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THE BREEDING BIOLOGY OF AN ISOLATED BOBOLINK POPULATION IN OREGON

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This study was initiated to evaluate the status and management of the isolated population of Bobolinks (*Dolichonyx oryzivorus*) breeding at Malheur National Wildlife Refuge in southeastern Oregon. It was conducted as part of a larger study concerned with habitat selection and the evolution of polygyny in Bobolinks (Wittenberger 1976). My purpose here is to report on the current status and breeding biology of the Malheur population. The results also provide some pertinent evidence for evaluating current mating system theory and suggest a new factor that may affect the timing of breeding events.

The Bobolink population at Malheur Refuge is of special interest because it represents the largest population west of the Great Plains (Hamilton 1962) and is the only remaining population in Oregon. As the entire population is confined to an approximate area of only 865 ha, it is potentially vulnerable to extinction in the absence of proper management. The population is also of interest because it has shown no propensity to expand its range, despite the availability of apparently suitable habitats in other parts of Oregon (Gabrielson and Jewett 1940). Hence, understanding the dynamics of this population may help clarify how geographical ranges of birds are limited.

Bobolinks have only recently colonized the Malheur Lake Basin, as Bendire (1877) failed to find them there during 1874–1877. Habitat suitable for Bobolinks was apparently nonexistent in the basin until 1872, when ranchers first began draining the lowland marshes to convert them into grazing lands (Brimlow 1951). The first specimens were collected there in 1908 (Gabrielson and Jewett 1940), and breeding was first recorded in 1918 (Willet 1919).

Smaller Bobolink populations have also been recorded in Oregon (now extinct; Jewett 1916, Gabrielson and Jewett 1940), northeastern California (now extinct; Dawson 1916, Maillard 1924), and other western states and provinces (A.O.U. Check-list 1957, Hamilton 1962, Bailey and Niedrach 1965, Marshall 1969, Weydemeyer 1973). The origin of these western populations is, however, open to question. Most authors (e.g., Ridgway 1876, Bendire 1895, Chapman 1909, Lincoln 1939, Bent 1958) have assumed that Bobolinks recently invaded the west with the advent of agriculture. Hamilton (1962) disputed this claim and argued instead that these populations represent relicts from an earlier widespread distribution when the Great Basin was covered by grasslands. Although the population at Malheur Refuge stems from a recent colonization, Hamilton's hypothesis may still be valid because the colonizers could have originated from other western populations. Nevertheless, the lack of subspeciation within these populations suggests that they stem from a recent range expansion, unless gene flow between western and eastern populations has remained high for long periods of time.

STUDY AREA

Malheur National Wildlife Refuge is approximately 100 km S of Burns, Oregon and includes most of the Donner and Blitzen River Basin. Surrounding uplands are covered by sagebrush (*Artemisia tridentata*) desert. The entire range of the study population is irrigated (Fig. 1), with water allocation managed according to priorities unrelated to Bobolink ecology. This water originates from snow melt off nearby Steen's Mountain, thus pointing to the role of winter precipitation in determining habitat conditions. Most Bobolink habitat on the refuge is mowed for hay in late summer and grazed by cattle in autumn, winter, and early spring.

My principal study area in 1973 was a 23.4-ha tract of meadows 2 km NW of P-Ranch Patrol Station at the southern end of the refuge. This area was chosen because it contained the highest density of territorial males on the refuge in 1972. It was centered around the major artery of an irrigation system that provided a consistent supply of water through June, even in dry years. In 1974 the western boundary was extended 180 m to the edge of surrounding cattail (*Typha*) marshes, thereby increasing the area to 27.3 ha. The entire 865-ha range of the population was censused every year from 1972 to 1976, and breeding chronology was studied throughout the population in 1975.

Bobolink habitat on the refuge consists of grassy meadows intermixed with sedges (*Carex*) and numerous forbs. Sedges occur as dark green patches, principally in poorly drained depressions and on dry, elevated terrain. Several prominent cow parsnips (*Heracleum lanatum*) grow near main irrigation channels and were frequently used as song perches. Willows (*Salix*) occur along many of the irrigation channels on the refuge, but only small seedlings were present on the principal study area. Bobolinks also used willows and fences surrounding cattle feedlots as song perches.

The most important source of seeds eaten by adult males during May was dandelions (*Taraxacum officinale*). Male Bobolinks spent much time eating

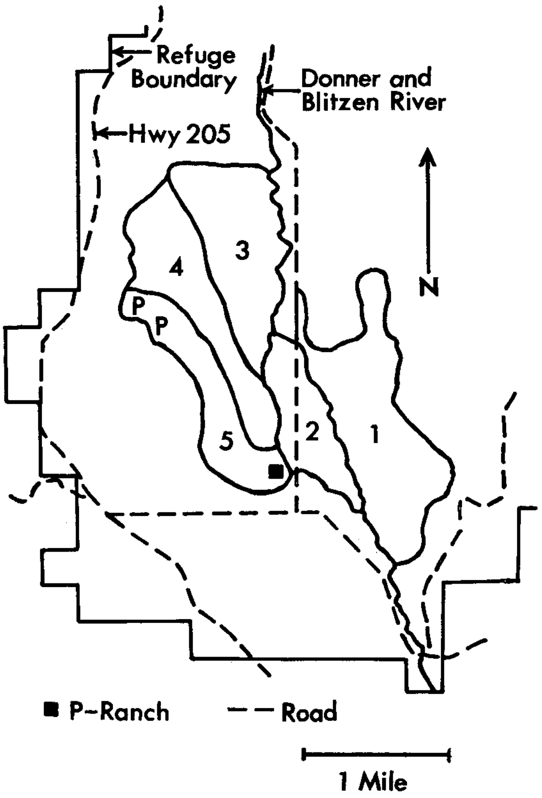

FIGURE 1. The contiguous range of Bobolinks at Malheur National Wildlife Refuge. The numbered enclosed areas are portions of the range subdivided by irrigation watersheds, with 1—Unmonitored-east, 2—Nursery, 3—Buckaroo, 4—Unmonitored-west, and 5—Barnyard. P—location and extent of the principal study area.

dandelion seeds directly from flower heads. I saw them eat cutworms and other insects only infrequently, except in 1975 when dandelions bloomed two weeks later than usual. Beginning in June, I also saw Bobolinks eat seeds of cinquefoil (*Potentilla glomerata*), yarrow (*Achillea millefolium*), Canadian thistle (*Cirsium arvense*), false lupine (*Thermopsis montana*), dock (*Rumex crispus*), and mallow (*Malva moschata*), although seeds of these species did not seem to be a prominent part of their diet. Other forb species not used for seeds included sweet clover (*Melilotus officinalis*), bur clover (*Medicago lupulina*), red clover (*Trifolium pratense*), vetch (*Vicia americana*), groundsel (*Senecio hydrophilus* and *S. hydrophobus*), false Solomon's seal (*Smilacina stellata*), and pepper grass (*Lepidium perfoliatum*). Most of these serve as host plants for caterpillars which were fed to nestlings (Tietz 1972). Scientific nomenclature of plant species follows Hitchcock et al. (1969).

METHODS

Individuals were identified by colored plastic leg bands and by various morphological and behavioral traits. I was able to identify most males by a combination of plumage characters related to the shape of the nape edge, color variation of the nape, scapulars, and rump, conspicuous patches or speckling patterns of buff- or gray-tipped feathers on all parts of the head and body, the number and width of back stripes, and partial albinism. About 20% of the male population also had distinctive songs. I could distinguish individual females by the length of the postocular stripe, the shade of yellow or white on the throat, breast, and belly, and in one case by the presence of ventral spots. Missing primaries and rectrices were useful for short-term identification but proved unreliable because the same feathers were sometimes lost by more than one individual.

Males were captured by placing on their territories a 1.22 × 1.22 m net drop-trap over a cage containing a live decoy male. Females were captured by placing the same drop-trap over their nests during the incubation period. This procedure never caused females to abandon their nests. The method used by Martin (1969) proved more time-consuming and did not reduce disturbance to the birds.

The population was censused by walking transects at 100–200-m intervals across all grassy meadows on the refuge within 3 km of the south boundary. This area contained nearly all Bobolinks on the refuge. A few individuals were seen in other areas by refuge personnel. These probably numbered less than five males each year, some of which were unmated. They were not included in the census results because they could not be reliably counted.

Transect counts were made of territorial males during mid-June in every year except 1974. Accurate censuses were possible because males circle in the air and sing whenever they detect an intruder. Females could not be counted at this time because they were incubating and hence difficult to find, so I waited until after all nests had fledged before censusing females. This may have introduced an error in the census results if some females left the census area before July. However, females probably do not begin to migrate that early following nest failure, since they are just beginning to molt, and few individuals of either sex were sighted on other parts of the refuge before August.

Transect counts of both sexes were conducted during the first 10 days of July in 1973 and 1974, when most individuals have gathered into post-reproductive flocks. Counting birds in large flocks is less accurate because not all individuals can be sighted simultaneously. Recognition of individuals facilitated counts, and all flocks were counted several times until I felt confident of the results. In 1975 the mated status of all males was determined by surveying the entire population every two days. These data allowed me to compute the number of females present that year.

Spring arrival dates were determined from surveys conducted in early May. I visited the principal study area daily beginning on 7 May each year. To do so, I traversed a 2.5-km transect between P-Ranch Patrol Station and the study area four times daily. In 1974 I also covered a 1-km transect between the principal study area and an auxiliary study area 600 m farther north twice each day. In 1975 I surveyed all areas within contiguous range of the population once every two days from 10 May until 18 June. Field work was terminated in mid or late July each year, after all active nests had fledged their young. Bobolinks are single-brooded, so field work spanned their entire nesting season.

I identified pair formation primarily on the basis of long-lasting association of a female with a particular male. Courtship behavior is conspicuous and follows a definite sequence that serves as a useful criterion for identifying mated pairs. Copulatory behavior was used whenever possible to confirm pair bonding. Polygynous matings were verified by simultaneously observing all mates and by locating all nests on each territory.

Most nests were found by watching incubating females returning to them. Females approaching their nests exhibit a distinctive pattern of wariness that distinguishes nest approach from other movements. This method was most efficient at dusk, when females return from their evening foraging bouts, but it was also successful at other times of day. Some nests were found by watching females carrying nesting materials, and a few were found by accidentally flushing incubating females. Because I located nests during incubation, I calculated dates of initial egg deposition by subtracting clutch size plus 11 days from the date of hatching. Mean duration of incubation is 11.8 ±1 days in Bobolinks, with incubation normally beginning on the penultimate egg (Martin 1971). Once found, nests were checked daily at midday to monitor their contents. Nest success data are easily biased when nests are found during incubation (Mayfield 1975). However, only seven eggs were lost to predators during the entire study, and I saw little indication that females abandoned the area prematurely. Therefore, this source of bias seems negligible and I did not attempt to correct for it.

The probable causes of nestling mortality were determined largely from indirect evidence. Brood losses were classified as predation losses, dead nestlings with full stomachs and/or wet bodies were classified as exposure victims, and dead nestlings with empty stomachs were classified as starvation losses. In some cases dead nestlings disappeared singly from nests before I was able to examine them. These were classified as losses due to uncertain causes. Parent birds usually remove dead young by carrying them in their bills and dropping them 50 or more meters away, so starvation or exposure are the most likely causes of death in these instances.

I banded nestlings with aluminum and colored plastic leg bands on the seventh day posthatching. Attempts to band older nestlings in 1973 sometimes induced premature fledging. Individuals returning in subsequent years were aged by their unique band combinations and by coding their hatching year with changes in the relative placement of the three color bands and the U.S. Fish & Wildlife Service aluminum band on their legs each year.

RESULTS

ABUNDANCE AND DISTRIBUTION

The number of Bobolinks breeding within 3 km of P-Ranch Patrol Station each year is summarized in Table 1. In every year except 1974 the census figures represent the number of birds actually seen. In 1974, 12 of 31 banded males (38.7%) and 6 of 21 banded females (28.6%) known to be on the refuge during May and June were missed during the July census. I calculated the total size of the population that year by assuming that an equivalent proportion of unbanded individuals were also missed by the census. The equations used for this purpose were $X = 0.387(58 + X)$ and $Y = 0.286(78 + Y)$, where X = number of males missed by the census and Y = number of females missed.

TABLE 1. The number of adult Bobolinks censused at the south end of Malheur National Wildlife Refuge during 1972–1976.

Year	Number of males	Number of females	Sex ratio
1972	144	—	—
1973	171	179	1.05
1974	95	106	1.11
1975	139	151	1.09
1976	139	—	—

The population fluctuated markedly in size during the 5-year study, but the data suggest no trend toward long-term change. No reliable censuses of the population are available for earlier years, but Gabrielson and Jewett (1940) stated that Bobolinks were scarce during the drought of the 1930's. The population has apparently increased since that time and now appears to be at equilibrium.

The sex ratio of the population appears slightly skewed in favor of females. Failure to include the few isolated males in the census results counterbalances this result to some extent, but the skew remains evident unless many more isolated males were on the refuge than were evident. Lack (1954) stated that a skew toward excess males probably exists in most monogamous song birds, but a skew toward more females is typical of polygynous species (Selander 1958, 1965). The near equality of sex ratios in Bobolinks suggests that only a small deleterious effect on male survival results from intrasexual selection arising from their polygynous mating system.

Bobolinks prefer to breed in mesic meadows rather than wet or dry ones (Wittenberger 1976). Males first settle in mesic habitats with low sedge cover and high forb cover. Later arrivals establish territories in wet habitats with high forb cover and high sedge cover rather than in flooded or dry habitats with low forb cover and high or low sedge cover. They avoid flooded areas that have not dried up and dry areas that are not near standing water.

Since Bobolink habitat preferences are correlated with soil moisture conditions, water distribution on the refuge should influence Bobolink distribution patterns. Bobolink range on the refuge includes parts of five irrigation watersheds (Fig. 1). Yearly changes in surface water conditions within these watersheds led to predictable changes in population dispersion (Table 2). A similar proportion of the

TABLE 2. The distribution of male Bobolinks in the five irrigation watersheds within contiguous Bobolink range on the refuge during 1972–1976.

	1972		1973		1974		1975		1976	
Watershed	#	%	#	%	#	%	#	%	#	%
Nursery	15	10.4	21	12.3	12	15.8	29	21.5	45	32.8
Unmonitored-east	8	5.6	19	11.1	9	11.8	21	15.6	14	10.2
Buckaroo	30	20.8	32	18.7	3	3.9	24	17.8	3	2.2
Unmonitored-west	65	45.1	64	37.4	25	32.9	25	18.5	18	13.1
Barnyard	26	18.1	35	20.5	27	35.5	36	26.7	57	41.6
Totals	144	100.0	171	100.0	76*	99.9	135[†]	100.1	137[†]	99.9

* Location of remaining males unknown.

[†] Remaining males not on territories at time of census.

total water supply entered each watershed in 1972 and 1973, although the absolute magnitude of flow was only half as great in 1973 (refuge records). As a result, the population showed little change in dispersion between these years. Water priorities were modified in 1974, with little water allowed into buckaroo watershed. This led to a significant decline in the proportion of territorial males established there (χ_1^2, $P < 0.01$). That watershed was again irrigated extensively in the unusually wet year of 1975, and the proportion of territorial males increased to its former level. In 1976 the watershed was again dry, and the population reverted to its 1974 level.

Similar patterns were evident in other watersheds. The northern half of the unmonitored-west watershed was dry in 1976, unlike previous years, and the proportion of males breeding there was reduced by half. Males breeding in that watershed in 1976 were all at the southern end, where irrigation flow was greatest. Bobolink habitat in the nursery and unmonitored-east watersheds consists largely of dry elevated terrain. Most of the irrigation water flows into low-lying areas that remain flooded through most of the summer. As a result, changes in irrigation flow have little effect on soil moisture conditions. However, heavy spring precipitation in 1975 led to more mesic habitat conditions than usual, and a significant increase in the proportion of males breeding within these two watersheds resulted (χ_1^2, $P < 0.001$).

I could not perform a similar analysis for females because they were not censused in most years until after breeding ended. Female habitat preferences are less closely attuned to moisture conditions, so their distribution pattern differed from that of males. In 1975 fewer males were polygynous and more males remained unmated in dry habitats than in mesic or wet ones (Wittenberger 1976), suggesting that the amount of suitable Bobolink habitat on the refuge probably decreases in dry years.

SITE FIDELITY

I determined the likelihood that individuals returned to the same area they occupied the preceding year by plotting where I sighted banded birds on aerial photograph overlays. All banding was done on the principal study area in barnyard watershed, where water conditions were least variable and population densities were most stable. Site fidelity should be lower in areas showing greater annual variations in habitat quality, so my estimates of site fidelity are almost certainly higher than the population average. This is made evident by the marked changes in population dispersion that followed annual changes in irrigation watershed conditions. Only 1975 data were used to estimate site fidelity because the locations of all banded individuals were not determined in other years.

Ten of 27 adult males (37%) established territories within 50 m of where they held territories the previous year, and 26 (96%) returned to within 1000 m. Only 1 of 8 yearling males (13%) established a territory within 1000 m of where it hatched, and 3 (43%) settled over 2000 m away. Significantly more yearling than adult males dispersed farther than 1000 m (Fisher exact prob. test, $P < 0.001$). Adult males dispersed a mean distance of 205 m (range = 0–1450 m), as compared to 1610 m (range = 120–3350 m) for yearlings.

Four of 13 adult females (31%) nested within 50 m of where they nested the previous year. Nine adult females (54%) nested within 200 m, and 12 (92%) nested within 1000 m. In contrast, none of 9 yearling females nested within 200 m of where they hatched, although 6 (67%) nested within 1000 m. Significantly more yearling than adult females dispersed distances greater than 200 m (Fisher exact prob. test, $P = 0.01$). Adult females dispersed a mean distance of 315 m (range = 0–2250 m), as compared to 810 m (range 240–2200 m) for yearlings. Fewer yearling females than yearling males dispersed farther than 1000 m (Fisher exact prob. test, $P = 0.025$).

Bobolinks in Wisconsin also showed strong site fidelity (Martin 1974). However, Martin could not estimate the percentage of surviving individuals returning to his study area because he studied only a fraction of the total population in the region. An average of only 33.9% banded females return to his study area each year, as compared to 62.8% for banded males. Therefore, females were less faithful to their former breeding sites than males. He suggested that this stemmed from a tendency for females to breed in new areas following nest failure.

BREEDING CHRONOLOGY

The earliest males arrived on the refuge on 13 May in 1973, 1974, and 1975. In each year I observed one male fly over the principal study area in mid-afternoon of that day. By the following morning several males were vigorously pursuing each other around the central parts of the study area. In 1976 I saw two males singing in a tree on the dike near P-Ranch Patrol Station on 12 May and several males displaying on the principal study area the following morning. The earliest previous records for Bobolinks arriving on the refuge were 20 and 21 May (Littlefield and McLaury 1973; pers. observ. in 1972). This discrepancy resulted from the fact that Bobolinks do not occupy habitats along roads until about a week after the earliest arrivals begin settling in less accessible areas.

Bobolinks occupied the principal study area before they settled in other areas except in 1976. At least 15 males settled on the principal study area before 20 May 1973, when I first saw males elsewhere. In 1974, two males occupied broadly overlapping home ranges on the study area and three additional males occupied an adjoining field during the rain and snow storms of 11–19 May. During 20–22 May, an influx of about 16 males entered the study area and its immediate environs. I did not see any males in other areas until 23 May. In 1975 I counted 26 males on the study area and its immediate vicinity by 21 May, when I first saw males elsewhere. This settling pattern changed in 1976, when there were nine males on the principal study area and seven males scattered throughout other parts of the population's range by 16 May.

Females first arrived on 18 May 1973, 20 May 1974, 17 May 1975, and 20 May 1976. They also settled on the principal study area before settling in other areas. Large influxes of females arrived immediately following these dates except in 1975, when the main influx was delayed until 22 May. Thus, females usually began arriving about four to eight days later than males. However, in 1974 most males and females arrived at the same time because the majority of males were delayed by snowstorms until 20 May.

Adult males generally arrived earlier than yearlings (Fisher exact prob. test, $P = 0.02$). In 1975, when I surveyed the entire population every two days, 16 of 21 banded adult males (76%) arrived before 27 May, as compared to only 2 of 7 banded yearlings (29%). The arrival date of one banded yearling was unknown that year.

Sample sizes were too small to evaluate age-related differences in female arrival dates. Martin (1971) stated that yearling females arrive about two weeks later than adults in Wisconsin, but this large a difference was not evident in my data.

Pairing and nesting on the principal study area were highly synchronous in every year (Fig. 2). Chronology data were not collected in 1972 or 1976. All males consistently obtained one mate before any male obtained a second one. This is consistent with Orians' (1969) prediction that females should not accept already-mated males until only marginal habitats remain open to them. Primary (i.e. first-mated) females did not accept mates until territory ownership was settled. In most years males were well established on territories before females arrived, but the simultaneous arrival of both sexes in 1974 allowed me to study male priorities when territory ownership is not settled before females arrive. During 20–22 May 1974 males devoted their full attention to delineating and defending territory boundaries. They completely ignored females who entered their territories until 23 May, and the first pair bonds were not formed until the following day. Hence, males apparently cannot afford to devote time to courting females until they are assured of possession of their territories.

The average intervals between major events in the nesting cycle provide a useful summary of breeding chronology. The interval between pair formation and laying of the first egg averaged 7.3 days for primary females in 1973 (N = 17, range = 2–17), 5.6 days in 1974 (N = 17, range = 3–12), and 6.1 days in 1975 (N = 18, range = 2–11). Secondary females spent an average of 5.8 days (N = 20, range = 2–11) between pair formation and

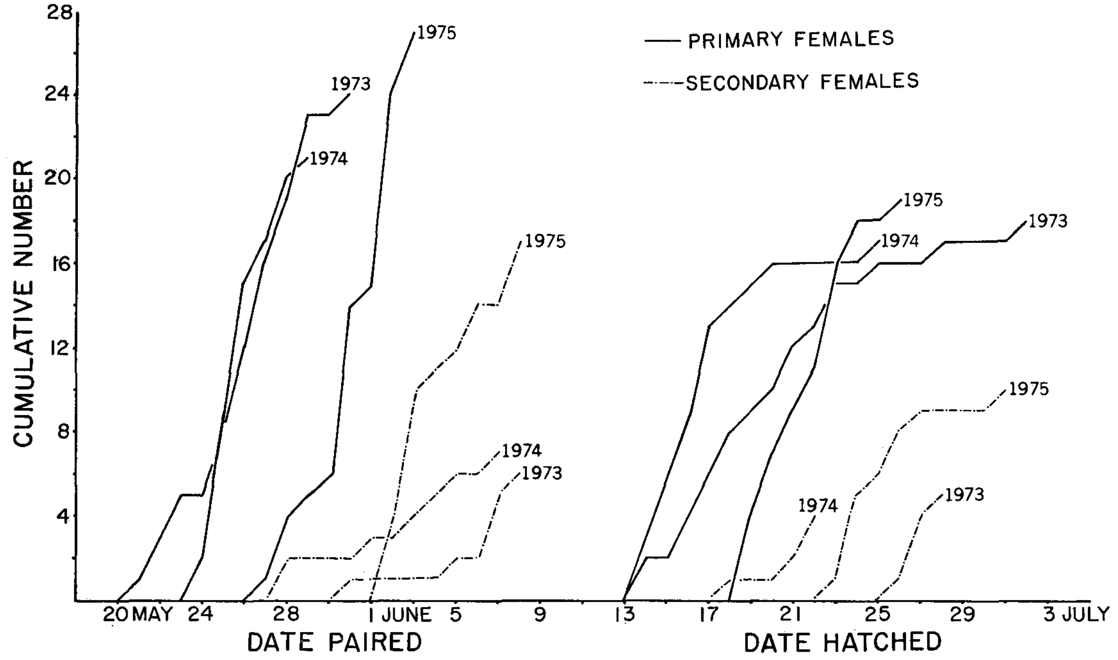

FIGURE 2. The breeding chronology of primary (solid lines) and secondary (dashed lines) females nesting on the principal study area. Primary females are the first mates of mated males and secondary females are the second mates of polygynous males (after Martin 1971, 1974).

initiation of laying for the three years combined. Martin (1971) found that females in Wisconsin usually began laying 5–8 days after pairing. The average interval in Oregon fell within this range, but some females delayed laying for much longer periods of time.

The length of this interval was correlated with the earliness of pair formation. In 1973 the first three primary females to accept mates began laying 12–17 days after pairing, as compared to an average of 6.3 days for females mating during the next 4 days ($N = 10$) and 4.6 days for females mating thereafter ($N = 5$). The difference between the earliest and later females is significant (t-test, $P < 0.05$). Early primary females did not delay laying any longer than later females in 1974, when pair formation was more synchronous. A difference between early and later females was again evident in 1975, when pairing was somewhat less synchronous. Primary females that paired during 28–29 May 1975 began laying an average 7.5 days after pairing ($N = 4$), as compared to 6.5 days for females that paired during 30–31 May ($N = 8$) and 4.5 days for females that paired in June ($N = 6$). The difference between the earliest and latest females in 1975 is significant (t-test, $P < 0.02$). It would be interesting to compare the delay in laying with foraging conditions, female weights, and weather, but my present data do not allow such an analysis.

The timing of pair formation by secondary (i.e. second-mated) females also varied between years. Polygynous males obtained their second mates 10.4 days after their first mates in 1973 ($N = 5$, range = 7–17), 7.6 days in 1974 ($N = 8$, range = 3–12), and 4.6 days in 1975 ($N = 17$, range = 3–8). The interval was significantly shorter in 1975 than in 1973 or 1974 (t-test, $P < 0.05$), apparently because primary females began pairing later than usual that year.

I was able to determine the status of 25 primary nests at the time when secondary females selected mates. Ten secondary females paired before the primary female began laying, 14 paired during laying, and one paired during incubation. A similar preponderance of secondary pairings before the primary female started incubating has also been reported for the Dickcissel (*Spiza americana*), another polygynous grassland species (Zimmerman 1966).

Breeding chronology on the principal study area is not representative for the population as a whole because Bobolinks usually occupied it a week or more earlier than other areas. I studied breeding chronology for the whole population only in 1975. In that year nearly all males had established territories before any males obtained their first mates (Fig. 3). Primary females selected mates relatively synchronously, especially during the

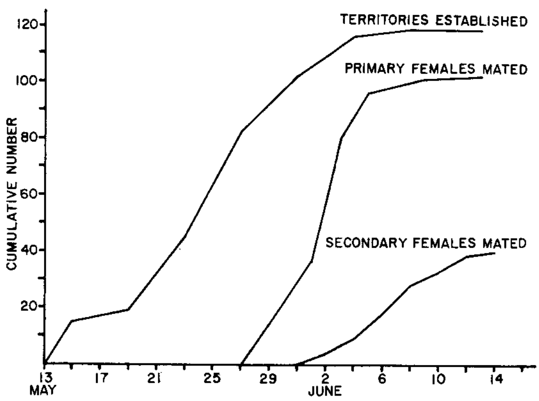

FIGURE 3. Breeding chronology of the entire Malheur Bobolink population in 1975.

peak pairing period of 2–3 June. This coincided with the time when polygynous males on the principal study area began obtaining their second mates. The significance of this timing will be discussed later.

Males on the principal study area acquired mates earlier than males in other areas. Sixteen of 27 males (59%) on the principal study area were mated by 1 June, and all were mated by 3 June. In contrast, only 20 of 77 males (26%) located elsewhere were mated before 1 June, and 25 (32%) were still unmated after 3 June. Therefore, females paired significantly earlier on the principal study area than in other areas (χ_1^2, $P < 0.01$). The same pattern was evident for secondary females. All 12 males who attracted second mates before 5 June were on the principal study area. These results imply that the principal study area encompassed the habitats most preferred by females as well as by males.

One factor that may influence the timing of nesting events is food abundance. I sampled the density of caterpillars, the preferred food items fed to nestlings, with a standard 38-cm diameter sweep net in 1975 and 1976. Procedural details are described elsewhere (Wittenberger 1976, unpubl. data). The results show that primary females began laying shortly after caterpillars first emerged in spring (Fig. 4). The interval between caterpillar emergence and laying was longer in 1975 than in 1974, possibly because of the cold rainy weather prevailing in 1975. The cold wet spring of that year probably affected the abundance of all insect resources, including those used by females to build up energy reserves for laying.

The nestling period coincides reasonably well with peak caterpillar densities, although the peak was prematurely terminated by rainstorms in June 1975. In both years, caterpillar densities declined considerably by the time nestlings fledged. Therefore, the fledgling period does not coincide with peak food abundance as it does in the Lapland Longspur (*Calcarius lapponicus*), an arctic species that also exhibits synchronous breeding (Custer and Pitelka 1977). Data from additional seasons are, however, still required before the relationship between timing of breeding events and food abundance can be fully evaluated for Bobolinks.

PREVALENCE OF POLYGYNY

Previous studies probably overestimated the prevalence of polygyny in Bobolinks because they were restricted to favorable habitats. The insular distribution of Bobolinks at Malheur Refuge allowed me to obtain a population-wide estimate. I determined the mated status of virtually every male in the population during 1975 and found that 40 of the 139 males observed that year (28.8%) were polygynous, while 69 males (49.6%) were monogamous and 30 (21.6%) remained unmated. Only 2 of the 40 polygynous males attracted three females, and none attracted more. Both of these held territories on the principal study area. I did not note any males with more than two mates in any other year. This differs from Martin's (1971, 1974) results for Wisconsin, where Bobolinks were often trigamous and in one case quadrigamous. Of the 30 unmated males, 21 held territories that never attracted mates, 6 were displaced from territories by other males and failed to establish new territories elsewhere (3 of these after becoming mated), and 3 never succeeded in establishing a season-long territory despite having held several temporary territories in succession.

Mating system theory predicts that polygyny should be more prevalent in superior habitats (Orians 1969). Two lines of evidence show that habitats on the principal study area were better than those in other areas. First, both males and females preferentially selected the principal study area over other areas. In fact, males did not occupy other habitats until a week or more after the first individuals had settled on the principal study area, and few females paired with males outside the principal study area until all males on the principal study area had been chosen. Second, territory size, the reciprocal of population density, averaged smaller on the principal study area (0.74 ha, N = 66) than in outlying areas (1.46 ha, N = 93), thus implying stronger competition for habitats on the principal study area. Hence,

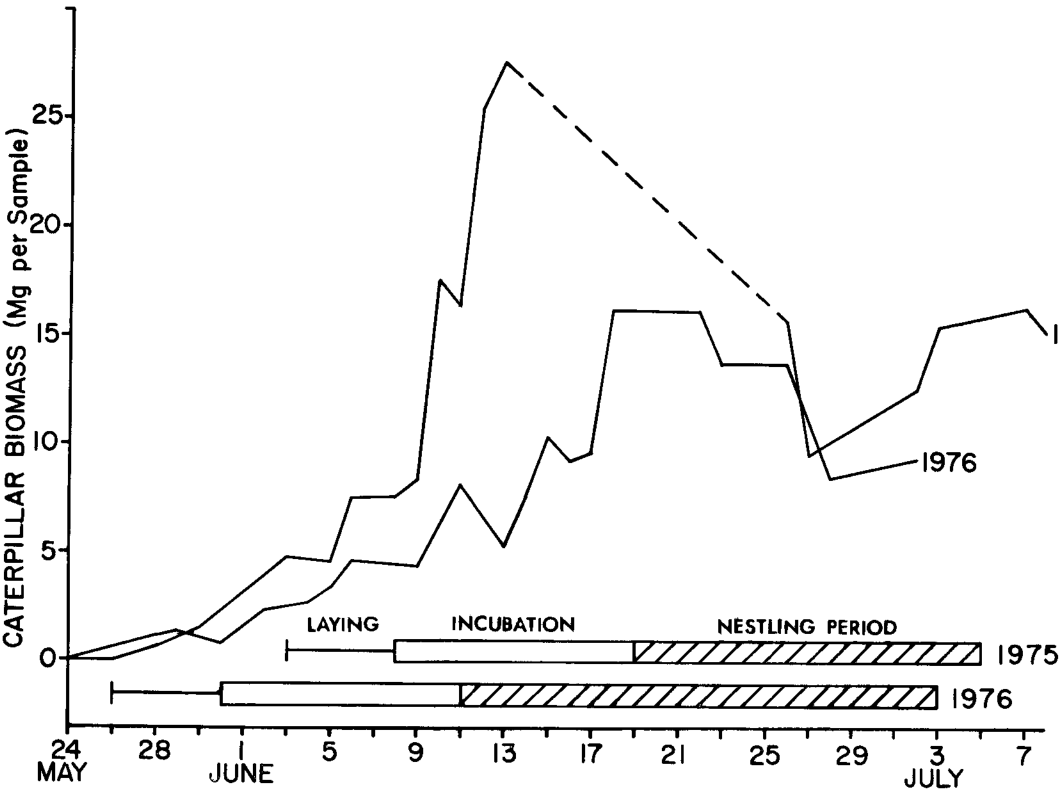

FIGURE 4. Caterpillar biomass on the southeastern section of the principal study area in relation to Bobolink breeding chronology. The dashed line in mid-June 1975 represents a period of continuous rainstorms when no samples could be taken.

theory predicts that polygynous matings should be more prevalent on the principal study area than on other parts of the refuge. The data confirm this prediction. Polygyny was more than twice as frequent on the principal study area (43.7%, N = 71 for all years combined) as it was in other areas (20.2%, N = 109) (χ_1^2, $P < 0.001$).

A second prediction of mating system theory is that the frequency of polygyny should increase as habitat heterogeneity increases (Orians 1969). This prediction can be tested by comparing my results with those of Martin (1971, 1974). The area studied by Martin was more heterogeneous than my principal study area in that it contained low-lying wet areas interspersed with higher ridges and surrounded by very dry elevated terrain. Males holding territories in low-lying areas always attracted mates, while males in dry peripheral areas rarely did. In comparison, my principal study area contained a gradient of mesic to wet meadows and completely lacked very dry areas with sparse vegetation. In conjunction with this difference, the incidence of both polygynous and unmated males was much higher in Wisconsin than on my principal study area (Table 3). The difference cannot be attributed to differences in the quality of the two study areas relative to surrounding areas, because territory sizes and breeding sex ratios were similar in both areas. Hence, the difference seems to have arisen from the greater heterogeneity of Martin's study area.

Young males were less able to attract females than older males in Oregon. Banded adults averaged 1.38 females in 1975 (N = 24), while banded yearlings averaged only 0.75 females (N = 8). No banded yearlings obtained more than one female, and 2 of them, along with 8 of 14 unbanded males presumed to be yearlings on the basis of aberrant songs, failed to obtain any mates. Since only 25% of the banded yearlings had aberrant songs, an additional 24 unmated males without aberrant songs should also have been yearlings. This is only a rough estimate because sample sizes are small, but it suggests that most unmated males were yearlings. Nevertheless, 2 of 21 banded adult males failed to obtain mates in 1975. One of these was banded as an adult in 1972 and was also unmated in 1974. Its mated status in 1972 and 1973 was not determined. This male dispersed further be-

TABLE 3. A comparison of Bobolinks studied in Wisconsin and Oregon. Data for Wisconsin are from Martin (1971, 1974).

	Oregon primary study area	Wisconsin riverbottom
Number of territories	66	64
Territory size (ha)	0.74	0.70
Breeding sex ratio	1.45	1.50
Percent trigamy	2.8	18.8
Percent bigamy	40.8	37.6
Percent monogamy	55.0	18.8
Percent bachelor males	1.4	25.0

tween successive years (1974–1975) than any other banded adult male in the population (i.e., 1450 m). The other unmated adult male was monogamous when banded in 1974. It also obtained a mate in 1975, but lost its territory to another male about five days later. Martin (1971) also found that bachelor male Bobolinks were usually yearlings.

In the polygynous Red-winged Blackbird (*Agelaius phoeniceus*) yearling males usually do not attempt to breed, but even two-year-old males are less able to obtain mates than older males (Yasukawa 1977). This suggests that experience rather than chronological age may be the critical variable. Whether the lower success of inexperienced males stems from a lower ability to defend high quality territories or from mating preferences expressed by females is uncertain. Evidence for Red-winged Blackbirds currently supports the former hypothesis (Searcy 1977; Orians, in press), but these alternatives cannot yet be evaluated for Bobolinks.

I did not band enough females to detect age-related changes in their mated status with any certainty. My small samples do not suggest any age effects. Five of 11 banded adult females were second mates in 1975, while 2 of 5 yearlings were first mates (both of monogamous males). These data do not support Martin's (1974) conclusion that most secondary females are yearlings.

NESTING SUCCESS

Fledging success exceeded 90% of hatched young from primary and secondary nests in 1973 and from primary nests in 1974 (Table 4). This is extraordinarily high for a passerine bird (Ricklefs 1969). Success was lower in 1975 and 1976, but the 4-year average remained high. The average primary nest fledged 3.4 young, while the average secondary nest fledged 2.3 young. In comparison, Bobolinks in Wisconsin fledged an average of 2.6 young from each primary nest ($N = 58$) and 1.5 young from each secondary nest ($N = 45$; Martin 1971).

Secondary females were less successful than primary females in 1974 and 1976 (χ_1^2, $P < 0.05$), but not in 1973 or 1975. The reasons for this will be discussed below. On average, secondary females produced fewer young than primary females, thus confirming Orians' (1969) assumption that females pay a price by accepting already mated males as their mates. The difference between primary and secondary females could have stemmed from an average younger age of secondary females instead of the difference in mated status, although my limited data do not support this interpretation.

I found no difference in clutch size between primary and secondary females. This result contrasts with the smaller clutch sizes laid by secondary females in Wisconsin (Martin 1974). Secondary females may lay larger

TABLE 4. Nesting success of Bobolinks on the principal study area during 1973–1976. 1° = primary females; 2° = secondary females.

	1973		1974		1975		1976		Totals	
	1°	2°	1°	2°	1°	2°	1°	2°	1°	2°
Number of nests	19	5	20	5	21	13	16	12	76	35
Number of eggs	108	28	109	26	116	71	89	63	422	188
Mean clutch size	5.68	5.60	5.45	5.20	5.52	5.46	5.56	5.25	5.55	5.37
Number hatched	92	26	97	23	106	61	83	49	378	159
Percent hatched	92.0*	92.9	89.0	88.5	95.5[t]	92.4[t]	93.3	93.7**	92.4	91.9
Number young died	6[+]	2	9	8	61	34	39	33	115	77
Percent young died	7.0[+]	7.1	9.3	34.8	57.5	55.7	47.0	73.3	30.4	48.9
Young fledged/egg (%)	83.5	85.7	81.7	57.7	38.9	38.0	49.4	19.0	62.8	43.1
Young fledged/female	4.8	4.8	4.3	3.0	2.1	2.1	2.8	1.0	3.5	2.2
Percent successful nests	100.0	100.0	95.0	80.0	61.9	61.5	62.5	33.3	80.3	60.0

* Excludes two eggs lost to predation and a clutch of six eggs abandoned because of observer interference.

[t] Excludes one clutch of five eggs lost due to flooding.

[+] Excludes five young lost when a female was banded at her nest.

** Excludes five eggs lost to predation and five eggs abandoned for unknown reasons.

TABLE 5. Probable causes of Bobolink nestling mortality on the principal study area during 1973–1976.

	1973	1974	1975	1976	Total	Percent of total
PRIMARY NESTS						
Total number of nestlings	92	97	106	83	378	—
Number of dead nestlings	6	9	61	39	115	30.4
Exposure	2	3	53	11	69	18.2
Predation	0	4	5	16	25	6.6
Starvation	0	1	3	8	12	3.2
Uncertain	4	1	0	4	9	2.4
SECONDARY NESTS						
Total number of nestlings	26	23	61	49	159	—
Number of dead nestlings	2	8	34	33	77	48.9
Exposure	0	1	16	2	19	12.0
Predation	0	0	0	17	17	10.7
Starvation	0	1	18	10	29	18.2
Uncertain	2	6	0	4	12	7.6

clutches in Oregon because they have a greater prospect of receiving male assistance in feeding young. Males rarely help feed secondary nestlings in Wisconsin (Martin 1974), but they almost always do in Oregon. Alternatively, the difference may stem from the apparently younger age of secondary females in Wisconsin.

The principal causes of nestling mortality varied between years (Table 5). The low nesting success in 1975 resulted from exposure of nestlings to the continuous rainstorms of 14–25 June. The storm killed a greater proportion of nestlings in primary than in secondary nests because the storm ended before most secondary nestlings had hatched. Nestlings also died with full stomachs on a few other occasions. Two primary nestlings died during a hailstorm in mid-June 1973. They were both in one of the only two nests that had hatched by the time of the storm. Other nestlings dying with full stomachs were found following unusually cold nights not associated with stormy weather. Martin (1971) also found high nestling mortality during severe rainstorms. In one year of his study fledging success was 60% below normal because of adverse weather.

The lower nesting success of secondary females stemmed largely from higher starvation rates of nestlings. This was especially evident in 1975 and 1976, when sweep samples indicated unusually low densities of caterpillars. The higher starvation rate of secondary nestlings in 1975 offset the lower mortality rate due to exposure, with the result that overall nestling survival was similar in both primary and secondary nests. The higher starvation rate of secondary nestlings presumably resulted from the substantially lower contribution made by males in feeding them.

Predation rates were very low compared to those in previous studies of Bobolinks. About 30% of nestling mortality resulted from predation in Wisconsin (Martin 1971), and nearly all of 40 nests found by Karr (1963) in an upland field were destroyed by predators. One reason for this disparity may be regional variation in predator or buffer prey densities.

I tested this possibility by assuming that predation on Red-winged Blackbird nests, which do not rely on concealment for safety, provides a reasonable index of predator pressure on passerine nests. In 1975 I monitored 60 blackbird nests situated in flooded lowlands around the periphery of my principal study area. Water under these nests was generally less than 50 cm deep, and most nests were placed in grass, sedges, or dock. Only 4.8% of 248 eggs and 16.7% of 192 young were taken by predators from these nests. This rate is lower than that reported in any other study, including those of Red-winged Blackbirds nesting in marshes where nests are supposedly safer from predation (cf. Smith 1943, Young 1963, Robertson 1972, Holm 1973, Caccamise 1976, Monahan 1977). As an alternative hypothesis, the low predation rates on Bobolink nests in Oregon may have resulted from better vegetation cover for concealing nests. This hypothesis seems unlikely to me, because it fails to explain the low predation rate on Red-winged Blackbird nests and the percent cover of forbs and other vegetation was similar on the areas studied by me and by Martin (1971) (see Wittenberger 1976). Roseberry and Klimstra (1970) also found that between-field differences in predation rates on meadowlark (*Sturnella*) nests resulted from variations in predator densities rather than variations in vegetation structure. However, meadowlarks construct domed nests, unlike Bobolinks or Red-winged Blackbirds, so vegetation cover may be less important for concealing their nests.

I identified several species of predators taking Bobolink nestlings. A Short-eared Owl (*Asio flammeus*) destroyed one primary nest containing four young in 1974. It frequently hunted near that nest, and it left a regurgitated pellet and one mutilated nestling there after finding the nest. I surprised a yellow-bellied racer (*Coluber constrictor*) that was in the process of eating a 10-day-old primary nestling in 1975. Sandhill Cranes (*Grus canadensis*) destroyed at least five nests containing five eggs and 20 nestlings in 1976. Cranes never hunted on the principal study area during 1972–1975, possibly because they were kept away by the mobbing behavior of Red-winged Blackbirds. Blackbirds were noticeably less abundant in 1976, and two pairs of cranes regularly hunted on the periphery of the study area that year. Cranes may have found nests by cuing on stakes used to mark nest locations, since three nests were destroyed in a small area during one morning. I moved the stakes that day to prevent recurrences, but the cranes subsequently found two additional nests.

Five of the six secondary nestlings dying of unknown causes in 1974 died after nighttime temperatures dropped nearly to freezing. They were all 4–6 days of age and not yet capable of thermoregulating. Four of these died in a single nest, despite provisioning by both parents. They were removed from the nest by the parents before I could examine them, but the indirect evidence suggests that they died of exposure. If so, the lower success of secondary nests in 1974, a year of abundant food resources, may have been fortuitous.

Four primary nestlings died of unknown causes in 1976. Three of these died following warm nights and one died following a night of freezing temperatures. Similarly, three of the four secondary nestlings dying of unknown causes in 1976 died following warm nights, with one dying after a night of freezing temperatures.

ADULT MORTALITY AND RECRUITMENT

I estimated adult mortality rates from the proportion of color-banded individuals resighted in years following banding. My data confirm Martin's (1973) conclusion that Bobolinks are exceptionally long-lived for a passerine bird (Table 6). An average of 56.9% of adult males returned to Oregon each year, compared to a return rate of 62.8% for Wisconsin Bobolinks (Martin 1974). However, Martin could not estimate the number of surviving birds who failed to return to his study area. Since his study area covered 11.3 ha, a better comparison can be obtained by excluding surviving males that dispersed more than 1000 m from my principal study area. This would suggest that the mortality rate of males is about 10% higher in Oregon than in Wisconsin. A similar difference should also hold for females, although no estimate is possible because of the low site fidelity exhibited by females in Wisconsin.

TABLE 6. Return rate of adult male and female Bobolinks during 1974–1976. Data are based on resightings of color-banded birds.

	Males		Females	
Year	N	Percent returns	N	Percent returns
1974	44	42.9	15	40.0
1975	31	77.4	21	76.2
1976	34	55.9	—	—
Totals	109	56.9	36	61.1

Adult survival rates in Oregon varied markedly between years. Survival was reduced to about 40% for both sexes in 1974, probably because they encountered snow and rain storms just before arriving on the refuge. These variations reduce the reliability of comparisons made between survival rates of Oregon and Wisconsin Bobolinks and make clear the need for additional data.

I estimated recruitment of yearlings to the population by subtracting the estimated number of returning adults, based on band returns, from total population size. To calculate the number of fledged young that were produced the preceding year, I multiplied the mean number of young fledged per female by the number of females breeding that year. Since the frequency of polygyny was known only in 1975, I used that value as an estimate of how many females accepted secondary status in other years. Errors stemming from this procedure would have little impact for 1973, when primary and secondary females enjoyed similar success, but they would have an important effect on the results obtained for 1974. These calculations allow an estimate of annual survival rate for successfully fledged young, given the assumption that emigration and immigration are negligible. This method probably overestimates total production of fledglings because all known nests were in nearly optimal habitat.

TABLE 7. The survival rate of juveniles and the recruitment of yearlings into the population each year. See text for an explanation of how estimates were obtained.

Year	One-half of fledglings produced in previous year	Estimated number of yearlings present		Percent survival rate of yearlings		Percent of total male or female population that were yearlings	
		Males	Females	Males	Females	Males	Females
1974	429.5	22	32	5.1	7.4	23	31
1975	208	65	70	31.2	33.7	47	46
1976	158.5	61	—	38.6	—	44	—

The survival rate of young fledged in 1973 was unusually low compared to other years (Table 7). As a result, few yearlings were present the following year. In more normal years about one-third of fledged young survive to the next year, and nearly half of the population consists of yearlings.

Independent confirmation of recruitment rate was obtained in 1975 from behavioral observations and band return data. In that year 14 unbanded males sang aberrant high-pitched or garbled songs reminiscent of abortive songs rendered by captive juveniles in autumn. One-fourth of the eight banded yearlings returning that year also had aberrant songs, suggesting that an additional 42 unbanded males with normal songs were also yearlings. Adding these together yields a total of 64 yearlings in the population, which is very close to the estimate obtained by the above calculations.

Fewer banded juveniles returned to the population than was expected on the basis of recruitment data. Resightings of birds banded as nestlings were consistently lower than my estimates of recruitment. Only 10.5% of banded female nestlings and 9.2% of banded male nestlings (assuming 1:1 nestling sex ratios) were seen again during the study, compared to estimated mean survival rates of 16.0% for females and 18.6% for males. Therefore, only about half as many banded nestlings were resighted as there should have been. Either the band return data are inaccurate, the banding process biased chances for juvenile survival, my calculated estimates of juvenile survival rates are too high, or significant immigration and emigration affect the population. I cannot evaluate these possibilities without additional evidence.

The low estimated survival rate of yearlings in 1974 probably resulted from the very dry conditions prevailing at Malheur Refuge in 1973 and not from differences in nonbreeding season mortality. Yearling males migrate later than adults and should not have been exposed to the stormy weather of early May 1974. Indirect evidence suggests that nest success outside the principal study area was substantially lower in 1973 than my data indicate. In that year approximately 25 males entered the principal study area before any nests there had fledged. Since males feed young in both primary and secondary nests, and nests on the principal study area were begun earlier than those built elsewhere, these males were probably emancipated from parental duties because their nests failed. The principal study area was not as strongly affected by drought in that year because it received irrigation water until later in the season than most other areas. Hence, low recruitment in 1974 probably stemmed from low overall nesting success in 1973, possibly in conjunction with poorer survival of newly fledged young.

DISCUSSION

TIMING OF BREEDING EVENTS

Initiation of breeding in Bobolinks is, of course, timed by the end of spring migration. The proximate timing of their spring migration depends on photoperiodic cues coupled with a progressive change in sensitivity to long daylengths (Engels 1969, Hamner and Stocking 1970). This is an adaptation to wintering south of the equator during the austral summer. Although the proximate stimulus of migration has been identified, the factors determining the optimal timing of breeding have not been studied.

In single-brooded birds the breeding season is usually timed so that the nestling period coincides with peak abundance of nestling food resources (Lack 1950, 1954, 1968, Moreau 1950, Skutch 1950, Marshall 1951, Immelmann 1971). However, this timing may be modified if seasonal changes in predation intensity are severe enough. Seasonal predation effects do not appear important for Bobolinks in Oregon, and their nestling period approximately corresponds to the period when caterpillars are most abundant. Food abundance peaked somewhat before the nestling period in 1975, but this resulted from premature cessation of caterpillar production owing to cold rainy weather in mid-June.

The beginning of the nestling period depends on when females begin accepting mates and how long they spend between pairing and laying. Female Bobolinks apparently time the nestling period by varying both factors. Spring was about two weeks later than usual in 1975, judging from the dates when forbs began to bloom, and females began laying a week later than usual in that year. This was due to later than usual pair formation and not to longer than usual delays between pair formation and laying.

The importance of delayed laying was revealed by comparing females who paired progressively later in the season. Despite small sample sizes, there was a consistent trend for early-pairing females to wait longer before laying than later-pairing females. This suggests that females who select habitats early cannot garner energy for making eggs as fast as later females or else wait until additional habitat cues become available before laying. Such cues might be used to make a better assessment of territory quality or to time the nestling period in relation to future food availability. Similarly, Great and Blue tits (*Parus major* and *P. caeruleus*) accelerate the nestling period in years of early caterpillar emergence by shortening the time between pairing and laying (Gibb 1950).

An important question concerns the ultimate factors governing when males and females should begin occupying habitats. Proximate factors are well studied and have been reviewed by Immelmann (1971, 1973), but most studies of ultimate factors have been restricted to timing of the nestling period. If indeed birds modify the interval between habitat selection and laying to adjust the timing of the nestling period, additional factors must determine when habitats are initially selected. One way to approach this problem is to consider the costs and benefits entailed by modifying the date of habitat selection for each sex.

Males can increase their chances of successfully establishing a territory in optimal habitat by settling in that habitat as early as possible. This advantage is especially important in polygynous species, because males stand to gain additional mates as well as higher than average success for each nest. The advantage would be less for monogamous species, especially if density-dependent effects lead to similar success in habitats differing with respect to intrinsic quality (see Fretwell and Lucas 1969, Fretwell 1969).

Early occupation of habitats is not without cost. To occupy habitats early, males must arrive earlier in spring, thus increasing their vulnerability to adverse weather conditions during migration or on the breeding grounds (e.g. Tompa 1971). Moreover, cues for assessing habitat quality are usually less reliable early in the season (Hildén 1965), so males sacrifice information in order to achieve earlier habitat occupancy. As a result, they risk making erroneous assessments of habitat quality that could cause them to settle in poor habitat.

My data confirm that male Bobolinks use less reliable cues than females to select habitats (Wittenberger 1976). Males select habitats before caterpillars emerge and are therefore unable to distinguish between habitats with future high and low caterpillar productivity. As a result, some males establish territories where caterpillar productivity will be low and consequently fail to obtain mates. Females usually do not select habitats until after caterpillars emerge, and even the earlier females to select mates are able to distinguish between habitats that will differ in the biomass of caterpillars available during the nestling period.

The best procedure for males would be to settle first in areas where they are assured of obtaining one mate and have a higher than average chance of obtaining additional mates. That is, the optimal habitats for males should be those where their predicted reproductive success at the time of selection is highest. Male Bobolinks generally follow this pattern. They first settle in mesic meadows on the principal study area, where irrigation flow is most reliable in every year. These males always attracted one mate, and they had a higher than average chance of attracting two mates. When I monitored the entire population in 1975, all but 1 of the 65 males establishing territories before 26 May obtained mates, and more of these males attracted two mates than did males who established territories later. Nearly all bachelor males selected habitats after 26 May but before caterpillars began emerging on 28 May.

The best procedure for females is more conservative. Females should also occupy habitats early, but they should not pay as high a cost as males to do so. This is because females do not benefit from the prospect of obtaining more than one mate by settling in a very good area. Since erroneous assessments of habitat quality may cost females an entire season's reproductive effort, they should not select habitats until more reliable proximate cues become available.

Female Bobolinks first chose mates on the principal study area, in places where caterpillars were consistently plentiful every year because of reliable irrigation flow. Irrigation flow was less reliable elsewhere, especially in June, so caterpillar abundance was less predictable in those areas (see Wittenberger 1976). As a result, females did not select mates in these areas until caterpillar productivity became more assessible. The large number of synchronous matings by primary females that occurred from 1–3 June 1975, along with the earliest matings by secondary females on the principal study area, coincided with the date when I was first able to detect differences in caterpillar biomass between physiognomically similar territories on the principal study area (Wittenberger 1976). Thus, females apparently select mates in predictable habitats as soon as males are well established on territories, but delay their choices in less predictable habitats until better cues for assessing habitat quality become available.

POPULATION DYNAMICS

Mortality of adult Bobolinks on their breeding grounds appeared low, although a pair of Prairie Falcons (*Falco mexicanus*) regularly hunted over my principal study area. I witnessed one unsuccessful attack on a male Red-winged Blackbird and found the remains of several kills of male blackbirds, but I never saw any signs of Prairie Falcon attacks on Bobolinks. Nevertheless, male Bobolinks usually crouch in the grass and remain still while Prairie Falcons are overhead. This response differs from the song-flight displays and vocalizations given in the presence of other potential predators (human and otherwise).

Adult mortality probably occurs mostly during migration. Bobolinks are granivorous in winter and exploit the extensive seed crops of South American pampas during the austral summer. It therefore seems unlikely that they encounter serious food shortages during winter. This may explain why their longevity is so high.

The costs of migration can be estimated by comparing the survival rates of Bobolinks breeding in Wisconsin and Oregon. All available evidence indicates that Oregon birds migrate across the prairie states and then follow a pathway similar to that taken by those that breed in Wisconsin (see below). Hence, Oregon Bobolinks migrate approximately 6000 km or about 32% farther each year than those breeding in Wisconsin (based on a round-trip distance of 19,000 km from Wisconsin to Argentina). This is accompanied by a 10% reduction in adult survival rate, which represents a 29% increase in annual mortality rate. If, in fact, most adult mortality occurs during migration, both my data and Martin's (1974) imply that survival rate decreases linearly at the rate of about 10% per 6000 km traveled each year. Alternatively, if a substantial fraction of adult mortality does occur on the wintering grounds, the data imply that migration mortality increases geometrically with path length.

There is little evidence that western Bobolinks migrate southward through California and Arizona into Central America. Most Bobolinks sighted in California are found in the southern end of the state, suggesting that they are eastern birds exhibiting mirror-image errors in migratory orientation (DeSante 1973, pers. comm.). These birds may well be the source of the regular wintering population on the Galapagos Islands, although banding data are lacking (see Swarth 1931, Kramer 1965). There are only two Bobolink records for New Mexico (Harris 1965), and Bobolinks are only casual migrants in Arizona (AOU Check-list 1957). Bobolinks are rare transients in Yucatan but migrate in small numbers through Central America (Oberholser 1920, Peterson 1973, Ridgely 1976). These observations are most consistent with the hypothesis that the Central American pathway originates in Texas rather than further west.

I measured the orientation responses of eight males captured at Malheur Refuge under clear natural skies in early September 1972 by means of Emlen funnel cages (Emlen and Emlen 1966). Statistically significant orientation was determined with a modified Raleigh test (Rabøl 1970). Six of these birds were active for a total of 23 bird-nights, and five were significantly oriented eastward with a mean heading of 96° (range = 76°–114°). The sixth bird was randomly oriented on all three nights it was active. Tests were conducted for only eight nights and activity levels were relatively low, but the direction taken by all oriented birds was consistently eastward. Hence, these results support the conclusion that Bobolinks migrate eastward rather than southward from Oregon in autumn.

Recruitment to the population depends upon nesting success, fledgling survival, and mortality of juveniles during migration and on the wintering grounds. At first glance nesting success appears uncorrelated with recruitment the following year. For instance, low recruitment in 1974 was preceded by high nesting success in 1973, and higher recruitment in

1975 and 1976 was preceded by lower nesting success in 1974 and 1975, respectively. However, my data were not representative for the population as a whole: overall nesting success was probably lower than on the principal study area in 1973 and higher in 1975. Low overall production of juveniles in 1973 evidently contributed to the population decline of 1974, along with higher than average adult mortality during spring migration in 1974. A similar decline did not occur in 1976 because overall production of juveniles was probably higher in 1975 than my data indicate.

Survival of first year males following fledging averaged 34.9% in 1975–1976, as compared to 66.7% for adult males in those years. I could not determine the causes of juvenile mortality, but it may be especially high shortly after fledging (Lack 1966). I observed the number of locations where parents fed fledglings from three nests and found that half of these young died during the first week after leaving the nest (Wittenberger 1976). If this preliminary estimate is representative, most of the difference between juvenile and adult survival occurs before migration. Otherwise, part of the difference must occur during migration or on the wintering grounds.

Gabrielson and Jewett (1940) pointed out that Bobolinks had not expanded their range into other seemingly suitable parts of Oregon. Several factors contribute to this situation. Since site fidelity is high, Bobolinks are not likely to colonize nearby areas unless old habitats deteriorate. Polygyny further reduces the likelihood that females will colonize new habitat islands, because females can simply become second mates of already mated males whenever they encounter habitat shortages. Hence, males that do colonize new habitats are not likely to attract mates. Finally, population increases and hence pressures for range expansion may be less likely because of the increase in adult mortality caused by their longer migratory path. The combination of high site fidelity, polygyny, and reduced adult survival may account for the lack of range expansion in discontinuous habitat.

The future of Bobolinks at Malheur Refuge appears good. The population is sufficiently resilient to withstand major fluctuations in density. Irrigation patterns appear to have a large influence on Bobolink habitat, but the refuge is currently developing a comprehensive management plan that will take Bobolink nesting requirements into account. Further research is needed to evaluate the effects of terminating grazing and hay mowing practices on Bobolink range. Bobolinks depend upon new growth of vegetation, so the continued presence of old vegetation in spring may reduce habitat quality. It is known that burning improves Bobolink habitat when old vegetation is otherwise left standing (Martin 1971). At present, winter grazing and hay mowing serve to recycle nutrients throughout Bobolink range on the refuge, because mowed hay is not removed. If these practices are discontinued, periodic burning may be desirable to maintain the quality of Bobolink habitat.

SUMMARY

Breeding biology and population dynamics are described for the isolated Bobolink population at Malheur National Wildlife Refuge in Oregon. Population size varied from 200–350 individuals, with slightly more females than males. Long-term changes in population size were not found despite large year-to-year variability. Bobolink distribution on the refuge was affected by irrigation patterns.

Males arrived in mid-May, and females arrived about a week later. Site fidelity was high for adults in optimal habitat but probably not in marginal habitats. The return rate of banded adults averaged nearly 60% annually.

About 30% of males in the population were polygynous. The frequency of polygyny varied with habitat conditions, as predicted by mating system theory. Most bachelor males were yearlings, but many yearlings did obtain one mate.

Fledging success of hatched eggs averaged about 70% for first mates of mated males and over 50% for second mates of polygynous males. The higher success for first mates stemmed largely from lower nestling starvation, even though exposure was a more important cause of mortality. Predation rates were unusually low, apparently because predator densities were low. Recruitment of yearlings was about 20–30% of fledgling production in good years but only 5% in one dry year.

The nestling period coincided with peak abundance of nestling food resources, especially caterpillars. Females began laying shortly after caterpillars were first evident in samples. This may serve to time the nestling period, since early females often delay laying for two weeks or more after pairing.

The costs and benefits that determine the timing of spring arrival are discussed for each sex. Males benefit from the prospect of obtain-

ing two mates, so they select habitats early. Females do not benefit from this prospect, and they risk losing an entire season's effort should they choose a poor habitat. Hence, females select habitat later than males and after reliable cues for assessing caterpillar productivity become available.

The most important factors regulating population density are apparently survival of newly fledged young and mortality of adults and juveniles during migration. The study population has not expanded into other areas, probably because site fidelity is high and because females faced with habitat shortages can become polygynous mates. In addition, further range expansion is made less likely because higher adult mortality caused by a longer annual migration route reduces chances for a population surplus.

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