reliably, for in 1969 and 1970 older males tended to comprise the bulk of colorbanded males in this category. Again, this is a result primarily of the low production of offspring in the preceding two years. The bulk of the drifters arrived during the last week of May but arrivals continued through the first three weeks of June. This arrival schedule corresponded to that of colorbanded yearling males hatched in the field the previous summer. It is a reasonable assumption that most unbanded drifters, then, were yearlings hatched in other areas. My early departure in 1970 precluded a complete tally of the drifters. The transient nature of their appearances suggests that drifters move individually over a fairly good-sized region. Nonetheless, at least some appear to migrate or arrive together, because in 1968 five yearlings and two unbanded drifters were observed simultaneously in late May, the first day that drifters

were noticed that year. Apparently individuals in these small flocks become solitary soon after their arrival. Some were seen almost daily, yet others disappeared for a week or more before reappearing for a short period, hanging loosely about the field for a day or less.

Because the provisions of the habitat quality hypothesis of polygyny depend on some males regularly being excluded from breeding because suitable habitat is in short supply, the availability of seemingly appropriate breeding meadows which are largely ignored by drifters poses some interesting problems which bear directly on the validity of the hypothesis. I will attempt to resolve this discrepancy when I discuss other features of the Bobolink's breeding biology which coincide with its non-monogamous breeding system, in Chapter 6.

#### Sex Ratios and Mating Levels

Whereas an accurate tabulation was obtained of the number of territorial males, only an estimate could be made of the non-territorial drifters because of their transitory habits and because some were not banded. Nevertheless, the number of floating males must be considered when determining the tertiary sex ratio, since they were potential territorial holders and comprised one component of the male population. The sex ratios given in Table 2 are based on the minimum number of males observed at the study area each year;

TABLE 2. SEX RATIOS OF ADULT BOBOLINKS, 1967-70

Year	Males			Females		Chi-Square
	Total # Territorial*	Minimum # Drifters**	Minimum Total	Total # in Season***	♀ / ♂	
1967	19	6	25	32	1.28	0.85 0.5 > P > 0.1
1968	16	9	25	19	0.76	0.81 0.5 > P > 0.1
1969	17	5	22	21	0.95	0.22 0.9 > P > 0.5
1970	14	5	19	28	1.47	1.72 0.5 > P > 0.1
1967-70	66	25	91	100	1.10	0.52 0.5 > P > 0.1

\* Includes males that established territories in June, after territorial configurations shown in Figure 8 were plotted.

\*\* Excludes mates classified as transients, and those that later became territorial in same year. Includes one unbanded drifter each year.

\*\*\* Includes females arriving late in the breeding season that probably experienced nest failure elsewhere.

the number of drifters was determined by adding one to the total number of colorbanded floaters present. Each year I observed unbanded males in the drifter class, and it is likely that many more than one were in this category of males. In no year did the ratio between the adult sexes differ significantly from unity (Chi-square test,  $P < 0.05$ ).

Of the 62 long-term territorial holders whose pairing status was known with certainty (males 68-3, 69-21, 69-39 and 70-U were excluded), 36 (58.0 per cent) were polygynists, 12 (19.4 per cent) were monogamists and 14 (22.6 per cent) remained unpaired (Table 3). Large yearly variation occurred in the per cent of males that achieved specific mating levels. The early flooding in 1968 probably prevented some bachelors that year from subsequently pairing. Bigamy was the commonest mating level.

#### Pair Formation and Courtship

Depending upon their past experience with the meadow as a breeding location, newly arriving females reacted in strikingly different manners. Those that had previously nested there showed little hesitation in settling in a territory close to the region of their former nest and establishing a pair bond within hours of returning. Because males also tended to return to the same location, when previous mates came to the field it was likely they re-paired. Unbanded females that were unfamiliar with the field sometimes moved over

TABLE 3. COMPARISON OF MATING LEVELS OF TERRITORIAL MALES, 1967-70

Year	Level of Pairing												Total Males
	Bachelor		Monogamous		Bigamous		Trigamous		Quadgamous		Polygynous		
	N	%	N	%	N	%	N	%	N	%	N	%	
1967	4	21.1	5	26.3	7	36.8	2	10.5	1	5.3	10	52.6	19
1968	7	46.7	1	6.7	4	26.7	3	20.0			7	46.7	15
1969	3	20.0	3	20.0	8	53.3	1	6.7			9	60.0	15
1970	0	0.0	3	23.1	5	38.5	5	38.5			10	77.0	13
Total	14	22.6	12	19.4	24	38.7	11	17.7	1	1.6	36	58.0	62

much of the meadow before pairing, sometimes for up to two days. All males reacted overtly by conspicuous short aerial song displays whenever small groups of females passed overhead, and when an unpaired female alighted in or close to a territory the male instantly initiated a stereotyped advertising-courtship sequence which was repeated up to five times per minute for intervals of 30-40 minutes if the female remained near by. Then after a brief period of foraging a new burst of display ensued.

The process of pair formation in the Bobolink had no formality-- the bond was simply formed when the female settled in a territory and remained. Pairing was evident when a female began closely associating with the male, following him within the territory as he continued to perform the courtship sequence. This sequence was probably multi-functional, primarily functioning to attract the female to the male and its territory. The display probably also served to delineate the boundaries of the territory. Finally, it probably functioned to stimulate the pair physiologically, coordinating and synchronizing reproductive readiness.

During the early courtship phases with one female, males usually paid little attention to newly arrived females. After the second day of courtship, however, some males displayed interest in other hens and by the first day of the copulatory period all males attempted to attract unpaired females to their territories. All

Bobolink male behaviors and strategies of time allotment were conducive to multiple acquisition of mates. The high song rates characteristic of the advertising period declined abruptly with onset of courtship after pairing. Late in the copulatory phase of the primary female, however, there was a recrudescence of song as the male sought to recruit a secondary female. If successful, song rate again declined with commencement of courtship and was renewed during the copulatory stage. Verner (1963) reported a similar adjustment of song rates in the Long-billed Marsh Wren. Under typical circumstances where female Bobolinks arrived over a period of about three weeks, the temporal spacing of the courtship-copulation-courtship sequence permitted a male to carry two successive secondary females through courtship and copulation before eggs hatched in the primary nest. Recurring renewal of advertisement and subsequent courtship activities requires the liberation of the male from duties associated with nest construction, incubation and feeding the incubating female. As will be noted beyond, this situation prevails in the Bobolink.

While engaged in courtship and copulatory activities with secondary females after the primary female was adequately serviced, males generally ignored the primary mate until her young hatched. The primary female, however, occasionally came off the nest for brief periods to follow her mate and vocalize as he chased the

secondary female during courtship. When hatching commenced, advertising and territorial behaviors ceased abruptly, and most male attention was directed toward care of these nestlings. However, if a male had an unserved secondary hen at the time of hatching, it divided its attention for a brief interval between the primary nest and the secondary mate. Often the courtship phase with the new female was accelerated under this circumstance. With few exceptions, males fed nestlings and fledglings of their first female only. When the primary nest was destroyed or deserted males then tended nestlings in the first of the secondary nests to hatch young. Usually, though, all duties of raising young in secondary nests were left solely to the female. Still, the male played an important role by "guarding" the secondary nest location through vocalization warnings or mobbing when potential predators approached the nest area. Thus the primary female derived special male attention that secondary females lacked.

#### Copulation and Nest Construction

The courtship phase, following a ritualized and predictable sequence, lasted two and one half or three days before copulations commenced. Mounting occurred throughout the day, but major concentrations of prolonged mating (15-20 consecutive mounts) were characteristic at about 0700-0900 (CDT) and again at approximately



1600-1900. Copulations normally took place within 40 m of the nest, which was under construction during the early stages of mating. The hen often was carrying nesting material in her bill at the time of servicing. The female alone built the nest, gathering dead grass stems and leaves at distances of up to 80 m from the nest and weaving these into a loose outer shell placed in a small depression made when she uprooted living vegetation at the nest location. Once the shell was completed a lining of fine sedge stems was placed in the nest. The time required for completion of a nest varied from 1-3 days. Additional lining material was sometimes placed in the nest after deposition of the first and second eggs.

#### Egg Laying, Incubation and Nestling Period

After the nest was completed, a day usually passed before deposition of the first egg. Eggs were laid, one per day, between 0615 and 0700 each morning and were not incubated until the penultimate egg was deposited. Copulations continued through the second day of laying and often into the third. After mating was finished the female became very shy and was rarely observed until incubation was underway. By this time males that had not yet attracted a second mate had retired to a different region of their territory and had begun vigorously advertising for another female. Table 1 shows the yearly variation in clutch size at the riverbottom meadow. The mean clutch

size of 114 incubated sets known to be complete was  $5.18 \pm 0.15$  ( $\alpha = .05$ ) ranging from 3-7.

Incubation, as measured from the laying of the last egg to the hatching of that egg, varied from 11 days, 20 hours to 13 days, 7 hours. In a majority of nests for which records are accurate, the length of incubation was approximately 12 days, 9 hours. With one exception where a monogamous male shared equally with the female in incubation duties of a very late nest, the Bobolink hen incubated unassisted by the cock. After young were hatched the egg shell fragments were removed from the nest by the female and she began feeding the young within an hour. Males began actively participating in care of the young of their primary female soon after the first young was hatched by bringing food to the nestlings and by brooding them. Brooding by both adults continued through about the fourth day and females occasionally brooded young through the seventh or eighth day, and at night until fledging. The tremendous pace required of the parents to feed their growing broods is illustrated in Figures 12 and 13. When nestlings were 9-10 days of age, food was delivered to the nest approximately every two minutes, or about 500 carries per bird day. The relevance of such a great expenditure to the adaptiveness of the polygynous mating system of this species will be developed more fully in Chapter 6. The bulk of food brought to the nest at the riverbottom site, as gauged by observation through a 20X spotting

scope of adult birds bringing food to the nestlings, consisted of lepidopterous larvae with lesser numbers of spiders, small beetles and coleopteran grubs, adult lepidopterans (small moths) and a few damsel flies. At Faville Prairie, where there was an abundance of dragon flies, this group comprised a relatively large proportion of the nestlings' food. In general, between 2-5 food items were brought per carry. Figure 14 depicts a growth curve of nestlings.

#### Fledging, Postfledging Period, and Breeding Success

Fledging occurred at undisturbed nests on about the 11th day. Usually all young fledged within a short interval, yet occasionally the smallest bird failed to fledge with its siblings and subsequently died of parental neglect. This suggests that concurrent fledging of all chicks is advantageous and that once some young have left the nest a loudly begging fledgling tends to stimulate adults more than a feebly begging nestling. While still in the nest, immatures rarely vocalized, except to give low quiet buzzes when adults appeared at the nest rim. Within five or six minutes after fledging, however, they began a loud begging note which continued periodically for approximately 20 days. Young scattered in all directions immediately on leaving the nest. Parents divided the labor of feeding the fledglings, each adult concentrating on feeding specific young for at least 3-4 days. At about 13 days of age young made short flights and by

16 days of age immatures were capable of sustained flight for up to at least 200 m; they frequently pursued one adult after another as they gave begging notes.

In most years there was synchronism in the onset of nesting of primary females, and the young of these nests fledged within a 3-4 day interval. About a week after leaving the nest these immatures and the associated adults congregated into a flock where they remained until departure from the field. The flock increased in size as additional immatures and adults from other nests joined. The group was mobile, and gradually moved over most of the field. Males still maintaining territories at this time were surprisingly tolerant of the congregation. Perhaps the fact that males within this feeding flock showed varying degrees of the post-nuptial molt, while territorial holders did not, in combination with distinctive behavioral differences provided clues that the former males did not constitute a threat to territorial birds. Within these groups adults continued to feed only their young, for up to 28 days after fledging. In most years the flock departed from the meadow about 20 July.

Nesting success over the five years is summarized in Table 1. Considering the devastating storms of 1968 and 1969, it is remarkable that success in 1968 was as high as 42 per cent. None of the early nests that year suffered nest losses, all successfully fledging virtually complete broods prior to the storm's arrival. The

destructive impact of the storms is expressed more decisively by the mean number of young successfully fledging from nests. For the three years where normal weather conditions prevailed an average of almost 2.5 young were fledged per nest. In 1968 only 1.68 young fledged the nest and in 1969 the mean was 1.08. In both these years it is likely that post-fledging mortality was exceptionally high, because the flooding also destroyed food resources, as evidenced by large quantities of dead adult and larval insects in the water. Moreover, the extended wet, cold conditions undoubtedly took a toll, especially in combination with the food shortage. Neglecting the stormy years, nesting success was directly related to the time of nest-building: nests constructed early had higher success than late nests (see Martin, 1967:66). The mean clutch size of earlier nests also was greater than that of later sets. Bobolinks never attempted a second nest after successfully fledging a brood, but in the event the original nest was destroyed some females renested (Table 1). In 1967 one female attempted three nests before she was successful; she returned the following two years and successfully fledged young in her initial attempt each year.

## CHAPTER 5

## TERRITORIAL QUALITY AND MATING STRUCTURE

Territory Dimensions and Pairing Success

Observations of male and female establishment in the river-bottom meadow demonstrate the birds exhibited strong preferences for specific sites in the field each spring. The schedule of male occupation of specific areas of the meadow was consistent from year to year. This was influenced to an extent by the earliest returning males maintaining attachments to previously occupied sites. In the event that a male holding an excellent territory (as gauged by the pairing success index, see below) one year failed to return the next, its area was still among the first to be occupied. Furthermore, the order of settlement by early arriving females generally paralleled the order of male occupation. During this investigation Bobolink females never distributed themselves evenly among all the available males (Figures 8, 9): each breeding season some males held concurrent bonds with as many as three females while others remained bachelors or paired with only one hen. These observations suggest that the different areas of the meadow did in fact differ in their attractiveness to both males and females.

Compared to qualities of the territories, characteristics of

Figure 8. Shapes and locations of territories as they appeared in late May, 1966-69. Territories of males that later established residency by either replacing disappearing males or by settling in regions left undefended by males caring for nestlings, are not included. The upper number in each territory corresponds with that identifying the male in Figure 7. The lower number is the pairing success index of the territory.

■ BACHELOR  
 M MONOGAMIST  
 B BIGAMIST  
 U UNKNOWN

T TRIGAMIST  
 Q QUADGAMIST  
 U UNKNOWN

O, U MALE NUMBER, OR UNBANDED  
 T MALE STATUS  
 9 PAIRING SUCCESS INDEX

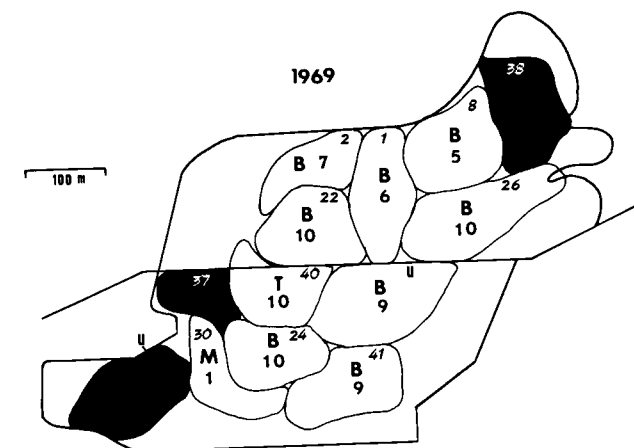
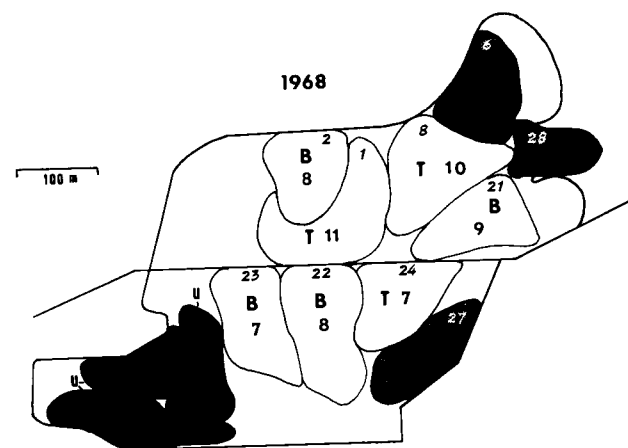
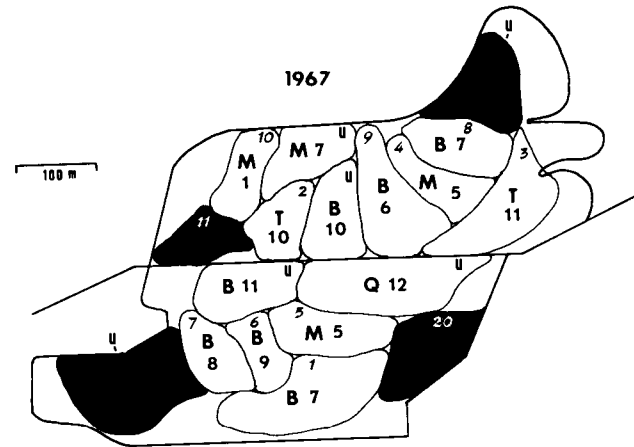
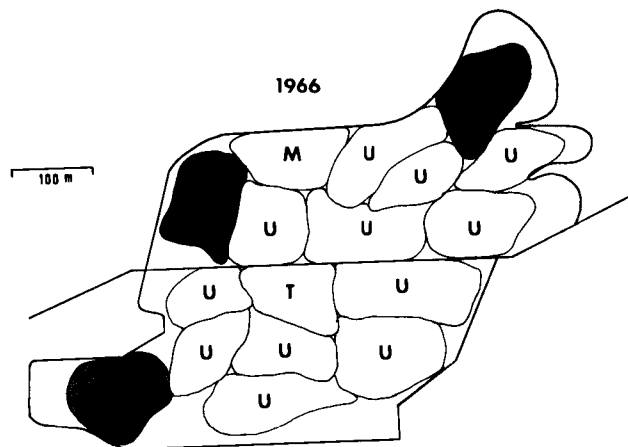
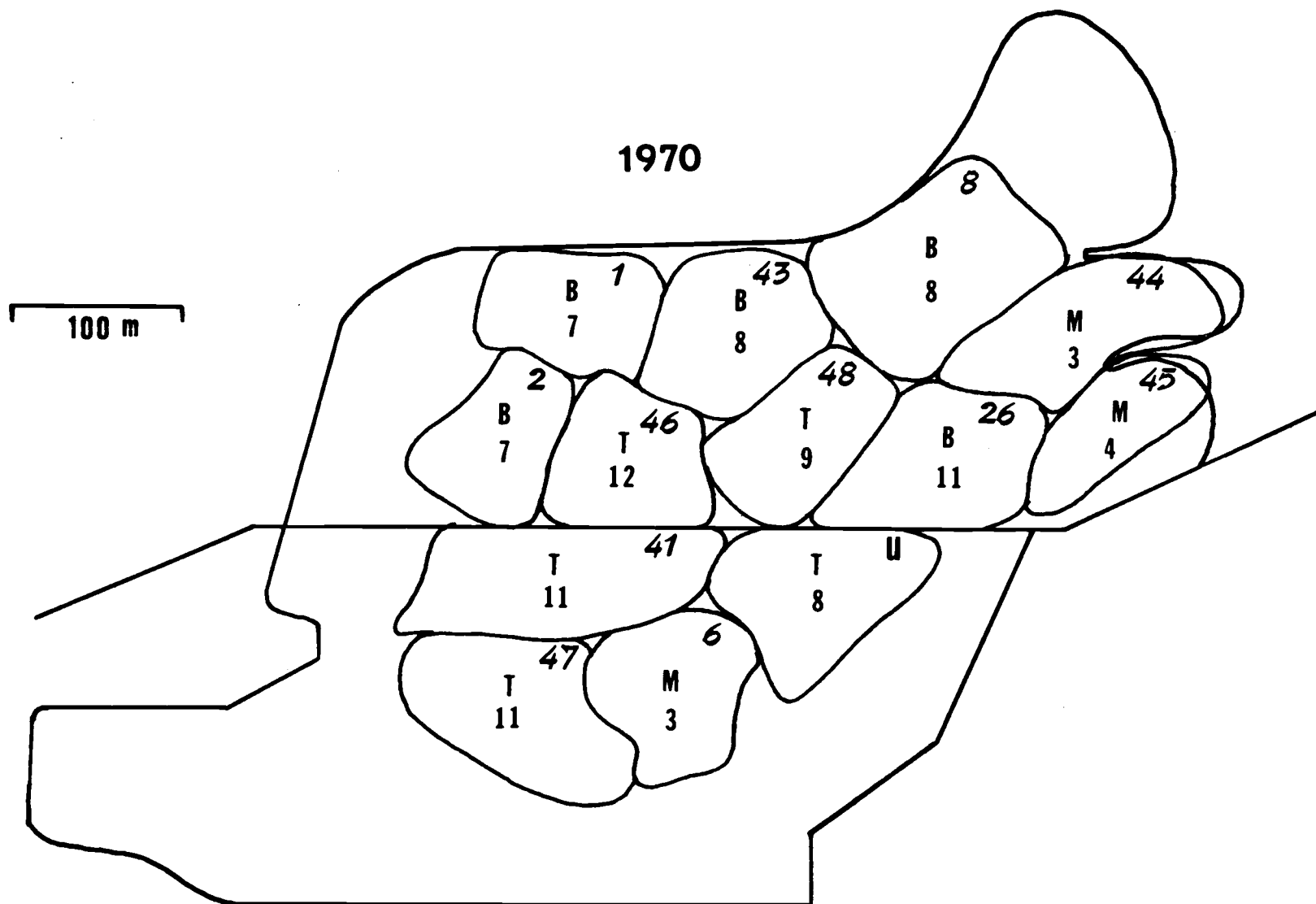




Figure 9. Shapes and locations of territories as they appeared in late May, 1970. Legend as in Figure 8.



individual males appeared to be of minor importance in the attraction of females. Despite frequent yearly changes in ownership of localized areas, there was a consistency from year to year in the general placement of territories held by bachelors and mated males (Figures 8, 9). Areas including territories occupied by bachelors one spring were generally ignored by females in subsequent seasons, while areas nested in one spring were utilized (usually by different females) in following years. Moreover, some males were able to modify their breeding status simply by moving to a different portion of the meadow, or by enlarging or shifting a portion of their territories to incorporate an additional chunk of suitable real estate.

Three factors must be considered when interpreting these territory maps: first, territory sizes, shapes and locations fluctuated throughout the season, and these figures thus represent a static and simplistic arrangement of territorial configurations as they appeared during the last few days of May each spring. In general, territories were initially large but contracted as more and more males arrived. Further reduction in size occurred when females appeared, as males allocated time to courtship at the expense of territorial maintenance. After most females were settled the sizes of territories again increased. Territorial areas and boundaries cited here and used as the basis for vegetation analysis were those determined during the last 10 days of May. I feel that this period is

most appropriate, for it is during this interval of maximum pair formation that the holdings of a male Bobolink are being evaluated by potential mates.

Second, because males ceased territorial defense soon after young hatched, new males were able to establish territories in mid June each year. These new territories usually overlapped extensively or completely with the former territories of feeding males. Unless these newly established territories were mutually exclusive (e.g., 69-30; 67-10) of late May territories, they were not plotted on these maps. Territories of late-establishers were usually larger than the original territories. Even though some of these males eventually paired successfully, properties of their territories were not included in the analyses of this chapter, because their late appearance at the meadow greatly diminished their opportunity to obtain multiple mates. Males in this class included some of the individuals that had drifted about the meadow early in the breeding season. The appearance of others coincided with early agricultural mowing of nearby alfalfa fields and I assume that the males were originally resident in these mowed fields. All females settling in the meadow at this time possessed well-developed brood patches. Vascularization ordinarily does not develop until the third or fourth day of egg deposition in the first nest, suggesting that their first nest had terminated unsuccessfully elsewhere.

Finally, the maps also fail to indicate disappearances and replacements of male Bobolinks in early June. Consequently, the numbers of territories depicted on the maps do not always correspond with the number of males of each mating level shown in Table 3, nor with the number of territories entering into the calculation of mean territory size.

An index of pairing success was determined for each territory to quantitatively compare differences in territorial attractiveness or quality. This index considers the total number of females a male paired with and the earliness of mate acquisition, based on the date when nest construction was initiated by each female. To determine an index value, five points were tallied for each of a male's females that began construction within seven days of the initiation of the earliest active nest in the meadow; four points were scored for nests started from 8-14 days later, and so forth. Thus, a trigamist could potentially tally a score of 15 if all three hens commenced building in the first seven days. In 1967 a monogamist (67-U) totaled seven, two points greater than the theoretical maximum for this mating level: the nest of its first female was destroyed and she was either killed or subsequently disappeared, the male acquiring a second mate shortly thereafter. Had the primary female's nest not been predated, the male in all probability would have attracted the second female regardless, thus becoming a bigamist. Bigamists occupied the same

general area of the meadow in the three following years.

The absence of natural limitations to territorial boundaries (other than the artificial ditch) which would standardize territorial locations year after year made it difficult to compare indices from the four springs. In their work with Long-billed Marsh Wrens, Verner and Engelsen (1970:563) had ideal conditions for determining year to year modifications in the status attained by males occupying the same areas, for water and emergent vegetation discontinuities in the marsh habitat forced perfect coincidence in locations of territories in consecutive springs. In only one of eight territories was there a change in the number of females nesting from one year to the next. In the present study specific regions of the meadow tended to have approximately the same pairing success index each spring. For instance, in the approximate location of the 67-U monogamous territory just mentioned, the index was 7-8-7-7 for four years (Figures 8, 9), while the area just to its south had index values of 10-11-10-12. In the general location of 67-3, values of 11-9-10-11 resulted. Bachelor territories, having a zero index, were situated in about the same areas yearly. For these and for some other locations the index values were remarkably stable through the study, despite rather large yearly differences in the number of females present (32-19-21-28 for 1967-70), which of course exerts considerable control over the range of possible index values. The heavy rains of 1968 and 1969

undoubtedly minimized the number of females nesting in the meadow those years, for additional hens would normally have arrived after the date the earliest storms struck.

The 1968 map beautifully illustrates the selectivity of females, for at the onset of the stormy weather that year only seven of the 13 territories had been settled by hens, resulting in high indices for those areas. Without exception, these regions attracted females early each season. Males 67-10 and 69-30 were bachelors early in the season but both successfully paired between 15 and 20 June. It is likely that at least one 1968 bachelor would have paired during this period had the thunderstorm fronts arrived a week later, as they did in 1969. As will be related later, by this date the stature of vegetation in certain areas of the meadow afforded concealment properties it lacked earlier. That is, by mid June, as a result of plant maturation and growth, certain areas that had habitat qualities below the habitat suitability threshold (c in Figure 1A) in May now exceeded the threshold, yet still failed to provide the best quality. At this time males holding superior habitat were preoccupied with tending young, forcing females to pair with either a bachelor in a moderately good area or a newly arriving male, or to forego an attempt at renesting. Hence, by this late date pairing with a male utilizing less than ideal habitat may be a better alternative to not renesting at all.

It should be apparent, then, that the pairing success index offers

a more sensitive measure of the dynamics of pairing than does simply an assignment to monogamous, bigamous and trigamous categories: males attaining the monogamous indices of M1, M3, M4, and M5 for example, differed substantially in their actual success at extended pairing. Moreover, from one M4 and two M5 territories a mean of 80.0 per cent of all eggs produced fledged young, compared with 22.2 and 13.6 per cent from two M3 and five M1 territories, respectively.

Although yearly differences in the mean size of territories (Table 1) were not statistically significant, there was a significant inverse correlation ( $r = -0.952$ ,  $N = 4$ ,  $0.05 > P > 0.01$ ) between territory size and male density from 1966-69, attesting to the compressibility of territorial holdings under high density conditions. Hence, sizes of territories held by males of different mating classes might vary slightly from year to year depending on male density. However, compared with the range of variation in territory sizes within any one year (Table 1), fluctuation in size as a result of density differences are of minor importance. Territory sizes averaged over four years for bachelors, monogamists, bigamists and trigamists are given in Table 4. Monogamous territories averaged significantly smaller ( $P < 0.02$ ) than bigamous ones, but territories of all other mating levels were statistically similar in size. The correlation coefficient for the relationship between territory size and mating level was insignificant ( $r = +0.402$ ,  $N = 4$ ,  $P > 0.05$ ). Other studies,



TABLE 4. TERRITORY SIZE AND MATING STATUS, 1967-70

Mating Level	N	Mean Size (acres)	S.E.
Bachelor	16	1.72	0.086
Monogamous	12	1.41*	0.131
Bigamous	24	1.86*	0.113
Trigamous	12	1.78	0.171

\* Paired values are significantly different ( $0.02 > P > 0.01$ )

likewise, have found a lack of a significant correlation between the number of females in a territory and its size (Haigh, 1968; Nero, 1956a; Orians, 1961; Verner and Engelsen, 1970; Zimmerman, 1966), in spite of a general tendency for territory size to increase slightly with increasing mating level. Interestingly, while the statistical relationship of increasing territory size with higher mating level is obscured by the large individual variations in size, a significant positive correlation does exist between the pairing success index and territory size ( $r = +0.660$ ,  $N = 12$ ,  $0.05 > P > 0.01$ ). This suggests that in general the more satisfactory territories, as gauged by the total number of females nesting and the earliness of nesting, are larger than the less desirable ones. But as illustrated by the conflicting results of these two tests, the relationship between mating level and territory size alone is a tenuous one, and I shall now turn to a discussion of other features of the territory that can be influential

in determining its quality and suitability for reproduction.

### Food Abundance

In species which concentrate their foraging for nestlings within territorial boundaries (e.g., certain populations of Yellow-headed Blackbirds, [Xanthocephalus xanthocephalus], Willson, 1966:54, 56), territory to territory differences in food resource abundance or in proximate indicators of food supply should be crucial stimuli to females evaluating potential breeding areas. Verner and Engelsen (1970) discovered that pairing success of individual male Long-billed Marsh Wrens was significantly correlated with the number of nests that each had constructed. They suggested that males inhabiting territories with abundant food could apportion less time to foraging and more time to nest building than could males defending inferior food reserves. Females might then actually evaluate the availability of food indirectly, by tallying the number of finished nests within a territory. Crook (1964) and Orians (1969) also stressed the powerful selective influence of differential food supply on the evolution of non-monogamous mating systems.

Some populations or species of polygynous passerines, however, gather all or a majority of nestling food outside the territory. For these species (Brewer's Blackbird, [Euphagus cyanocephalus], Horn, 1968; Red-winged Blackbird, Haigh, 1968; Tricolored Blackbird,

Orians, 1961; Dickcissel, Zimmerman, 1966) differences in food supply cannot operate importantly in the development or maintenance of this mating strategy, for there will be no selective pressure on females to settle in territories rich in food. In fact, foraging for nestling food at distances from the territory appears to be common among polygynous species (Verner, 1964).

The Bobolink fits the conditions of this second category during the nestling stage. The continuous commitment to territorial defense and prevention of stolen copulations obligated males to perform all their foraging activities within the territory from the time that females appeared in the meadow until young hatched. Throughout the egg deposition and incubation periods females respected territorial boundaries for foraging, but to a lesser extent than males. They occasionally flew to foraging locations within territories of other males or to undefended regions of the meadow. However, after young hatched both sexes made frequent trips to distant areas of the field in search of food. Males sometimes foraged more than 1 km from the meadow during the nestling stage. The parents rarely foraged together or in the same general locations. Once young had fledged, however, each adult tended to gather food reasonably close to the young under its care. I suspect this enabled the parents to maintain better contact with the mobile young, which dispersed in all directions soon after fledging. Because so little foraging was done by

adults within the territory during the period of maximum food consumption, it is unlikely that territorial differences in food abundance above a certain minimum level are of major importance to Bobolink females in their selection of a mate.

### Vegetative Structure Surrounding Nest Sites

The variation in the pairing success index from territory to territory and its relative stability in specific parts of the meadow from spring to spring suggest that differences in habitat quality exist and that these differences take a patchy distribution over the meadow. If this is so, all males should be unable to incorporate equally suitable habitat patches within their territories, and this should influence their mating level. In order to appraise differences in quality between territories held by different males it is necessary to use a standard or baseline for comparisons. A female's evaluation of the quality of a male's territory may be strongly influenced by the availability of vegetation which will adequately protect and conceal her nest from adverse weather and predators. The nature of the vegetative structure immediately surrounding nest sites was accordingly chosen as this baseline.

Females showed a strong preference for constructing their nests at the base of large forbs (the major forbs of Table 5), especially Meadow Rue and Golden Alexander, which formed an overstory

TABLE 5. VEGETATIVE SUBSTRATE OF 127 NESTS

Substrate	N	Per cent
Major forb	106	83.5
Sedge with scattered minor forbs	14	11.0
Woody overstory	4	3.1
Arched over by litter	3	2.4

stratum above the sedge. Beecher (1942) noted a similar propensity for Bobolink nests to be associated with Thalictrum and other forbs. The frequency of utilization of this physiognomic type for nest placement greatly exceeded that to be expected by the low coverage (10.6 per cent) of major forbs over the entire field ( $P < 0.001$ , Table 6). By contrast, sedge was essentially ignored as a principle nesting substrate despite its distribution over vast portions of the meadow (72.1 per cent coverage). In most of the 14 instances where sedge was selected as nesting cover (Table 5), rich growth of small forbs in the immediate nest vicinity provided the primary concealment. Furthermore, these nests were usually among the latest to be built. A few nest cups were located beneath short, bushy willows which formed a canopy similar to that of large forbs. None of the 127 nests was placed where grass afforded the major source of concealment, despite the wide coverage (63.8 per cent) of grass in the meadow.

TABLE 6. CHARACTERISTICS OF VEGETATIVE STRUCTURE  
SURROUNDING NEST SITES, COMPARED WITH VALUES  
FROM RANDOM SAMPLES IN THE ENTIRE MEADOW

Habitat Feature	Total Field		Nest Vicinity		Field-nest Difference
	Sample points	Value	Sample points	Value	
Per cent coverage of:					
Minor forbs	632	34.2	374	57.0	**
Major forbs	632	10.6	374	25.5	**
Total forbs	1694	44.2	374	82.5	**
Sedge	1694	72.1	374	89.6	*
Grass	1694	63.8	374	29.8	**
Woody	1694	0.9	374	0.9	ns
Total vertical density <sup>1</sup>	1734	8.66	260	11.35	**
Per cent open skylight at:					
Ground	984	34.3	146	14.5	**
10 cm	984	57.9	146	29.8	**
20 cm	984	79.4	146	48.6	**
Litter depth (cm)	1736	1.39	298	0.92	**
Nearest major forb:					
Mean height (m)	1921	0.73	292	0.77	*
Mean distance to (m)	1921	4.03	388	2.02	**

<sup>1</sup> Mean number of total contacts

\* Differences significant ( $0.05 > P > 0.01$ ) by chi-square or t-tests

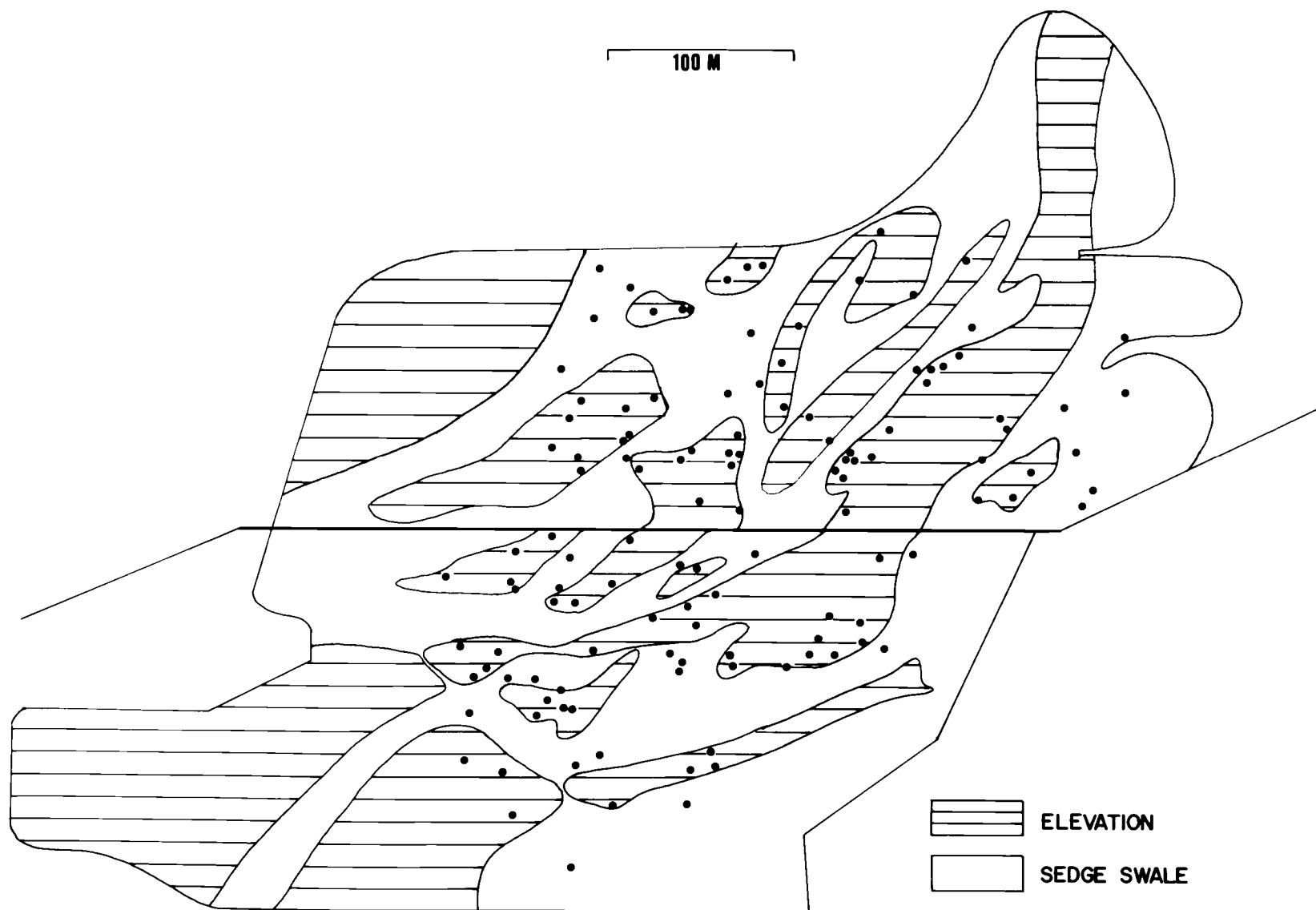
\*\* Differences significant ( $P < 0.001$ ) by chi-square or t-tests

ns Differences between means insignificant

Although sedge was not used extensively to provide cover directly over the nest cup (Table 5), it was nonetheless associated closely with nest sites (Table 6), for its per cent coverage around nests was significantly higher than over the entire meadow. This apparent paradox can be explained by a brief consideration of the vegetation stature found in the meadow in mid to late May when most females selected nest locations. At this time sedge and grass had a low, open appearance, and each furnished poor cover for nests. Some of the major forbs, however, already provided an overstory to the gramoid forms of vegetation. Their dense foliage produced shading and concealment properties afforded by no other physiognomic type in the meadow this early in the growing season. These large forbs grew most abundantly on the slightly elevated ridges in association with bluegrass (Figure 2). The dryness of the sandy ridge tops retarded the growth of herbaceous vegetation. In the transition zone along the slopes of the ridges, on the other hand, more mesic conditions prevailed, grass was replaced by sedge, and early in the nesting season the forbs were fuller and provided better protective conditions than did those higher on the ridges. Major forbs growing in scattered clumps on small knolls within sedge swards had a similar accelerated growth. As a result, most early nesting females took advantage of the extra cover by placing nests under forbs along the edges of ridges (Figure 10) or in the scattered

Figure 10. Locations of the 127 nests found from 1966-70, accurately plotted by measured distances referenced to the grid system. Only major elevations are illustrated, and thus certain nests seemingly located in sedge swales were actually on slight elevations.





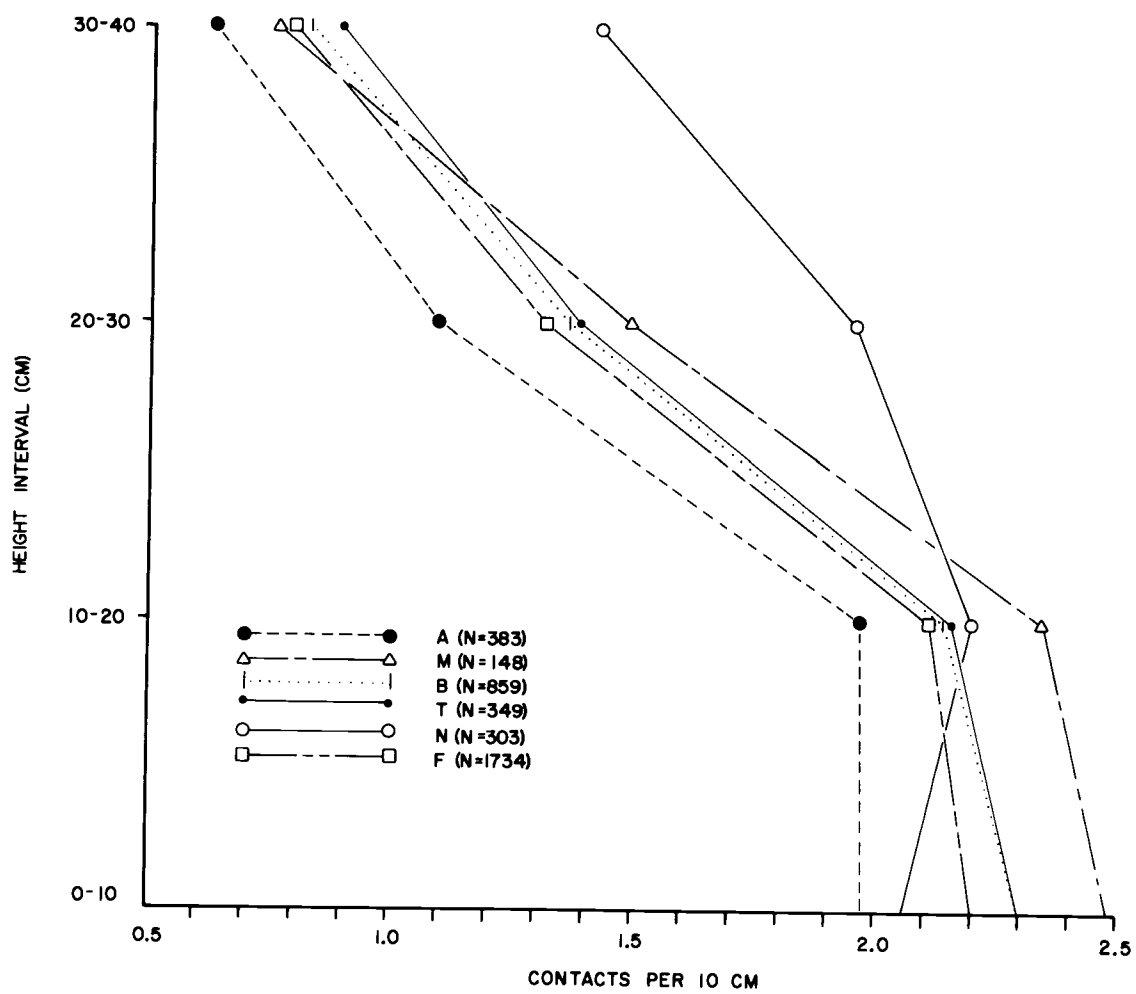
small clusters of rue (as in Figure 5A), where sedge formed the general low coverage. In mid June the average height of major forbs growing in the nest vicinity was significantly greater ( $P < 0.05$ ) than the mean height of forbs sampled randomly over the entire field (Table 6), probably as a result of the growth boost from these moister conditions. In May when females selected these forbs as nest sites they were probably reacting more to the full, lush nature of forbs growing in these favorable locations than to forb height, for it is questionable whether females could discern the less than five per cent height difference between nest vicinity forbs and randomly sampled forbs (Table 6).

By the point-centered quarter method, the mean distance to major forbs from random points in the meadow was twice as great ( $P < 0.001$ ) as the mean distance from nest cups (Table 6). Hence, the average density of major forbs in nest vicinities was 99 stems per 0.1 acre, compared to 30 stems per 0.1 acre over the entire field (Table 8).

A comparison of the total vertical density of vegetation (as measured by the mean of the total vegetation contacts at point samples) close to nests and those at non-nest samples in the field (Table 6) also emphasizes the tendency of females to select heavy concealing cover about nests. Furthermore, the vegetation profile above nests contrasted markedly with the profile of the meadow as a

whole (Figure 11). In the decimeter interval above ground level the density was less about nest sites. This likely permitted the incubating hen a freer view, and at the same time allowed a less impeded escape through the sparser vegetation when predators approached. Despite the more open nature of the vegetation near ground level, nest sites were extremely well-concealed by the increased density of the vegetation at heights above 10 cm. Wiens (1969:59) described a similar increase in cover in the 11-20 cm interval over that in the first decimeter above Bobolink nest vicinities. The heavy overstory cover also may have permitted an undetected running escape from potential predators. When diversionary behavior was performed to lure predators from the nest vicinity the hen awkwardly climbed or flopped onto or over the tops of vegetation in order to be visible.

Another measure of the concealing properties of vegetation is the per cent of skylight which penetrated through the plant cover. Nests were placed in deeply-shaded situations compared to the mean light penetration properties of the entire meadow (Table 6). The nest site preference of females for the fuller forbs also influenced the properties of the litter surrounding the nest. Deep shade cast from the forbs prohibited heavy growth of gramoid types in the immediate vicinity; litter, then, was often composed of small flat forb leaves which were subject to blowing and which settled flat on the ground. Consequently litter depth was significantly less around nests



than at other point samples ( $P < 0.01$ ) and the litter was generally more compacted.

Of all the variables of habitat structure that I measured at the riverbottom site, litter depth is likely the least important to the female in her choice of nest location, for it plays no role in nest concealment or sheltering. This is not to say that litter is unimportant in the Bobolink's nest site selection in other regions, however. In the fallow strip adjoining Faville Prairie the dominant forb was Common Goldenrod, which provided poor cover to nests. Here 30 per cent of the 27 nests found were fashioned beneath a heavy overhang of litter, and high litter afforded lesser degrees of concealment to a number of other nests. Thus, in this field deep litter substituted for forbs as the chief protection for many nests. In the contiguous Faville Prairie large forbs grew abundantly and their bases were generally used as nesting locations, just as in the riverbottom meadow. In his upland study areas, Wiens (1969:56) found that accumulated litter in the immediate vicinity of Bobolink nests was substantially deeper than the average depth in Bobolink territories. These fields were similar to the fallow land contiguous with Faville Prairie in lacking numerous large forbs (Wiens, 1969:58) which could provide necessary nesting concealment. Intermediate depths of litter were found correlated with Bobolink presence by Tester and Marshall (1961) in a region which apparently had a scarcity of large forbaceous

species. Therefore, in lieu of forb cover, litter may be an important criterion in nest site selection.

Tables 5 and 6 and Figure 11 demonstrate without question that females actively chose structural habitat features which differed significantly from the typical habitat present in the meadow. Had the nest site measures been restricted to points at the nest cup, rather than including additional points at half-meter distances from the nest, these differences would have been accentuated. For example, per cent coverage of major forbs would have been close to 83 per cent (Table 5) rather than 25.5 per cent, had the samples been taken only at the nest cup.

The tendency for nests to be located along the transitional habitat where the dry ridges and moist lowlands interdigitated is apparent in Figure 10, which illustrates that a number of localized areas were heavily utilized for nest sites year after year. The correspondence of nest placement and the well-defined spatial organization of vegetation in the meadow is clear. No nests were located on the broad, dry, sparsely vegetated ridges covered with Fleabane bordering the field along the west (Figure 1), or on the very dry peninsula of spindly rue extending north from the small building. In addition to the moister conditions which permitted earlier phenological development of forbs along the periphery of ridges, the visual freedom afforded by nests under the more scattered forb clusters

found there over that allowed by the dense forb aggregations on certain areas of the ridge tops might have influenced this nest placement pattern in the Bobolink.

In wet sedge meadows such as the riverbottom field and Faville Prairie, nesting in the lower sedge swales should be heavily selected against. In most sedge marshes the stature of sedge early in the season is low and lawn-like. It thus affords protective cover so poor that very likely the habitat suitability threshold is not exceeded. By mid June, on the other hand, sedge usually provides exceptionally good cover, yet as it was in these locations, it should still be generally ignored as nesting substrate. At these two fields any rains of greater than approximately 1.3 cm caused standing water in the low sedge areas and waters collecting from downpours of more than 2 cm chilled eggs or killed nestlings in those occasional nests that were placed in low open expanses of sedge. In southern Wisconsin it is not unusual for 1.5-2.5 cm of rain to accompany thunderstorms three or four times during May and June. Thus, despite the remarkable cover characteristics of this physiognomic form late in the spring, mechanisms should develop which prohibit choice of sedge for nesting sites. Beecher's (1942) observations of Bobolink occupancy of sedge meadows in Illinois augment this conclusion, for he noted that the species preferred habitat within the fields which was too dry for the Short-billed Marsh Wren (a species that nests on

elevated stools in the low sedge swards in the riverbottom field) and which had an abundance of large forbs (characteristic of slight elevations or ridge edges in the riverbottom meadow).

### Vegetative Structure of the Territories

Results of the vegetative analysis of bachelor and mated male territories are summarized in Tables 7-10, and in Figure 11. In general, there were marked differences between the territory classes in vegetation structure and in the abundance and distribution of physiognomic types. The relative quality of the various territory classes was judged using the criterion of the "closeness of fit" of each measured variable to those conditions surrounding nest sites.

TABLE 7. PER CENT COVERAGE OF PHYSIOGNOMIC TYPES  
ACCORDING TO TERRITORY CLASS

Territory type	Number of points sampled	Physiognomic Type		
		Forb <sup>1</sup>	Sedge	Grass
Bachelor	366	37.15	54.37	72.32
Monogamous	147	43.54	74.15	68.43
Bigamous	845	45.21	76.80	62.02
Trigamous	336	49.70	78.57	57.12
Nest value	374	82.53	89.61	29.78
Total field	1694	44.21	72.09	63.81

<sup>1</sup> Includes both major and minor forbaceous species



TABLE 8. DENSITY AND HEIGHTS OF MAJOR FORBS ACCORDING TO TERRITORY CLASS

Territory type	Forb Density		Number of samples	Forb Height	
	Number of distance measures	Density per 0.1 acre		Mean (m)	S. E.
Bachelor	504	8.3	429	0.80 <sup>c</sup>	0.014
Monogamous	156	33.4 <sup>a</sup>	151	0.77 <sup>c</sup>	0.022
Bigamous	918	48.4 <sup>a</sup>	834	0.72	0.009
Trigamous	352	117.7 <sup>b</sup>	285	0.67	0.013
Nest value	388	98.8 <sup>b</sup>	290	0.77 <sup>c</sup>	0.015
Total field	1930	29.7	1699	0.73	--

Paired letters indicate insignificant differences. All other value pairs are significant ( $P < 0.01$ ). Total field values were not statistically compared with territory means.

TABLE 9. TOTAL VERTICAL DENSITY AND DEPTH OF ACCUMULATED LITTER  
ACCORDING TO TERRITORY CLASS

Territory type	Vertical Density			Litter Depth		
	Number of sample points	Mean number of contacts	S.E.	Number of sample points	Mean	S.E.
Bachelor	380	7.73*	0.205	367	1.16	0.030
Monogamous	148	9.48	0.391	152	1.50	0.041
Bigamous	858	8.91	0.146	865	1.50	0.018
Trigamous	348	8.73	0.219	352	1.34	0.029
Nest value	260	11.35**	0.312	298	0.92***	0.034
Total field	1734	8.66	---	1736	1.39	---

\* Significantly less ( $P < 0.001$ ) than all other mating levels

\*\* Significantly greater ( $P < 0.001$ ) than all mating levels

\*\*\* Significantly less than bachelor level ( $P < 0.05$ ) and other mating levels ( $P < 0.01$ )

TABLE 10. SHADING PROPERTIES OF VEGETATION IN DIFFERENT TERRITORY CLASSES

Territory type	Number of points sampled	Per cent open skylight penetrating to:					
		Ground level		10 cm above ground		20 cm above ground	
		%	S.E.	%	S.E.	%	S.E.
Bachelor	280	45.3	1.93	68.8	1.95	85.6 <sup>e</sup>	1.45
Monogamous	66	33.0 <sup>a</sup>	3.32	53.6 <sup>b, c</sup>	4.25	80.6 <sup>e, d</sup>	3.14
Bigamous	491	32.0 <sup>a</sup>	1.19	56.2 <sup>b</sup>	1.52	78.9 <sup>d</sup>	1.26
Trigamous	147	21.8	1.91	44.8 <sup>c</sup>	2.65	69.0	2.61
Nest value	146	14.5	1.31	29.8	1.91	48.6	3.22
Total field	984	34.3	--	57.9	--	79.4	--

Note: Paired letters indicate insignificant differences. All other value pairs are significant ( $P < 0.01$ ). Total field values were not statistically compared with territory means.

Bachelor Territories. The habitat structure in bachelor territories was characteristically open, showed less vertical density, and possessed fewer and more widely dispersed large forbs than did the habitat in territories occupied by paired males. Bachelor territories were usually located in the drier, peripheral regions of the meadow (Figures 8, 9), where rather short sparse bluegrass formed the principle cover early in the spring, broken only occasionally by forbs or small patches of sedge growth. Hence, coverage of grasses was more extensive than in other territory classes while forbs, and especially sedges, had their lowest coverages in bachelor territories (Table 7). Coverages of all three types in bachelor areas deviated more from the nest values than did coverages in other territories.

The chief forb in these regions was Fleabane, a spindly species which provided virtually no shading or concealment. Density of major forbs (Table 8), the principle Bobolink nesting substrate, was significantly lower ( $P < 0.001$ ) in areas defended by bachelors than in all other territories, but these forbs were the tallest and, aside from monogamist territories, most closely fit the nest value for forb height (Table 8). The significant negative correlation ( $r = -0.971$ ,  $n = 4$ ,  $P < 0.05$ ) between major forb height and forb density in the four territory types demonstrates that forbs were tallest where they were sparse and shorter where they grew densely. It is not surprising, then, that forbs in bachelor territories were tall. Aside from

height, no measures were taken of the physical structure of these forbs. However, visual inspection of Meadow Rue and Golden Alexander growing in the sparse cover of bachelor territories clearly demonstrated that most lacked the fullness and breadth of those found in territories of paired males.

The total vertical density measured in bachelor territories was significantly less ( $P < 0.001$ ) than in all other territories (Table 9). Consequently, the vegetation was much thinner and more open. Furthermore, the vegetation profile was lower than in other territories (Figure 11). Both the low total vertical density and the flattened profile allowed significantly greater ( $P < 0.001$ ) light penetration through the vegetation than in other territory types at the ground and at 10 and 20 cm increments above ground (Table 10).

Because the cover in bachelor territories was so sparse, little plant remains were present to accumulate as litter (Table 9). In fact, although litter in bachelor territories was significantly deeper than litter about nests, it approached the nest value more closely than did litter depth in territories of paired males. As discussed previously, litter was shallow around nests because the deep shade from the overstorying dense forbs seemed to prevent heavy growth of gramoid vegetation. Hence, the low litter depths in bachelor territories and around nests were a consequence of two strikingly different causes.

Monogamous Territories. Monogamists utilized habitats of two contrasting types. Males 67-5, 70-6 and 70-45, for instance, occupied tracts of heavy sedge that were broken only occasionally by small clumps of rue on slight rises. Males 67-10 and 69-30, on the other hand, held fairly marginal dry habitats possessing extensive grass coverage. They were bachelors in May and paired rather late in the breeding season, as evidenced by their low pairing success indices. The wide range in pairing success indices for territories of both monogamists and bigamists signifies that not all males within each group were equally successful at pairing early in the season. If I were to analyze values from all sample locations according to the pairing success index of the territory rather than to the male's mating level, such differences in territorial quality as those suggested above for monogamists would be more apparent. However, the analysis of vegetational data was completed before I developed an index which would more realistically expose individual differences than did comparisons of values between the four mating classes. Such analyses with the index levels are planned.

In general, most monogamous territories were in fairly dense sedge growth, but vegetation samples from territories on the dry grass ridges tended to bias the summary values by increasing the variances of the measured parameters, and by increasing the coverage of grass. The value for sedge coverage was correspondingly

decreased. Nevertheless, the influence of the more typical location of monogamous territories in areas of high sedge coverage is apparent when comparing the total vertical density (Table 9) and the vertical stratification profile (Figure 11) of monogamous and other territory types. Where sedge is dense it grows profusely close to the ground, but decreases in vertical density faster above 20 cm than do forbs and more scattered sedges. As a result monogamous territories had a vertical vegetation density profile which had more contacts per decimeter close to the ground and fewer high contacts than did other territory types. The large number of sedge stems and leaves close to the ground accounted for the large total vertical density in monogamous territories. Although this value most closely approached that found around nest sites (Table 9), it was still significantly less ( $P < 0.001$ ) than the nest vertical density. Furthermore, Figure 11 demonstrates that the concentration of vertical density in monogamous territories differed from the nest profile more than did profiles from all other territories of paired males, due to the high density close to the ground.

As a result of the denser stature of vegetation near ground level, light penetration to the ground and 10 cm levels was significantly reduced ( $P < 0.01$ ) in monogamous territories over that in bachelor territories, but at 20 cm both territory types had similar shading properties (Table 10). Vegetation in monogamous and bigamous

territories did not differ appreciably in shading qualities. Because thin sedge blades were less effective at intercepting light than were broad leaves of forbs which were more widely dispersed in trigamous territories, monogamous vegetation permitted significantly more ( $P < 0.01$ ) light to reach the ground and 20 cm levels than did the vegetation in areas utilized by trigamists. Considerable statistical variance, however, obscured the statistical difference between these territories in per cent of open skylight at 10 cm, despite the large measured mean difference (Table 10).

The density of major forbs in monogamous territories was four times greater than forb density in areas owned by bachelors (Table 8). Forb densities in monogamous and bigamous territories were not statistically different, yet both had significantly fewer forbs per unit area ( $P < 0.001$ ) than did trigamous areas. With an increased forb density, forb height declined. Forbs were significantly taller ( $P < 0.05$ ) than those in bigamous territories.

Bigamous Territories. Areas inhabited by bigamists were generally intermediate in quality between monogamous and trigamous territories. Coverages of forbs and sedges were more extensive, but grass coverage declined compared to the coverages of these physiognomic forms in monogamous areas (Table 7). Major forb density in bigamous territories was less than half that in areas utilized by



trigamists ( $P < 0.01$ ) but was not appreciably different ( $0.1 > P > 0.05$ ) from forb density in monogamous holdings. Mean forb height was greater ( $P < 0.01$ ) than in trigamous territories, and also differed significantly from heights of forbs around nest sites (Table 8). There were no significant differences in either total vertical vegetation density or mean litter depth between territories of all classes of paired males ( $P > 0.05$ ). The per cent of open skylight reaching various levels (Table 10) was similar to that in territories utilized by monogamists, but vegetation in areas inhabited by bigamists allowed significantly more light ( $P < 0.01$ ) to these levels than in areas defended by trigamists. In general, the vegetation structure found in bigamous territories was more similar to the habitat occupied by monogamists than to trigamous habitat.

Trigamous Territories. Trigamists inhabited the more central regions of the meadow, where the horizontal heterogeneity imposed by the patchy distribution of the slight ridges and bordering swales of sedge was most prominent. These ridges were much lusher than the drier peripheral elevations held by bachelors. In contrast to these drier ridges, the vegetation on the more central elevations structurally provided good cover by mid June, and in the zones of sedge-bluegrass interspersions along the ridge-lowland interfaces the vegetation was phenologically well-developed and structurally complex

by late May. Bigamist territories were also dispersed within these very favorable areas, yet the significant difference ( $P < 0.01$ ) between trigamous and bigamous territories in shading characteristics at all heights above ground (Table 10) and in the density of major forbs (Table 8) in the two territory types demonstrates that there were major differences between the holdings of these two groups. Major forbs were 2.4 and 15 times denser than in bigamous and bachelor territories, respectively. The considerable discrepancies in per cent coverages of forbs and grasses (Table 7) further illustrates quantitative differences between territories of bigamists and trigamists. Moreover, per cent coverage values suggest that the ridges in trigamist areas possessed greater sedge coverage at the expense of grass distribution than did elevations in other territory classes. In this meadow ridges having only slight relief were liberally covered with sedge growth and dense clumps of rue, apparently in response to the more mesic conditions. Nest values for shade, for the vertical vegetation profile above 30 cm, for per cent coverage values of forbs, sedges and grasses, and for the density of major forbs were most closely approximated by the habitat in trigamous territories.

Clearly, differences in male pairing success were associated with quantitative differences in the habitat physiognomies they defended. Territories of unmated males were deficient in those features most closely related to nest protection and concealment for this

species in this meadow, for they departed significantly ( $P < 0.001$ ) from territories of paired males in values of the more important ecological conditions measured in the immediate vicinity of nests. For certain factors rather large differences existed between territory types. For instance, the average bachelor territory of 1.72 acres contained on the average only 142 stems of major forbs, which, when in combination with other necessary habitat features that were also scarce in bachelor territories, could potentially provide adequate overstory protection for nests. This compares with 467 forb individuals in an average monogamist territory, 900 in a bigamist area and 2095 in an average-sized trigamist territory.

In general, trigamous territories were statistically of better quality than bigamous territories. Habitat differences between bigamous and monogamous areas were not so apparent. Obviously quantity alone is only one of the possible factors of potential importance; the structural features must also be dispersed in the proper configurations and proper combinations to provide the composite conditions favored by hens for nesting. Knowledge of quantity does, however, permit a rough assessment of the likelihood that these special conditions are prominently available within the various territory types. Moreover, many habitat factors other than those analysed here could play a role in influencing the pairing success of male Bobolinks. Only those features which were relatively easy to measure were

considered. However, the significant coefficients of correlation shown between pairing success and certain of the ecological variables analysed illustrates that many of these parameters actually comprise or are tied to the stimuli which females do in fact evaluate (Table 11). As previously suggested, the correlation between pairing levels and major forb height is superfluous, owing to the inverse association between forb density and height.

TABLE 11. CORRELATION COEFFICIENTS ( $r$ ) BETWEEN  
VARIOUS FEATURES OF HABITAT STRUCTURE  
AND MALE PAIRING LEVEL

Habitat Feature	$r^1$
Major forb:	
Mean density	+0.9748
Height	-0.9897
Per cent coverage of:	
Forbs	+0.9766
Sedges	+0.8864
Grasses	-0.9961
Per cent skylight penetration to:	
Ground	-0.9594
10 cm above ground	-0.9035
20 cm above ground	-0.9556
Total vertical density	+0.4571
Number vegetation contacts in:	
First decimeter	+0.3632
Second decimeter	+0.4267
Third decimeter	+0.5339
Fourth decimeter	+0.9561
Litter depth	+0.4304

<sup>1</sup> A coefficient of correlation greater than  $|0.9500|$  is significant ( $0.05 > P > 0.01$ ).

These results decisively support the habitat quality hypothesis and the natural selection model (Figure 1). They suggest that in the riverbottom meadow some males were forced through high density to occupy habitats which lacked suitable conditions for nesting, and that females were responsive to the range in available habitat quality and settled in the superior areas. One advantage accrued the female by a polygynous mating organization, then, is that it grants each individual an opportunity to breed in a favorable location.

#### Effects of Habitat Manipulation on Pairing Success

Quantitative analysis of vegetative structure was not conducted at Faville Prairie and the adjacent fallow field. However, my observations of the Bobolink's response to major alterations in habitat at the prairie as a result of burning routines are pertinent to this discussion of site preferences and habitat utilization, especially with respect to female pairing responses. The prairie segment was completely burned in late April of both 1968 and 1969, but not in 1970. In years of burning the meadow was still blackened when Bobolinks arrived in the vicinity. Resurgence in plant growth became apparent by 10 May but by late May the stature of new growth was still too low and open to provide suitable breeding habitat. However, by mid June vegetation cover, shade and vertical development in the prairie equalled or surpassed that in the unburned fallow strip, which was

characterized by its extreme structural simplicity and monotony. Aside from open clusters of goldenrod, the unburned area possessed few forbs and was covered almost entirely by rather low, matted Kentucky Bluegrass, broken occasionally by small patches of bare ground. Nonetheless, deep litter and early growth of grasses provided moderately good nesting cover.

At the height of plant production in early July the coverage of major forbs in Faville Prairie exceeded even that in the riverbottom meadow, and in combination with smaller forbs and widespread coverage of deep sedge provided exceptional nesting conditions. With no burning in 1970, the quality of the prairie as a breeding habitat was far superior to that of the surrounding fallow land at the time when female Bobolinks appeared in the region. Approximately the same percentage of adults banded in these meadows returned to the area as did adults at the riverbottom site.

On 6 June 1968 when I first visited the Faville region no males were established in the prairie. Twelve males were territorial in the fallow land, and most were paired. By 14 June nine additional males had arrived, and all were settled in the burned prairie, two being paired. In 1969 a similar establishment schedule existed, nine males occupying sites in the unburned region on 1 June. By 7 June three males were territorial in the prairie and by 14 June, 10 were territorial, including two males that had relocated there after being

unsuccessful at pairing in the adjacent field. By 17 June, 12 males were exhibiting territorial behavior in the prairie and the number in the fallow meadow had declined to six. Most males in the prairie were paired. In 1970 I visited the area only twice. On 18 May eight males were established and paired in the prairie (unburned that year) and none were present in the fallow area. By 1 June the prairie population had increased to 12 and the adjacent field held two males. The average date of nest construction of 27 nests located in the unburned area in 1968 and 1969, as extrapolated from the date of hatching, was 28 May; that of 16 nests in the burned prairie was 20 June. No attempts were made to locate nests in 1970, since my tight time schedule did not permit my following nest chronology. In 1969 a female whose nest was predated in the fallow field deserted her mate and renested with a different male in the prairie.

Several conclusions can be drawn from these observations. First, the fact that banded males utilizing sites in the fallow meadow in 1968 and 1969 defended territories in the prairie in 1970 attests to the flexibility in male site preference responses. Here the availability of far superior habitat in Faville Prairie in 1970 outweighed tenaciousness to specific breeding territories of past years. There is little doubt, then, that male Bobolinks are quite responsive to alterations in habitat. Second, following the conspicuous change in the appearance of the two meadows from early May 1969 to 1970, a

striking difference in occupation schedule occurred in the two fields. Whereas in 1968 and 1969 the prairie served as an overflow area for yearling males which arrived in June, in 1970 the fallow area was the overflow. This suggests that territorial behavior of older males relegates the yearlings either to occupancy of the less satisfactory habitats, or to the drifting group of males. It is interesting that the most desirable mid May habitat one year was the least desirable the next. Moreover, in years when the prairie is burned the yearlings likely have their best opportunity for pairing, for by 20-25 June they hold exceptionally fine territories and readily attract late-arriving females or those that lost their first nests. When the prairie is not burned, however, the structure of the vegetation they occupy is not attractive to females relative to that in the prairie.

Third, because in 1969 some males that were unsuccessful at pairing in the fallow plot moved to the prairie in June, it appears that bachelor males evaluate surrounding habitats and change location in mid-season when appropriate. In this area where the two adjacent meadows differed substantially in vegetation I could determine the new settling location, whereas at the riverbottom site some bachelor males disappeared and were not observed again. It is likely that they settled elsewhere after more favorable habitat became available. The process of evaluation might correspond with the "distant flight" phenomenon of bachelor Dickcissels, as described by Zimmerman



(1970). Fourth, the instance of a female breaking pair relations with her first male after predation of her nest and settling in the prairie 100 m away with another male illustrates that females also show flexibility, and attempt to improve their opportunities for producing offspring. There should be a reevaluation of relative territorial qualities whenever renesting is eminent, and this shift attests to this process. At the riverbottom site, where most females nested in habitat superior to that found in the fallow field, none of the renesting females changed mates or territories. This is indicative that the territories in this meadow did not fluctuate in relative qualities through the season as they did in the prairie-fallow field situation.

## CHAPTER 6

DISCUSSION: DIFFERENTIAL BREEDING SUCCESS,  
THE ADAPTIVE COMPLEX, AND BEHAVIORAL  
ASPECTS OF POLYGyny

In the preceding chapter I showed that female Bobolinks distributed themselves unevenly over a spatially heterogeneous habitat, concentrating in the areas providing the most suitable nesting conditions. When the better quality habitat is too limited to accommodate all males within the population, the males in superior habitats become polygynists, and those in less suitable or inferior areas monogamists or bachelors. Regardless of which specific environmental factors or collage of factors influences the development and maintenance of the polygynous system, once this mating form becomes a regular reproductive phenomenon, selective forces should adjust other features of the breeding organization so they reinforce polygyny by diminishing the mean reproductive loss ( $\bar{e}$  in Figure 1B) resulting from secondary pairing. That is, selection should ultimately temper an integrated adaptive complex differing from adaptive patterns found in monogamous species. Here I will discuss the factors which account for the reduced success of secondary birds, and the features of the breeding biology and behavior of the Bobolink which I feel represent adaptations to offset the disadvantages imposed on secondary females. It should be

clear that by the "disadvantage" of being a secondary female in good habitat I mean the relative disadvantage compared to that of being a primary female in similar habitat (again, e in Figure 1B). Obviously, for polygyny to evolve, a secondary status must be advantageous in the sense that the hen's reproductive success on the average will be greater than that which she would experience in the alternate role of primary female in a habitat of poorer quality.

### Differential Breeding Success

Despite the complex of adaptations described later which help reduce the reproductive disadvantages of a secondary status, primary and secondary females still differed significantly in their production of progeny (Table 12). Primary females fledged more young, on the average, than did secondary hens. The tabled values also demonstrate the effects of the two flood years on Bobolink reproductive success. Because this rare flooding phenomenon produced much greater nest mortality than would normally impinge on this population, the fledging values for "all nests" are biased heavily downward. On the other hand, the values for "unflooded nests" are too high, since a percentage of the flooded nests that were eliminated from the calculations would have experienced nest destruction by other factors. Consequently, the norm should lie somewhere between the paired values given in Table 12. Despite the fact that primary nests fledged significantly

TABLE 12. COMPARATIVE BREEDING SUCCESS OF PRIMARY AND SECONDARY FEMALE BOBOLINKS, 1966-70<sup>1</sup>

Feature Compared	Mating Status		Significance Test
	Primary	Secondary	
Number of individuals	58	45	
Mean clutch size <sup>2</sup>	5.33	4.77	t = 2.41 0.02 > P > 0.01
Mean brood reduction/nest <sup>2</sup>	0.3 (range 0-2)	1.1 (range 0-3)	t = 4.57 P < 0.001
Mean number fledged <sup>2</sup>			
All nests	2.64 (58) <sup>3</sup>	1.47 (45)	t = 2.32 0.02 > P > 0.01
Unflooded nests	3.19 (47)	1.97 (33)	t = 2.13 0.05 > P > 0.02
Per cent eggs fledging young <sup>4</sup>			
All nests	52.20 (58)	31.00 (45)	$\chi^2 = 8.21$ 0.01 > P > 0.005
Unflooded nests	59.98 (47)	41.50 (33)	$\chi^2 = 5.69$ 0.025 > P > 0.01
Per cent successful nests <sup>4,5</sup>			
All nests	58.62 (58)	44.44 (45)	$\chi^2 = 3.44$ 0.1 > P > 0.05
Unflooded nests	68.08 (47)	57.57 (33)	$\chi^2 = 1.47$ 0.5 > P > 0.1

<sup>1</sup> Nests included only if all information is accurately known; nests from 1966 included only when female status is known with certainty.

<sup>2</sup>  $\sqrt{x + 1/2}$  transformation used for t-tests, but untransformed means are tabled.

<sup>3</sup> Parentheses refer to the number of nests in each category.

<sup>4</sup> The percentages for secondary nests are compared with those for primary nests, using the primary value as the norm.

<sup>5</sup> Per cent of nests which fledged at least one young.

more young (judging by either measure) and had a greater percentage of eggs produce fledged young than did secondary nests, there was no statistical difference in the per cent of nests which fledged at least one young, especially in unflooded nests. This means that in general secondary nests were less successful because they lost individual eggs or young within broods more frequently than did primary nests. Loss of entire broods in secondary nests, although greater, was statistically the same as in primary nests. Because predators usually took the entire clutch or brood, this suggests that factors other than predation were more effective in killing some but not all eggs or chicks in secondary nests than in primary nests.

From the standpoint of maximizing offspring production it is clearly advantageous to hold a primary status. In contrast to these findings, Haigh (1968:89) showed that as the harem size of male Red-winged Blackbirds increased, the average number of young fledged per female increased. In the redwing all females are of similar status, for the male does not assist any females in caring for nestlings (Haigh, op. cit.; Orians, 1961). Thus, one would not expect a decline in reproductive success of a male's second or third female, and as a consequence the curves in Figure 1B should be superimposed. Haigh's work demonstrated that females in the larger harems were the most successful because these harems nested in territories possessing excellent habitats while smaller harems or individual females nested

in poorer quality areas. Behavioral characteristics of the male red-wing, then, aside from those which prompt him to capably choose and defend a good site and warn of and attack predators, are superfluous to the survival of nestlings. In the Bobolink, as will be clear shortly, male cooperation at the primary nest contributed in great share to the higher breeding success. If male Bobolinks, like redwings, failed to assist their first female the theoretical average success of primary nests would be similar to the mean value for secondary nests. Thus, the polygynous systems of the Bobolink and Red-winged Blackbird are strikingly different.

For polygyny to be selected for in a species, in addition to the advantages gained by females, polygynous males must experience higher mean reproductive success than monogamous males. Comparisons of male breeding success (Table 13) show that trigamous Bobolinks fledged significantly more young than bigamists and monogamists. Large nest to nest variation in the number of young fledged probably accounts for the insignificant difference in the mean number fledged by monogamist and bigamist males. Nonetheless, it is apparent that the exploitation of the most favorable nesting habitats and the allotment of time to behaviors associated with procuring and holding secondary females is selectively favored in Bobolink males, for with each additional female the male on the average makes a greater contribution to succeeding generations. Von Haartman (1951), Williams

(1952) and Haigh (1968) have shown this to be the case in three other polygynous species as well.

TABLE 13. COMPARATIVE BREEDING SUCCESS OF MONOGAMOUS, BIGAMOUS AND TRIGAMOUS MALE BOBOLINKS, 1967-70<sup>1</sup>

Feature Compared	Monogamous	Mating Status		Trigamous
		Bigamous		
Number of individuals	12	24		11
Number of nests	12	48		33
Mean clutch size/male	4.77	10.01		15.28
Mean number fledged/ male <sup>2</sup>	1.79	t=1.70 (0.1>P>0.05)	3.89 t=2.53 (0.02>P>0.01)	7.00
Per cent eggs fledging young	38.71	38.26		45.45
Per cent successful nests	57.14	42.31		48.48

<sup>1</sup> Tabulates all nests, including those flooded.

<sup>2</sup>  $\sqrt{x + \frac{1}{2}}$  transformation used for t-tests, but untransformed means are tabled.

#### Factors Influencing Differential Breeding Success

Even when the range of habitat quality is sufficient to create a wide range of territorial suitability and when male density is sufficient to force some into marginal patches, polygyny will be selected against if females are incapable of rearing healthy young without the full

cooperation of the male. Thus, polygyny should occur only in plant communities where insect abundance is concentrated or where food is rapidly replenished. Marsh and prairie communities possess these characteristics (Verner and Willson, 1966; Orians, 1969). Moreover, females must be capable of a sustained and rapid food delivery tempo to the nest in the absence of male assistance.

Figure 12 illustrates the increase in the pace of feeding deliveries made by the sexes to nestlings as a function of nestling age. Secondary females exhibited a significantly greater ( $P < 0.01$ ) rate of feeding than primary females. No statistical difference existed between the combined feeding tempo of male and primary female and the delivery rate of unaided females. Hence, solitary birds effectively compensated for the lack of male cooperation. Kendeigh (1952) and von Haartman (1954) found that unassisted female House wrens (Troglodytes aedon) and Pied Flycatchers (Muscicapa hypoleuca) were able to compensate, but to a lesser extent, for the work that was not done by the male. In Figure 13 these same data are plotted without respect to the number of nestlings, to more dramatically illustrate the tremendous pace required of adults while feeding young. From about the seventh day until fledging, approximately 28-30 food deliveries were made each hour (450-500 trips per day-light interval). Primary females and their mates divided the feeding responsibilities equally between them (Figure 12), each sex averaging about four



Figure 12. Differences between primary pairs and secondary females in the number of food carries per nestling per hour as related to nestling age in days. Sample sizes are given in Figure 13.

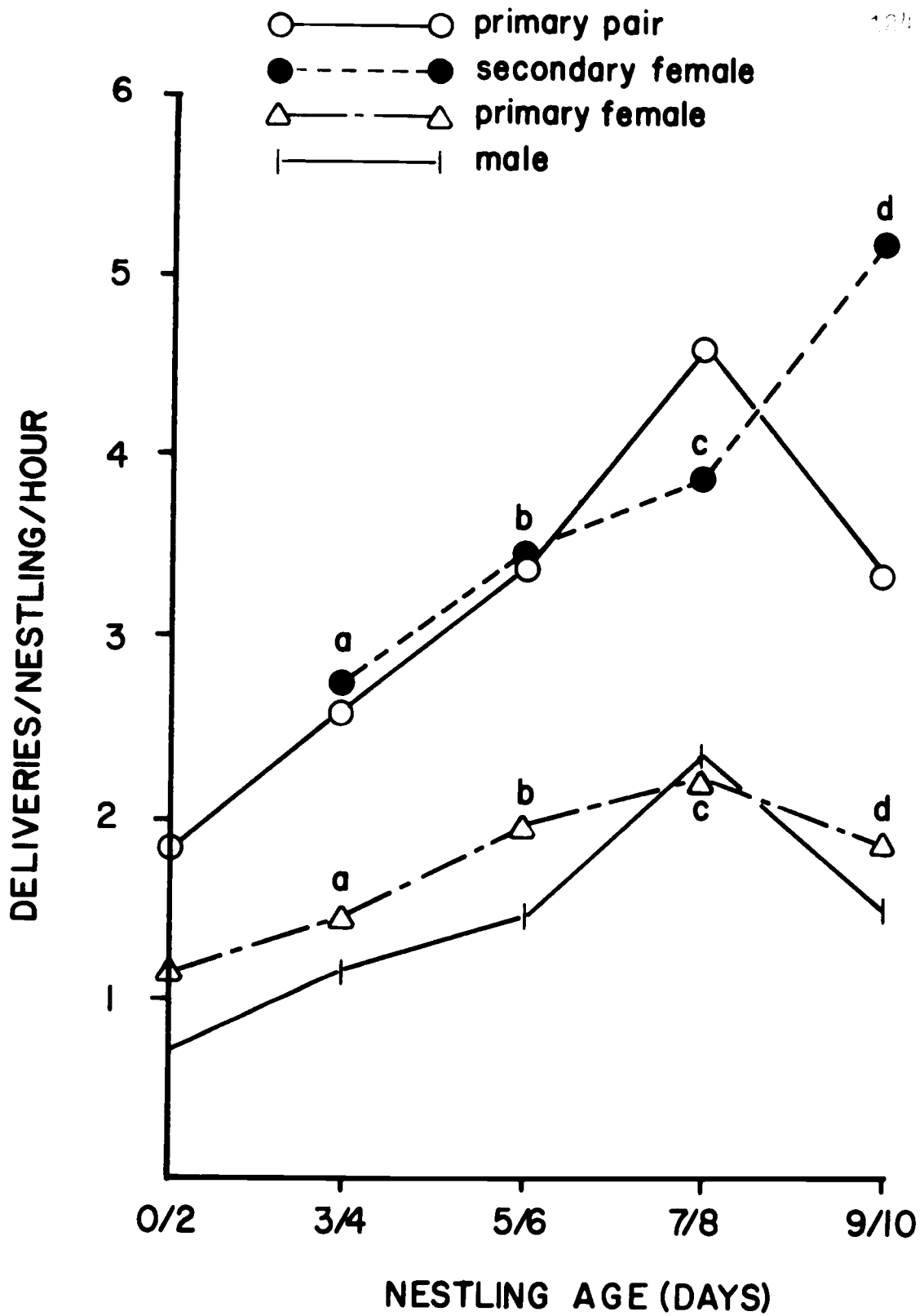
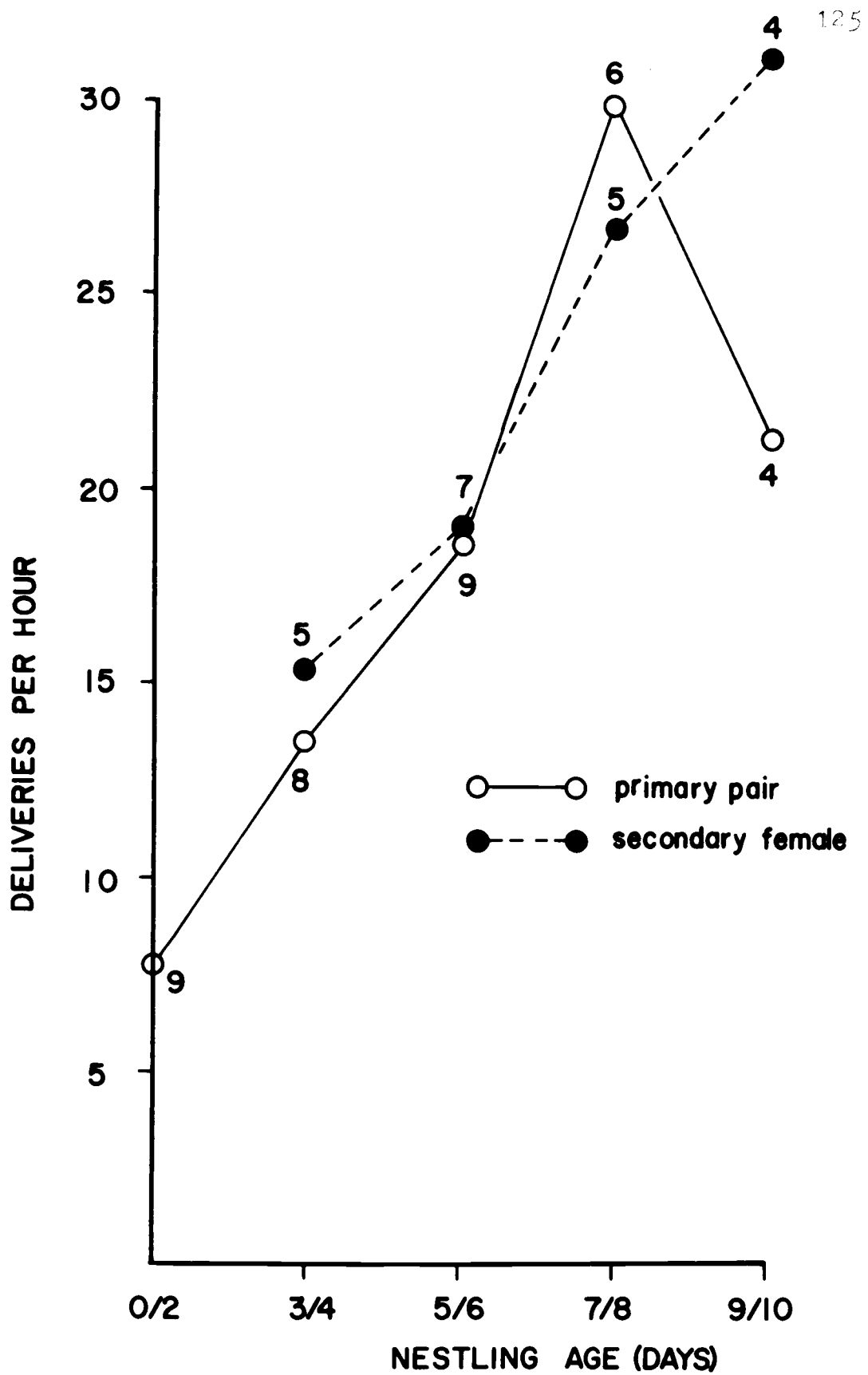


Figure 13. Differences between primary pairs and secondary females in the total number of food carries to the nest per hour. Sample sizes (in hours of observation) are indicated by the number beside each plotted value.



minutes on a round trip foray late in the nestling stage. Secondary females, on the other hand, maintained a steady, unbroken delivery tempo of about one carry every two minutes when nestlings were this old.

The differences between primary and secondary females in allocation of times budgeted to garnering and delivering food pose some interesting questions of the selective advantage of relaxation of the primary female's foraging tempo. What ultimate advantage is accrued to the female and to her progeny by conveying food at a rate well below her capabilities? Presumably a hen's young would be healthier and stronger at fledging, being better able to survive and reproduce (the true measure of her fitness) if they were fed more frequently as nestlings. One possible explanation is that in regions or times of food abundance nestlings fed by both adults are receiving adequate nourishment for maximum vigor and health, and that any increase in food delivery rate will not result in a corresponding increase in survival. In this situation a relaxation of the female's maximum feeding rate undoubtedly allows her to ingest more food herself while simultaneously decreasing the time and energy she devotes to foraging flights. The increased food coupled with decreased energy expenditure may well increase her own likelihood of survival and future reproduction.

The above argument somewhat parallels Lack's (1954:63) explanation of delayed sexual maturation in monogamous birds. That is, if

delayed breeding decreases stress and energy expenditure of inexperienced birds so ultimately a greater cumulative progeny production results than if breeding were to commence in the first year, then selection will favor delayed maturation. Regarding the present question, selection would support a smaller investment of time and energy by a primary female in feeding young if the relaxation on the average increased her chances to ultimately produce more young through a longer breeding span than that cumulative reproductive output produced by more intensive parental care in a shorter life. That is, optimization of feeding rate rather than maximization should be favored. In this sense, where long-term fitness of the female influences the selection for feeding rate optimization, an occasional young might in fact be poorly nourished; brood reduction (see beyond) does occur in primary nests, despite the cooperation of both adults (Table 12). In any event, a primary female's long-term fitness should be greater than the fitness of secondary hens: indirectly her fitness increases because the relaxed tempo possibly extends her breeding life. Directly it increases if the male's help in brooding and feeding young bolsters her mean reproductive success to a level higher than that attained by secondary females. Secondary females, on the other hand, invest more energy for fewer young surviving to the reproductive age (Table 12). As will be shown shortly, chronological advancement in female status is controlled in great part by age. Selection, therefore, should

work to minimize the length of the secondary role, while simultaneously allowing each female the flexibility of taking either status depending upon the relative advantages of each under the ecological alternatives open to them in the territories of receptive males. Adults do in fact lose weight while caring for young. Five males weighed during the period of attention to nestlings averaged 3.6 g (approximately 10 per cent of the pre-nestling stage body weight) less than eight territorial males weighed in late May and early June. Seven females weighed during the nestling feeding period averaged 3.7 g (ca., 13 per cent of the pre-nestling stage body weight) less than five captured during the incubation stage. Fairly large weight variations existed as a result of individual differences as well as the variation in the length of time individuals were feeding young prior to weighing. The data are too few to partition into primary and secondary categories. I suspect, however, that secondary females averaged substantially less than primary females by the time they were feeding fledglings.

A second explanation of the slower food delivery pace of both male and primary female is that it probably permits more selective food gathering tactics, enabling the adults to provide more numerous, more nutritious, more succulent and larger items per carry than unassisted females can find in the briefer foraging interval. Or, additional time could permit farther foraging flights to heavy concentrations of prey. With regard to secondary females, Willson (1966:72) pointed

out that they might

...increase their success by maintaining a steady and rapid flow of food to the offspring, even if little food is brought on each trip. When the young are under-nourished...they might die quickly if left without food for frequent, long periods, so that a female frequently bringing in a few items might rear more young than one delivering the same total amount at longer intervals.

Most adults returning with food for young perched briefly on a forb before dropping to the nest. On some occasions I enumerated food items brought to nestlings, while I watched through a spotting scope. Although these counts are not entirely free from error because small food items could escape my view, they are still useful for comparing the relative insect numbers delivered by secondary females and primary pairs. A mean of 3.0 (range 1-6) items per carry were brought on 36 deliveries by unassisted females to nestlings 8-10 days old. At nests tended by both adults an average of 3.3 (range 1-7) items per carry were brought on 102 deliveries to nestlings of the same age. Males averaged slightly more insects per carry than females. There was a general tendency for the size of delivered insects to increase as chicks became older. Rarely were large items brought to birds 1-3 days old, but deliveries to older nestlings often contained a wide variety of insect sizes. It was, therefore, difficult to gauge the relative insect biomass per carry, despite attempts to categorize items on a subjective size scale. Obviously a quantitative



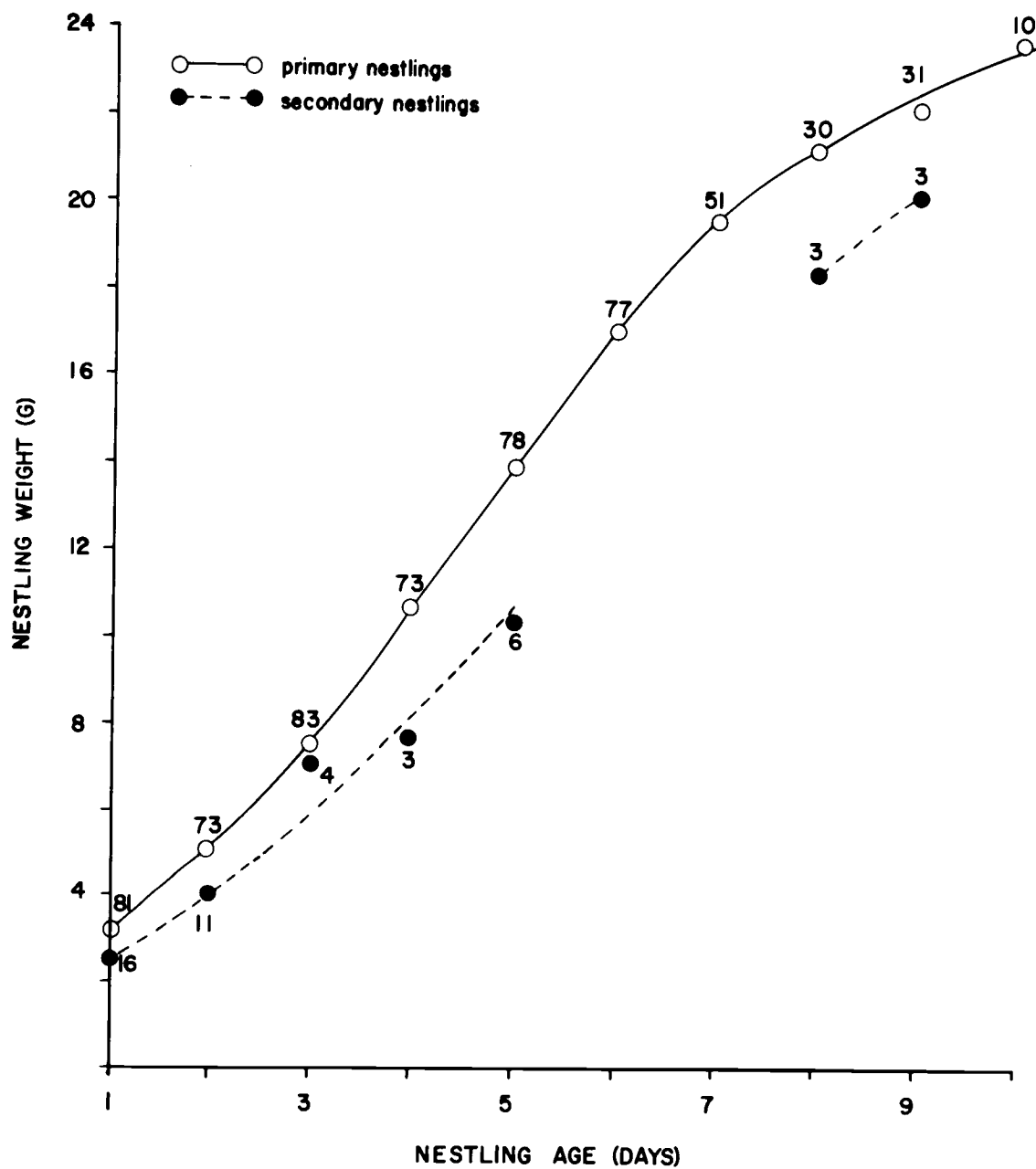
sampling method must be employed to obtain suitable information of this nature. The use of pipe cleaner collars on nestlings (Willson and Orians, 1963; Orians, 1966) was rejected because extended manipulation of nestlings might induce considerable behavioral modifications in adults that were the subjects of time budget studies.

Despite the few observations of carries by unassisted females, these data suggest that the slower delivery pace of each member of a pair indeed allowed them to increase the quantity of food brought to nestlings, by permitting longer searching periods or longer flights to more abundant food sources, and perhaps by permitting a more selective foraging routine. At the average delivery tempo late in the nestling period, secondary females delivered nine fewer insects per hour (ca., 2.25 fewer items per nestling per hour to a brood of four), or approximately 145 fewer per day, than did a pair. The sharp decline in the combined feeding rate of pairs (Figures 12, 13) just prior to when their young fledged might be an artifact of insufficient observations. More likely, however, the decline resulted from satiation of young and a concurrent reduction in begging stimulation. By contrast, secondary females continued to increase their delivery tempo, evidence that their chicks were hungry and demanding food at an increasing rate.

Age-weight relations of nestlings in primary and secondary nests are graphed in Figure 14. As a result of the thunderstorms

Figure 14. Differential growth of primary and secondary young, with sample sizes indicated by the number beside each plotted value. The curve of secondary weights was drawn to emphasize apparent weight divergence. T-test comparisons between weights of primary and secondary nestlings are:

<u>Age in Days</u>	<u>T-Value</u>	<u>Significance Level</u>
1	2.68	$P < 0.01$
2	3.30	$P < 0.01$
3	0.57	$0.9 > P > 0.5$
4	3.51	$P < 0.001$
5	4.95	$P < 0.001$
8	1.75	$0.1 > P > 0.05$
9	1.29	$0.4 > P > 0.2$



and subsequent floods in 1968 and 1969, few secondary nests were active during the time I had access to a balance. Consequently sample sizes are small from these nests. Nonetheless, young from the two nest types differed significantly in weight through at least the fifth day of age. The small sample size probably accounts for the insignificant difference at three days of age, for early in the nestling stage there is a distinct divergence in weights. Adults differ dimorphically in weight, and it is reasonable to expect that the weight separation commences in the nestling stage, as it does in other dimorphic icterids. Thus, by the eighth and ninth days the statistical differences between nest types are probably concealed by the large variability in nestling weights resulting both from this sexual divergence and from individual variations in weight gain within the sexes. Secondary nestlings averaged 28.7, 26.3, 13.6 and 9.1 per cent less in weight than primary nestlings at four, five, eight and nine days of age, respectively.

Young began gaping for food within minutes after hatching. Early in the nestling period individuals of the primary pair frequently exchanged positions, one brooding while the other foraged. Thus as long as nestlings continued to gape they were continuously provided with warmth and food. Secondary females had to budget their attention between brooding and foraging during the first two or three post-hatching days when warmth was crucial. Thus, secondary young

received much less food early in the nestling period, as attested by the weight gain differences (Figure 14). Moreover, there was a greater likelihood of chilling during the parent's foraging trips. By the fourth day secondary females were making more feeding trips per hour than the combined tempo of the primary pair (Figures 12, 13). Observations of food delivery rates were usually made from mid-morning to late afternoon and thus the figures fail to take into account the substantially lower delivery rate to secondary nests in the cool early morning hours, when secondary females had to sacrifice foraging time for brooding. Once the warmer mid-day temperatures emancipated secondary hens from brooding they maintained a steadier and more rapid foraging schedule than primary pairs, in response to the more continuous begging from their hungrier, lighter young. Prior to the development of the fear crouch reaction, young in primary and secondary nests contrasted markedly in the amount of begging when I weighed them. Secondary nestlings usually begged vigorously and continuously through the procedure, whereas only the smallest primary young begged.

Brood reduction, the death of nestlings from causes other than predation or severe weather, was significantly greater ( $P < 0.001$ ) in secondary nests than in primary nests (Table 12). Brood reduction was apparently caused by starvation or susceptibility to disease from malnutrition or chilling. The victims were always the smallest,

last or next-last nestlings to emerge, and deaths usually occurred within three days after hatching. The extent of brood reduction varied from nest to nest of secondary birds, probably as a result of two factors. First, during the study a wide range of temperatures, wind velocities, or precipitation amounts impinged upon different nests in the first few days after hatching; these different climatic regimes might have permitted some hens to break brooding attentiveness for longer or more frequent periods than could other females. Second, female experience was perhaps important. Two females that had nested successfully as primary birds in the meadow returned the following year and were serviced by males that later vanished. Both laid large clutches (six and five egg sets), and fledged complete broods, unaided by males. Thus, under favorable circumstances females are capable of successfully feeding large broods. As will be shown shortly, most secondary females were yearlings<sup>2</sup>, and their lack of experience might have caused sloppy or inefficient exploitation tactics and imprudent time budgeting, thus influencing their ability to raise complete broods. After this reduction of young, secondary hens were better able to provide for the nestlings which remained. This, in addition to the increased foraging time permitted when brooding demands ceased, probably accounted for the marked decrease in the weight differential between primary and secondary chicks late in the nestling stage.

Hence, the chief factor governing the differential reproductive success of primary and secondary females is the decline in the number of secondary young when conditions did not permit females to adequately and simultaneously nourish and brood all their young. The male thus made a substantial contribution to the welfare of the primary young. The price of polygyny for secondary females, however, resulted from the inattention of the male to their nest.

#### Minimization of Secondary Reproductive Failure

Four unassisted females fledged complete broods of five and another fledged six young. Hence, secondary hens were capable of fledging as many young as primary pairs when conditions were favorable. Nonetheless, many secondary females failed to provide the same biomass to their nestlings as primary nestlings received and as a consequence, weights of their young were lower and the starvation rate was higher. A collage of several adjustments of Bobolink breeding biology (here termed the adaptive complex) may circumvent even heavier losses of secondary young, while still permitting a relatively high reproductive output under favorable circumstances.

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<sup>2</sup> A yearling is a one-year old, a bird in its second spring. During the breeding season a two-year old is in its third spring.

### Clutch Size Differences

Lack (1947, 1948, 1954) hypothesized that a species' clutch size is adjusted to maximize production of young in relation to food availability. Obviously primary and secondary nestlings usually experienced different feeding conditions. Hence, according to Lack's view, a reduction in clutch size in secondary nests should insure higher success if a female produced more young on the average from a well-fed, smaller brood than from a larger undernourished brood. The average clutch size should, however, be large enough to take advantage of occasional exceptionally good conditions for production. Indeed, secondary clutches averaged 0.56 eggs less than primary clutches in the riverbottom meadow ( $0.02 > P > 0.01$ ; Table 12). A comparison of clutch size between intrafamilial polygynous and monogamous species (von Haartman, 1955), on the other hand, showed no correlations between clutch size and the degree of assistance given by the male.

However, the influence on egg numbers of the contrasting ecologies and life histories of the species compared were generally overlooked.

A combination of three factors probably accounted for the smaller size of Bobolink secondary clutches. First, older females produced larger egg sets. The sequence of female migration was such that the earliest arriving banded hens, and thus those that became primary females, were at least two years old. Eight females that nested as



primary mates (and thus were older than yearlings) in their year of banding returned among the earliest females the following year (average date 16 May), and one of these returned early for two consecutive years. The 17 clutches they laid averaged 5.41 eggs (range 5-7). Two of these birds increased their clutch by one egg in their second year as a primary mate. With one exception, which is discussed shortly, none decreased their clutch size. In the Faville Prairie region seven adult females (a mixture of primary and secondary birds in their year of banding) returned to nest the year following banding. All were among the vanguard of arriving females and established primary pairbonds. One that had been a secondary female in 1968 with a clutch of four was a primary female in the succeeding two years, when she laid clutches of six and seven eggs. Another increased her clutch size by one. Three females that hatched in the riverbottom meadow returned as yearlings. Their average arrival date was 4 June, they paired in secondary relationships, and their clutch size averaged 3.67 (range 3-4). One of these returned before 18 May 1970 as a two year old and laid a clutch of six in a primary role. This was the only secondary female at the riverbottom field to return in following years. Another female that hatched in the meadow returned as a two year old and as a four year old. In her first appearance she arrived early and was a primary female with five eggs. Two years later she arrived on 9 June with a vascularized incubation patch,

indicative that her first nest was destroyed elsewhere. She again laid a set of five eggs. Clearly, then, older females tended to lay larger clutches. Moreover, the delayed migration of younger females in great part determined their breeding status, for they arrived too late to be the first mate of a male defending good habitat.

Second, the brood patches on at least 20 per cent of the arriving secondary hens revealed that they had first attempted to nest at a different location. Most of these arrived concurrently with early mowing of other fields, starting about 10 June. The six females nesting in the research meadow that renested there after nest destruction all laid new clutches which were 1-2 eggs smaller than that of their first nest. Accordingly, clutch sizes of the renesting birds that had originated from other meadows were probably also reduced, thus contributing to the smaller average egg numbers of secondary nests.

Finally, it is possible that physiological adjustments are made so that manufacture of eggs corresponds with the optimum for the pairing status which the female assumes. Behavioral cues from the male and the primary female might trigger these physiological responses. Unlike the overt animosity shown toward one another by female Red-winged and Yellow-headed Blackbirds (Nero, 1956b, 1964; Orians and Christman, 1968), Bobolink females were relatively tolerant of one another. Nevertheless, primary females occasionally directed bill-flipping and song-spread displays (Martin, 1967:75, 81)

toward secondary females, and also followed the sexual pursuits of their mate and the secondary female. The individual that nested in the meadow for at least three years laid clutches of seven, six and seven eggs. The first and last year she was a primary female. In her second year she arrived early, paired with a returning male and was in final stages of the precopulatory sequence when her mate suddenly disappeared. The following morning I observed three males copulate with her. She constructed her nest in a small but excellent undefended section of the meadow and laid the clutch of six, successfully fledging the full brood without male support. It might be coincidental that hers was the only clutch size of a returning female to decline. It was certainly adaptive under the circumstances.

#### Asynchronous Hatching

At first appearance the high incidence of brood reduction in secondary nests seems disadvantageous in that it reduced the number of young that might eventually fledge. However, brood reduction was in fact adaptive, for it operated to efficiently cull the smallest chicks in nests where food deliveries were insufficient (cf., Ricklefs, 1965). Under these circumstances the smallest one or two young are at an extreme disadvantage, unable to compete for food with the larger, stronger, more vociferous siblings. Consequently the excess is rapidly trimmed before a share of food is wasted on them. The

alternate strategy for dealing with unpredicted poor feeding conditions, an even further decrease in the mean secondary clutch size, could not take advantage of years where an exceptional food supply would allow all young to be well-nourished, or where favorable weather would permit extended foraging by secondary females in the first few days after hatching. Here the largest siblings would become satiated and inactive, allowing ample opportunity for the smaller birds to obtain food.

Incubation in the Bobolink commenced after deposition of the penultimate egg. This schedule resulted in asynchronous hatching, the last young emerging a full day later than the others. Even in primary nests this young occasionally died from inability to compete with the larger nestlings. In secondary nests, especially, asynchronous hatching provided the means whereby the brood size could be adjusted to the food-providing capabilities of the unassisted female. Under favorable conditions no adjustment was necessary and the late-hatching young survived. Assuming that all eggs hatched, the average number of young in primary nests after brood reduction was 5.03, while that in secondary nests was 3.67.

There is much evidence that asynchronous hatching and/or brood reduction are common in a number of polygynous species (Haigh, 1968:18, 31, for Red-winged Blackbirds; Orians, 1961:300, for Tricolored Blackbirds; Willson, 1966:60, for Yellow-headed Blackbirds; Verner, 1965c, for Long-billed Marsh Wrens), yet the significance

and adaptiveness of these features to polygynous birds where some nestlings do not derive food from both adults has been generally neglected. A comparative examination of other species practicing polygyny would indeed be profitable, and might prove that hatching asynchronism and frequent brood reduction are the rule. Needless to say, the same strategy is also adaptive to primary pairs, for starvation of the runt under unfavorable circumstances will better guarantee survival of the others. A number of authors (Gibb, 1950; Lack, 1954; Kessel, 1957; Ricklefs, 1965) have speculated or reported data on the differential survival between large and small young under varying food availabilities in a number of monogamous species as well.

The interrelation of lower clutch size and asynchronous hatching may thus permit a flexible success program for secondary nests, which is sensitive to the varying environment. Under suitable conditions brood reduction would not occur and unassisted females would raise an entire brood. When food was insufficient to provide for a full brood, the late-hatching young would be quickly, efficiently removed. In the latter case, however, an additional egg (i. e., a higher clutch size) would require the culling of two young. One of these would hatch synchronously with the survivors and would utilize a portion of food that was better spent on the survivors, thus weakening all young. Consequently, brood reduction is an important backup to a lowered clutch size, yet works optimally only when the clutch size of secondary

nests is finely attuned to the long-term average secondary food supply. Hence, these two features of the Bobolink's reproductive biology in combination with the behavioral flexibility of male feeding (see below), form an effective adaptive complex which diminishes reproductive loss associated with secondary roles.

#### Flexibility of Male Feeding Attention

As we have seen, polygyny placed constraints on a male's time budget, so that it could not share in the pre-hatching duties at any nest (see Snow, 1963). Once primary young hatched, however, it would be to the male's advantage to aid in the care of the young, increasing the probability that at least some progeny would result from its courtship and mating efforts. Even during the incubation period males paid casual attention to the contents of their primary nest by occasionally visiting the nest site briefly. If not engaged in courtship or copulation with a new secondary hen, some males displayed anticipatory food-bringing behavior (Nolan, 1958) at the primary nest in the day or two before hatching. Once feeding commenced at the primary nest males began infrequent visits to their secondary nests also, apparently inspecting the contents. On two occasions each, when secondary nests hatched unusually large broods of six and five, the associated male unevenly divided its time between the primary and secondary young, still concentrating on the care of the much

larger nestlings or fledglings from the primary nest. However, assistance at these second nests was never begun until the young were at least four days old, and by that time brood size had been reduced in three of these four nests. Nonetheless, the added help undoubtedly contributed to healthier, stronger fledglings. Perhaps the more intensive begging of the large undernourished brood stimulated male care.

The flexibility and adaptiveness of male feeding behavior was demonstrated clearly when I added six three-day old young from flooded nests to four three-day young in a secondary nest. This nest previously had been ignored by male 69-26, who was engaged at feeding seven eight-day young in its primary nest. Within two hours it began carrying small items to the secondary nest while still directing a major share of its attention toward the primary nestlings. Three chicks died in the overloaded nest, but the female, with the male's assistance, fledged the remaining seven. The full primary complement also fledged. Except late in the season (see below) males never fed at secondary nests having broods of less than five. It is particularly significant that the two broods of six cited above were the only secondary broods of more than five (except for the one belonging to a female that had no mate) which I discovered. Hence, males were alert to situations where secondary females were heavily overworked, and their latitude in feeding at secondary nests circumvented heavier losses.

The foregoing raises the question of why males do not always provide similar light assistance at secondary nests, if by so doing more secondary young are fledged. I can only speculate on the reason or reasons. If by apportioning feeding care to young from two nests the male loses primary fledglings that would have lived with additional food, and if this loss is not equaled or exceeded by an increase in secondary young which live to reproduce as a result of male attendance, the behavior would be selected against. That is, under the ordinary situations of low secondary brood size (a consequence of the smaller clutch and the typical brood reduction under conditions of secondary female stress) the female parent is usually capable of fledging the adjusted brood unassisted. Then it is more advantageous for the male to feed the larger primary brood which has already lived through many dangers the younger birds still face, and therefore has a greater chance of surviving. With exceptionally large secondary broods, however, male help might make the difference between complete failure or partial success if the male can afford to reduce its feeding rate to the primary young under the existing food supply. Under these circumstances it would be adaptive for the primary female to increase her feeding tempo, but I have no data on this.

It follows from this argument that late in the season after primary fledglings became less dependent upon adult feeding, males could increase their total production by feeding nestlings in their last



nest. They in fact did. Generally males with active nests did remain at the meadow tending these chicks after the post-fledging flock had departed. The time schedule of a trigamist's courtship and copulation with three females delayed the third nest by an interval which minimized the overlap in the dependent periods of the offspring. Thus, the third female usually had the advantage of male assistance that the second lacked. Verner (1963, 1965c) showed that the two nests of males in a population of Long-billed Marsh Wrens inhabiting a region where food shortage forced full male cooperation at all nests were timed so the fledglings from the first nest were strong and well-nourished before male assistance was required at the second nest. Here, however, subtle behavioral and physiological mechanisms were intimated in adjusting the nest chronologies. The only instance where a male Bobolink shared in incubation duties also occurred so late in the breeding season that this monogamist (67-10) had only a remote possibility of attracting an additional mate. The time it shunted from advertisement into incubation possibly decreased the incubation period, although I was unable to determine the incubation period for this nest.

These flexibilities in feeding tendencies of males, then, certainly contribute to the adaptive complex of behaviors and features of Bobolink breeding biology which have been adjusted through natural selection to maximize production of young.

### The Relation of Male Age and Behavior to Mating Status

In general, older males obtained the better territories in the riverbottom meadow (Figures 7, 8, 9) and in the Faville Prairie region. Only one yearling, 67-1, established a territory immediately upon its arrival in late May. The quality of its territory was poor, except for two small regions (where its nests were located) which bordered the territories of 67-6 and 67-5, and I feel the male was lucky to have paired bigamously. Still, it illustrates that yearlings are sexually mature. The following year this male relocated in one of the better areas of the meadow and held territories in that general region in succeeding years (Figure 8, 9), always pairing polygynously. Two of the birds which hatched in 1967 (males 27, 28), the only year-class prior to 1970 which contained large numbers of fledglings, established territories in 1968 after being drifters in early June. Both settled in marginal regions. Four other banded yearlings remained drifters throughout 1968. In 1969 male 27 again settled late, and paired in an excellent territory vacated by a male tending young. Three others from the 1967 cohort (all 1968 drifters) were territorial in 1969; male 69-36 took a good territory and paired in a vacated area. The other two settled earlier as bachelors in poorer regions. In 1969 male 28 (a 1968 bachelor) didn't appear until after the storms. Apparently, it had taken up successful residence elsewhere but its nest

was destroyed. Only two of the 1967 cohort were observed in 1970, although more may have been present before or after my presence. Male 37 established a territory in the meadow south of the riverbottom field and was a bigamist. The other returnee was a drifter that was not identified because of band loss. A 1969 immature was a drifter in 1970.

The above chronology of territorial establishment by the male 1967 age-class is rather undefined, partly because the floods of 1968 and 1969 probably prevented some from pairing successfully late in the breeding season. This poor success might have influenced the propensity for searching out alternative breeding sites. The chronology does establish that most yearlings were drifters and that some established territories late that season. The 1969 hatchling that drifted in 1970 supports the conclusion that most yearlings belonged to the drifter class. All two-year olds established territories and, assuming that 69-28 paired in a different meadow (which its early July appearance suggests), 60 per cent were successful at pairing; with favorable weather more might have paired. The paucity of 1970 returns prevents further speculation. The fact that two bachelors (69-37 and 68-28) left the meadow and paired successfully elsewhere the following year attests that these males were searching for potentially good alternate breeding locations. Observations of similar relocations at Faville Prairie were previously mentioned. As discussed earlier,

the behavior and arrival agendum of the drifter group suggested a similar strategy. Hence, the scarcity of 1967 age-class males in 1970 may be attributable to their finding alternate sites.

Most likely, then, males are drifters or bachelors as yearlings, become territorial and pair as two-year olds and later improve their mating status by relocating in better areas when vacancies permit. The movement of male 1 from its rather poor 1967 territory to its location in following years is an example. In 1969 male 22 relocated in perhaps the best nesting habitat in the meadow, but flooding conditions probably prevented its becoming trigamous. Male 69-41 also improved its position in 1970. Once settled in a good area males continued to return to the same general location (note males 1, 2, 8, 26). The history of male 26 (Figure 7) demonstrates that a drifter pairing late in the season (1968), successfully fledging young, can become a regular breeder. In 1969 and 1970 it returned early and was a bigamist.

If male breeding is usually postponed until the third spring, male longevity must be reasonably long. Males 2, 3, 6, 8 and 13 were all banded in early May, 1967; this suggests they were at least two-year olds when banded. All were observed at the meadow in 1970, in addition to male 1, hatched in 1966. Others banded as adults in 1967 may have bred elsewhere in 1970.

Each year unbanded males established early in the season.

Their early arrival coincided with that of previous residents which were at least 2-3 years old. Hence, these males were either birds that had lost former breeding meadows to land alterations or males that as drifters in past years arrived early enough to establish territories in areas where former residents failed to return. Their status, however, remained uncertain until all past residents had returned, as evidenced by an extremely interesting series of events occurring in May 1969. In that year males 1, 8 and 2 arrived on 3, 5 and 6 May, respectively, but all disappeared within a few hours. Perhaps the fact that each had lost its nest to flooding in the previous year, coupled with their overt distress at my daily weighing their young in 1968, caused them to desert the meadow after observing me back in my customary position atop an observation tower. In their absence their former territorial areas were settled by two of these unbanded males and by male 26. All successfully paired, and male 26's hen was serviced. She nested in an area held in past years by male 8. The three former residents suddenly reappeared on 22 May and quickly displaced or drove away the two new males. When male 26 restricted its territorial holdings its nesting female was left in the newly-established territory of male 8. These observations demonstrate that the intensity of behavioral characteristics associated with gaining and holding a territory vary from individual to individual depending at least partially upon experience with the area. Moreover, they raise

interesting questions as to how former residents could so easily evict well-established and paired males, whereas birds with no previous experience in the meadow that attempted to replace defending males had no chance of success. The mechanisms are unknown.

The cumulative records of male appearances and statuses illustrate that the behaviors and strategies of most males led to the eventual establishment in a territory of good quality and then continued yearly breeding in that area. However, occasional striking variations from this adaptive norm occurred for which I have no explanation.

(1) Male 67-3 was a trigamist and successfully fledged young. It returned in 1968, paired and progressed through precopulatory sequences (Martin, 1967:105-107), and vanished. I assumed that it had been killed. However, in June of 1970 it reappeared for a number of days, displaying behavior characteristic of drifting males.

(2) Both nests of 67-6, a bigamist, were predated in the nestling stage, its females left, and it attempted unsuccessfully to feed young at two other primary nests, being repelled by the attending males. Eventually 67-8 permitted it to feed at a nest and thereafter both males and the female fed the nestlings and fledglings. The individual adaptiveness of aiding the survival of unrelated young eludes me. In 1968 male 6 reappeared in early May, establishing a territory in the location of its 1967 holdings. By the next morning, however, it had

vacated this good habitat and settled in a region of low, dry and sparse vegetation abutting with the territory of 68-8, fairly close to the nest where both males had fed in 1967. Apparently the experience of the 1967 "success" in this vicinity overrode its earlier choice of appropriate habitat. After approximately 15 days with no success at pairing it disappeared. Male 6 did not appear at the meadow in 1969 but in 1970 it defended a territory fairly close to that of the original 1967 location. It paired and mated, had no success in attracting a second female, and then disappeared!

(3) Another male, unbanded, serviced a female in 1967 and later disappeared.

(4) Male 67-12 vanished after a copulation sequence. Male 67-8 took the undefended area and later tended young of the deserted female. Once its own female's young hatched it began feeding only these. A few days later male 6 began assisting at this nest. Let me emphasize that in all these instances identification of individuals was certain.

(5) Finally, male 67-13 was banded at the field too early in May to have been a yearling. It disappeared after a few hours and was not seen again that year. I assumed that it bred elsewhere. In both 1969 and 1970 this male frequently harassed territorial males through much of late May and early June, yet made no attempt to settle in undefended sites.

The foregoing examples illustrate the occurrence of rather curious divergences from the normal male strategy of attempting to settle and remain in a good location. Generalizations and models dealing with the organization or structure of highly adapted biological systems, especially those describing the operation of systems within the behaviorally complex birds and mammals, are beset with peculiarities and abnormalities which inevitably are disclosed by careful study. The behavioral quirks associated with the experiences of feeding foster young or with the attachment to male 8 by male 6, for instance, overrode the built-in selective habitat response processes which were initially manifested upon male 6's return to the meadow in 1968. The other examples demonstrate equally-imprudent strategies which reduced the fitness of these individuals. Nonetheless, male 3 fledged young in 1967 prior to its unusual behavior; male 8, who fed at the nest of a female serviced by male 67-12 (whose young later fledged) successfully fledged young in 1967, 1968 and 1970; the deserted female of male 70-6 also fledged his young. Consequently, if genetic bases exist for these deviant behaviors they were probably retained in the gene pool.

#### A Reexamination of the Drifting Class

Selander (1965:132-137) developed an argument for the advantages of delayed male maturation and for the resultant skewed sex



ratio favoring females in some non-monogamous species. Briefly, if suitable breeding habitat is unavailable to all males, there should be exceedingly keen inter-male competition for the choicest areas. As a result, a selective premium should be placed on the development of secondary sexual characters functioning in the competition for prime habitat and females. Thus, polygynous species should show strong sexual size and color dimorphism (Selander, 1958). Increased male size permits intensified physical competition while color dimorphism promotes instant sexual recognition, thereby minimizing excessive antagonism by males toward females. However, an increase in the male's conspicuousness and the departure of male size from the optimum size for ecological efficiency exhibited by females (Amadon, 1959; Selander, 1966; Orians, 1969), increases the vulnerability to predation and foraging inefficiency of males. Selander (1958, 1965) in fact demonstrated that the prominently larger adult male Great-tailed Grackle (Quiscalus mexicanus) suffered greater mortality than females, thus heavily skewing the tertiary sex ratio away from the nestling ratio (Selander, 1960, 1961). The sex ratio deviation from unity is accentuated in most icterids because first-year males are non-breeders while yearling females breed (Nero, 1956a; Orians, 1961; Selander and Hauser, 1965; Willson, 1966). Deferred maturity results if the intensified territoriality characteristic of polygynous species diminishes the probability that yearling males can obtain a

satisfactory territory and mate when in competition with older, experienced males; delayed maturation would be favored if postponement of breeding ultimately permitted greater reproductive output by decreasing the stress of useless competitive interactions and by granting the opportunity to appraise the value of other localities as potential breeding sites.

In contrast to most other sexually dimorphic icterids where yearling males fail to achieve full adult plumage (Selander and Giller, 1960; Orians, 1961) and apparently have retarded gonadal development (Selander and Hauser, 1965), Bobolink yearlings attained the same morphological development as older males. Further, the early pairing of male 67-1 attests that at least some yearlings were reproductively capable early in the breeding season. Nonetheless, in competition with experienced males, yearling Bobolinks clearly had reduced opportunities for establishing a territory and for mating, and they did not effectively participate in breeding. In general, then, yearlings which establish territories early after their arrival are relegated to poor habitat, and the time and energy expenditures involved in maintaining a territory and in futile advertisement might be better used in becoming acquainted with and evaluating surrounding meadows for future breeding potential. Thus, a drifting existence should be advantageous. At the same time, if a satisfactory site becomes vacant under special circumstances of death or disappearance

of an older male, the yearling Bobolink possesses the fully developed sign-stimuli necessary to attract a female, and the sexual maturation to service her. Hence, drifters should opportunistically exploit good openings, and their wandering schedule interspersed with short evaluatory stops at different meadows permits such a strategy. In this connection, Figure 7 illustrates that each year some bachelors, after an interval of no success at pairing, became drifters. In the Faville area some bachelors relocated later in the season. Bachelors were restless even while holding a territory, for they occasionally left the field for up to a day. Paired males were never absent from territories.

Zimmerman (1970) described similar brief vacation of territories by bachelor Dickcissels, and felt these birds were searching for more suitable habitat.

The very fact that Bobolink yearling drifters harassed only those males inhabiting the best quality sites is evidence that they recognized differences in habitat grade. The interactions with territorial males probably kept the drifters physiologically primed to opportunistically meet the challenge of a good vacancy. In mid June when older males were busy with the care of chicks, drifter males settled in the best of these opened habitats. Postponing territorial establishment until late in the season, then, permitted their appraisal of all breeding locales and the opportunistic settling in excellent habitat. Moreover, once established in an appropriate meadow their chances for gaining a

territory there in subsequent years were good. This establishment period coincided with the appearance of females that had experienced nest loss elsewhere. Consequently, the drifters provided a nucleus to inseminate these females. The energy apportionment of these males to territoriality and sexual advertisement, then, was delayed until chances for success were the greatest. The weather of June 1968 and 1969 prohibited the full development of late season occupation and pairing. It is likely that among the four drifters of the 1967 cohort which did not establish late 1968 territories in the riverbottom meadow, some might have settled in other fields.

The tendency of drifting yearlings to ignore suitable habitat in meadows unoccupied by the species suggests that choice of a specific territory is a two-staged process, governed at the first level by social behavioral stimuli which guide the selection of the field, and next by specific habitat cues which guide the choice of specific sections within the field. The efficacy of social behavior in influencing the distributional pattern of breeding congregations within the entire breeding range and in developing local populations of a species has been generally ignored. In each of three meadows (30, 40 and 70 km from one another) where I studied Bobolink behavior, all territorial males possessed well-developed song dialects, distinct from the dialects at the other locations. At the riverbottom site I occasionally heard floating males singing an improper pattern. These were never

successful at establishing there. This implies that specific behavioral mannerisms impose limitations on distribution of individuals. In the Bobolink there must be strong selective pressures to establish territories in locations where other birds are settled. The nature of these pressures is problematical. On both legs of the long migration the Bobolink is extremely gregarious, as are other polygynous icterids. In the wintering grounds the species roosts, moves, and forages in enormous flocks. Thus, the tendency of individuals to settle adjacent to others during the breeding season is not surprising. The heightened stimulation of the intense heterosexual chases (Martin, 1967) so conspicuous in breeding groups would be diminished in sites having only one or two males. Such social stimulation is probably important in coordinating reproductive readiness of primary pairs, which permits males to terminate courtship and coition with their first females and to attract secondary mates rapidly.

Shifting agricultural land use patterns during the past century should tend to facilitate selection favoring young birds which eventually settle in traditional breeding meadows. Whereas in the past the eastern grassland communities afforded relatively predictable, stable conditions throughout the breeding season, now modern crop rotation, early silage haying, grazing intensity changes, and burning schedules have disrupted the stability or predictability of many fields. Of species using the eastern grasslands for breeding, the Bobolink is the

latest nester, and is consequently the most subject to the ramifications of earlier mowing practices. In general, meadows which have a high breeding density of Bobolinks are utilized annually for nesting. Hence, these fields obviously provide extended conditions which permit completion of the full nesting cycle. Many other plots possessing habitat which appears appropriate in May might be mowed prior to fledging. Birds that delay and finally settle in fields inhabited by other individuals, then, might on the average experience a higher life time reproductive success than those choosing unoccupied fields where a greater chance exists that energy spent in advertisement and mating is wasted when the nest is subsequently plowed or mowed. For yearlings the most advantageous strategy would be to drift until a vacancy permitted establishment in a traditional breeding meadow; thereafter relocation in prime stable habitat coupled with male longevity would best assure high long-term fitness.

Clearly, the actual factors or factor interactions selecting for cohesion of drifters to traditional nesting locations are unknown; despite the speculative nature of the above arguments, the social organization and social behavior of the species seem to be very important in influencing the ultimate establishment patterns of young birds.

### Effects of Polygyny on Time Apportionment

Polygyny has importantly influenced the time males devote to song and territorial defense. Whereas song ends abruptly upon pair formation in most monogamous species, it is advantageous for polygynous males to maintain high song rates and active territorial defense to attract additional mates while simultaneously reducing the possibility of stolen copulations. From 93 hours of summarized time budgets of male Bobolinks (Table 14), a consistent adaptive strategy of time partitioning emerges which differs markedly from that characteristic of monogamous passerine time allotment. Only a few of the recorded activity categories are tabulated here, but the total values for agonistic and intersexual behaviors are the five-minute means of all recorded behaviors falling in each group. Long Song (see Martin, 1967) functioned both in territorial and sexual advertisement, but is included only in the agonistic totals. Song Flight was used chiefly as territorial notice, but also accompanied courtship flight songs associated with the Circle Flight display. Here it is partitioned into the proper total depending upon the context at occurrence, but is also tabled as the combination of all Song Flights regardless of context.

During the pre-pairing period when territories were established, a major share of time was devoted to agonistic or territorial behaviors, with limited expenditure to intersexual activities when a

TABLE 14. MEAN NUMBER OF OCCURRENCES<sup>a</sup> OF SELECTED MALE<sup>b</sup> ACTIVITIES PER FIVE MINUTE INTERVAL, IN DIFFERENT STAGES OF THE REPRODUCTIVE CYCLE (See text for explanation)

Stage <sup>c</sup>	Number of 5-minute intervals	Agonistic Behaviors					Intersexual Behaviors				Total of all intersexual behaviors	Miscellaneous Behaviors			
		Long song	Dis-placement preening	Face off with males	Attacks another species	Total of all agonistic behaviors	Circle flights	Courtship notes	Buzz vocalization	Copulation		Main-tenance activities	Foraging	Total flight	Song flight
Pre-pairing	121	11.87 (0.749)	0.70 (0.353)	2.48 (0.213)	0.32 (0.084)	20.07 (0.088)	0.28 (0.043)	1.48 (0.365)	0.72 (0.091)	0	3.07 (0.020)	1.65 (0.037)	9.71 (0.998)	4.48 (0.081)	2.40 (0.065)
Courtship	260	6.69 (0.461)	0.15 (0.060)	1.21 (0.171)	0.20 (0.033)	13.57 (0.056)	1.64 (0.211)	5.05 (0.632)	1.68 (0.183)	0	12.73 (0.048)	1.59 (0.025)	7.33 (0.518)	6.76 (0.078)	4.37 (0.086)
Copulatory	301	4.54 (0.309)	0.24 (0.095)	0.73 (0.091)	0.13 (0.021)	9.11 (0.036)	0.28 (0.054)	4.66 (0.540)	0.48 (0.050)	0.19 (0.050)	10.91 (0.049)	2.06 (0.024)	10.87 (0.590)	4.85 (0.055)	2.07 (0.040)
Egg-Laying and incubation	272	5.45 (0.447)	0.40 (0.111)	1.37 (0.136)	0.20 (0.046)	11.43 (0.051)	0.45 (0.074)	3.83 (0.554)	0.66 (0.077)	0	6.50 (0.028)	3.57 (0.058)	8.86 (0.588)	5.22 (0.066)	2.44 (0.052)
Nestling	159	0.99 (0.015)	0.06 (0.049)	0.11 (0.051)	0.04 (0.017)	1.52 (0.015)	0 (0.136)	0.41 (0.136)	0.01 (0.004)	0.01 (0.010)	0.59 (0.006)	1.35 (0.030)	18.19 (1.343)	2.98 (0.054)	0.50 (0.022)

<sup>a</sup> For discrete activities (song, notes, attack, copulation, etc.) the number of occurrences per five minutes are averaged; for continuous activities (foraging, flight, preening, etc.) the total number of 10 second metronomic intervals (see page 48) within which the behavior occurred per five minutes are averaged.

<sup>b</sup> Data from males of all mating statuses are combined here.

<sup>c</sup> See Chapter 4 for stage descriptions.

<sup>d</sup> Standard error of mean in parentheses.



female occasionally alighted close to or within a male's territory. A conspicuous shift in time allotment commenced when courtship began; agonistic behaviors declined markedly in frequency as the proportion of sexually associated behaviors increased. Time in flight and Song Flights increased when Circle Flights became prevalent during courtship. In the copulatory stage the pair was usually in close association, often foraging together for extended intervals between bouts of coition. Time devoted to foraging, therefore, was greater while agonistic postures and vocalizations directed toward other males or given as general territorial advertisement declined further. Intersexual behaviors also declined after the courtship Circle Flights and associated Buzz vocalizations ceased. Later in the copulatory stage a resurgence of territoriality and sexual advertisement began, as males resumed vigorous defense of their entire territory. Thus, in the period of egg deposition and incubation, agonistic activities were more frequent and intersexual activities waned. During this stage males continued emitting notes to the primary female and directed sexual behavior toward prospective mates. Chases of drifter males increased the amount of flight. If successful in attracting a secondary female the male immediately reverted to the courtship time allotment. If unsuccessful, the song rates characteristic of the incubation period continued unabated until nestlings hatched, when agonistic and sexual behavior virtually ceased and foraging became the principle

activity. In a few instances males were paired with unserviced hens when nestlings hatched. These individuals continued territorial and sexual behavior during the nestling stage until copulations terminated. These cases account for the tabulated agonistic and intersexual behavior totals in the nestling stage.

## CHAPTER 7

## CONCLUSIONS

The central aim of this investigation was to discover if sufficient ecological differences existed between territories occupied by males of varying mating levels to account for the maintenance of the Bobolink's non-monogamous mating pattern. The results decisively demonstrate that territories defended by bachelor, monogamous and polygynous males (Figures 8, 9) differed enormously (Tables 7-10; Figure 11) in the quantity of almost all structural habitat features which I measured. Of the various factors considered, the distribution and abundance of those providing concealment and protection properties were most strongly correlated with the ability of males to attract females (Table 11). Territories of the various male classes differed significantly in the density and distribution of major forb types, which furnished the only source of dense concealment about nests early in the nesting season. Such forbs were poorly represented in bachelor territories, which were covered by low, sparse vegetation of such an open nature that protective cover was virtually absent. The "quality" of monogamist and bigamist territories, as measured by the abundance and distribution of habitat features characterizing nesting areas (Tables 5, 6), was improved over that of bachelor territories, and areas defended

by trigamists were generally superior to all others. Clearly, bachelors inhabited areas deficient in the major features important in female nest site selection, and their holdings were thus marginal or unsatisfactory for successful breeding.

The existence of the substantial habitat quality differential between territories of paired and unpaired males coupled with the yearly consistency of female responses to this quality gradient, substantiates the argument and model developed by Verner and Willson (1966) and Orians (1969) (Figure 1). Each year in this meadow and in the Faville Prairie region competitive interactions excluded some males from satisfactory breeding habitat and these settled in regions providing little opportunity for successful reproduction. When the resultant disparities in habitat quality were great, females distributed themselves unevenly along the gradient, resulting in polygynous pairing by males occupying good areas. Presumably females making the proper habitat choice could raise more offspring unassisted by the male than could be fledged with the full cooperation of both parents in a poor territory. Consequently, polygyny permitted each female the opportunity to maximize her potential seasonal fitness by choosing the most suitable nesting conditions available from territories of all males in receptive stages of the advertising-courtship cycle. Wiens (pers. comm.) found no evidence of polygynous pairing in Bobolinks inhabiting a dry upland site in southcentral Wisconsin. Here male density was so low that

territory size averaged four times larger than in my meadows. It is likely that no males were forced to occupy habitat which was markedly poorer than that of others, and hence the polygyny threshold was not exceeded at this field.

In different habitats different environmental factors are likely operational in influencing the females' evaluation of the breeding potential of various territories. At the riverbottom meadow forb density and distribution, shading properties of the vegetation and the vertical density of vegetation above 30 cm were highly correlated with female choice, while the depth of accumulated litter seemed of minor importance. At other meadows of contrasting physiognomies, however, deep litter appears to serve as an important substitute for suitable forb configurations.

Morphological and behavioral qualities of males, aside from those characters associated with the males' ability to establish and defend satisfactory territories, were apparently of relatively minor importance compared with the powerful selective influence of habitat quality. Differences in food reserves within different territory types were also of little importance to females in their choice of male and territory, for food for nestlings was generally gathered off the territory. The possibility of higher nestling predation associated with the increased foraging activities of more than two parents within territories (Horn, 1968:685) coupled with fast depletion of territorial food

supply by extra females and nestlings, might have favored the development of the off-territory foraging habits of polygynous species. Nonetheless, for some populations of Bobolinks where food abundance within reach of the nesting meadow is inadequate for secondary females to properly nourish their brood, a polygynous strategy would not be favored despite the existence of large differences in territorial suitability. Hence, the natural selection model of polygyny is realistic only in situations where food is abundant and quickly replenished.

Under the habitat quality hypothesis the conditions necessary for polygyny to be favored by natural selection require that male density be high enough so that some males are forced into marginal overflow areas. My observations that drifting unmated males avoided suitable breeding habitat in fields unoccupied by Bobolinks suggest that the tenants of the contemporary hypothesis must be broadened and generalized. Clearly, behavioral propensities complicate the model, and males are in fact "psychologically excluded" from undefended suitable habitat if the proper social stimuli are not concurrently evident at these meadows. Moreover, these observations cast doubt on the validity of arguments concerning the role of territorial behavior in population regulation (see Brown, 1969a, 1969b).

A corollary to the central objective was to determine if the pattern of resource distribution in space importantly influenced the attractiveness of different areas to females. This involves assessment

of bird responses to habitat heterogeneity, and whether individuals treat their requisites as "fine-grained" or "coarse-grained" resources (see MacArthur and Pianka, 1966; Levins, 1968)--that is, whether individuals utilize a series of patch types for different activities (fine-grained) or whether they specialize in one specific patch type (coarse-grained). The measurement of heterogeneity poses difficult problems; obviously, human perception of patchiness might differ strikingly from that which is meaningful to various bird species. The confinement of heterogeneity to a narrow horizontal belt in grasslands, however, provides exceptional opportunities for its measurement and for observational determination of patch utilization and of the impact of heterogeneity on bird distribution. Although my vegetative measurement procedures permit determination of heterogeneity indices, my time budget has prohibited preparation of these quantitative indices for the different territory types. Nonetheless, differences were visually apparent. Figures 2-5 in fact illustrate that abrupt structural discontinuities were characteristic of the meadow. The Bobolink's selective use of specific "edge" patch types for nest placement (Table 5, Figure 10), the heavily utilization of large forbs for display and advertisement sites, and the concentration of foraging within sedge swales demonstrate that this species was indeed treating the habitat as a fine-grained mixture. Thus, areas favored by females should possess a proper mixture and distribution of patch types which assure good reproductive potential and which are appropriate for all activities.

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The response to the habitat mosaic by the other bird species regularly breeding in the riverbottom meadow was apparently also fine-grained. Obviously each species responds to different physiognomic cues, those of special importance to its niche requirements, and consequently extreme care must be taken in generalizing that the pattern of structural heterogeneity affecting one species is operational in influencing the micro-distribution and habitat utilization of other species. Nonetheless the wide range of features which were structurally patterned in the meadow provided a variety of quality gradients so that territories defended by males of other species might also have differed widely in their suitability for breeding regardless of which habitat features served as sign stimuli. The habitat quality hypothesis predicts this is an ideal situation for polygyny to be prevalent. My casual observations documented that Red-winged Blackbirds and Eastern Meadowlarks were polygynous in this meadow. It is likely that the Short-billed Marsh Wren also engages in polygynous mating (Verner and Willson, 1969) when male density forces some males into marginal habitat, but in this field density was too low to warrant polygyny. The mating system of the other common breeding species, the Savannah Sparrow, remains undetermined. Savannah Sparrow density was generally lower than the Bobolink's and sparrow territories were smaller. It is likely that no Savannah Sparrow males were forced into marginal areas of the meadow during the course of this



study.

The other objectives of this study, the evaluation of breeding success differences between males and between females of different mating statuses, and the demonstration of an integrated complex of adaptive patterns involving behavioral and breeding biology phenomena, were discussed in detail in the preceding chapter, where major conclusions concerning these results were given. Here I wish to comment briefly on the diversity of elements which comprise what I have called the "adaptive complex". One of the most apparent adaptations serving to maximize reproductive output is a pairing system flexibility which assures all females the opportunity to breed in a habitat where conditions provide a reasonable chance for success. Thus, the permissive polygynous system is the foundation of the complex, and the sensitive habitat screening and evaluatory processes of females are its girders, and both must be under constant selective refinement to adjust to environmental changes. The tendency for secondary females to deposit smaller egg sets combined with the evolution of asynchronous hatching, providing the potential for bringing brood size into correspondence with food availability, are of obvious adaptive significance. More subtle aspects, such as optimization of primary feeding rates to permit a relaxation of delivery tempo, and possibly extend breeding longevity, must also be included as important components of the adaptive complex. The ability of secondary females to

compensate for the loss of male assistance by increasing their food delivery pace is yet another adaptation. In general, females attain a primary status in their second breeding season; consequently, the stress of the secondary role is a temporary one. The pacing of behavioral energy expenditures demonstrated by yearling males in their opportunistic drifting and evaluatory phase is probably also adaptive. By postponing energy and time apportionment to advertising until the time when satisfactory habitat becomes available, the probability for successful offspring production is increased, as is the opportunity to settle successfully in following years within an established "stable" breeding locality. Their establishment at a time when females whose nests had been destroyed are in quest of an unoccupied male is especially convenient. Moreover, the flexibility which some males displayed in feeding young at secondary nests which had unusually large broods, and in feeding secondary nestlings late in the season after the primary young were independent, forms a particularly important link of the complex. For the male, any secondary young that fledge and live to reproduce represent the bonus which prime the system and maintain the selective advantage of the males' heightened and extended territorial and advertisement behaviors. The male time budget strategy alone is a very sophisticated adaptive system. The adaptive complex, therefore, involves a number of flexible and interrelated adaptations, which working in concert affect virtually all breeding biology and

behavioral tendencies of the Bobolink.

Finally, I feel the long-term behavioral observations of individual males and females permitted by the intensive color-banding program used in this study have demonstrated conclusively the need for more investigations of this nature. The behavioral complexity of birds and the impact of past experiences on behaviors create striking individual and populational divergences from the generalizations ethologists and ecologists are so prone to making. These generalizations simply are not always supported by careful field studies, and field investigations are prerequisite to the refinement and true utility of generalizations and models.

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