REPRODUCTIVE RATE AND TEMPORAL SPACING OF NESTING OF RED-WINGED BLACKBIRDS IN UPLAND HABITAT

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THE literature contains numerous studies on Red-winged Blackbird (*Agelaius phoeniceus*) reproduction. Francis (1971) summarized eight studies dealing with nesting success. These and other studies have also provided information on breeding chronology, clutch sizes, sex ratios, survival rates for eggs and nestlings, reproductive physiology, and other life history aspects of reproduction. With few exceptions, these studies have provided no data on the number of young fledged per female, per territorial male, or per unit area. This is especially true for upland nesting habitats where, at least in the midwestern United States, most Red-wings now nest (Graber and Graber 1963, Dyer et al. 1973). Also insufficient quantitative information is available on the extent and nature of renesting (i.e. nesting more than once in a nesting season) and on movements of adult females during the nesting season.

A better understanding of these aspects of reproduction is critical for the development of an accurate population-dynamics model for the species. Such a model is sorely needed to evaluate the impact and effectiveness of proposed population management strategies in places where blackbirds are deemed a health or safety hazard, or cause damage to agricultural crops (Tosh et al. 1970, Solman 1971, Stone et al. 1972).

This study had three objectives: (1) to determine the distribution, size, and number of Red-winged Blackbird territories for an old-field habitat; (2) to determine the number of nesting females, nesting success, extent of renesting, and number of young fledged for these territories; and (3) to examine movements of female Red-wings during the nesting season.

METHODS

The study was conducted from April to early August 1973 and 1974 in an old-field habitat at the southern edge of NASA Plum Brook Station, Erie County, in north central Ohio. The study area, hereafter referred to as Mason Field, has not been cultivated since 1967 but the vegetation has been mowed annually in late summer. Dominant plant species include golden rod (*Solidago* sp.), daisy fleabane (*Erigeron annus*), Canada thistle (*Cirsium arvense*), yellow rocket (*Barbarea vulgaris*), and various grass species. Mason Field adjoins intensively farmed land on the south and west and a mixture of woodlots and hayfields on the north and east.

Mason Field encompassed 6.50 ha in 1973. In 1974 as 2 ha of the western side were planted to wheat, Mason Field was expanded on the north side to include an additional

1.75 ha of old-field habitat, making the 1974 study area 6.25 ha in size. In both years, Mason Field was marked off at 50-m intervals with 2-m wooden stakes that were used as reference markers.

From 20 April through mid-May, observations were made for 1 to 3 h daily, generally 5 days weekly, to map male Red-wing territories. Nest searching commenced on 1 May after females were first observed on territories and continued until late July or early August when all territorial and nesting behavior ceased. Normally one to four people searched 4–8 h daily, 5–6 days weekly to assure that all nests were found. Nests were usually found by watching a female's movements until she revealed her nest location. Active nests (i.e. containing one or more eggs or nestlings) were then checked at 1- to 3-day intervals.

Dates of nesting events (e.g. hatching), when not directly observed, were estimated by dating from observed events. I assumed that: (1) nest building lasted 3 days, (2) eggs were laid at the rate of one per day, (3) incubation lasted 12 days after completion of clutch, and (4) nestlings remained in nest 10 days (Wood 1938, Beer and Tibbitts 1950, Young 1963, Case and Hewitt 1963). Nestlings that disappeared from a nest 8 days or more after hatching were considered successfully fledged if no evidence of predation was noted.

I attempted to band each female nesting in Mason Field. In 1973 a nest trap (Fankhauser 1964a) was used to capture females after they began incubating. This method was quite successful (90% of trap sets caught females) but caused some disturbance to the vegetation immediately surrounding the nest.

In 1974, 10–15 funnel traps (Reeves et al. 1968: 17) baited with cracked corn were set throughout Mason Field from 15 April to 10 June to trap and band females before they started nesting. When set, traps were checked at least every 2 h. Females that began nesting before being banded were caught by setting a mist net 1–3 m from the nest and flushing the bird into the net. These two methods left nest sites undisturbed.

Upon capturing a female, a USFWS band was placed on one leg, and usually one 2- × 1-cm vinyl plastic leg marker (Guarino 1968) was attached with an additional aluminum band The use of various shaped markers of four colors allowed observers with binoculars to recognize individual females.

Upon capture in 1974, most females were classified as either second-year birds or after-second-year birds on the basis of color of the marginal wing coverts (Payne 1969: 57; Holcomb 1974). Payne (1969) found a 20% error in this method, and in 1974 I classified 3 of 17 females returning from 1973 as 1-year-old when, in reality, all were at least 2 years old. Thus results based on this method must be interpreted with caution.

RESULTS

Territorial males.—Males began territorial behavior in Mason Field in early April. By mid-May 17 territories covering 6.50 ha were established in 1973 and 14 territories covering 6.25 ha were established in 1974. Although some boundaries shifted, all territories remained occupied in 1973 and 1974 until late June when some males left the field. The last teritorial male left during the first week of August in 1973 and on 27 July in 1974.

Nesting chronology.—I believe the intense searching located all active nests in Mason Field in both years. In 1973 we located 105 active nests.

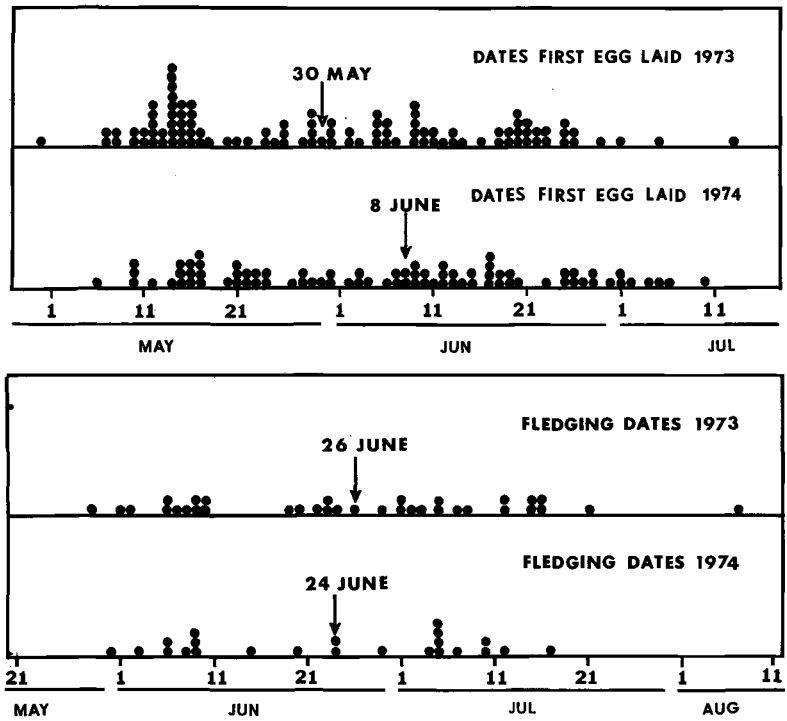

Fig. 1. Chronology of nesting, 1973 and 1974. Each circle represents date when first egg was laid in a nest or when young were fledged from a nest. Arrows indicate median dates.

The first egg was laid on 30 April and the last young was fledged on 6 August, a span of 98 days (Fig. 1). Except for a peak during mid-May, nesting activity, as evidenced by nest starts, remained rather constant from 10 May to 30 June 1973, declining rapidly thereafter. In 1973 young fledged (Fig. 1) mainly from 1–10 June and from 19 June to 15 July. Median dates for nest starts and fledging were 30 May and 26 June, respectively.

In 1974 we located 81 active nests. The time from the first egg laid (3 May) to the last young fledged (17 July) was 75 days (Fig. 1). Nest starts were rather evenly distributed throughout the period 10 May to 30 June. As in 1973 most fledging occurred in two periods 1–10 June and 5–12 July (Fig. 1). Median date for nest starts (8 June) was 9 days later than in 1973, but median fledging date (24 June) was 2 days earlier than in 1973.

Nesting females.—A total of 68 nesting females was banded in the 17

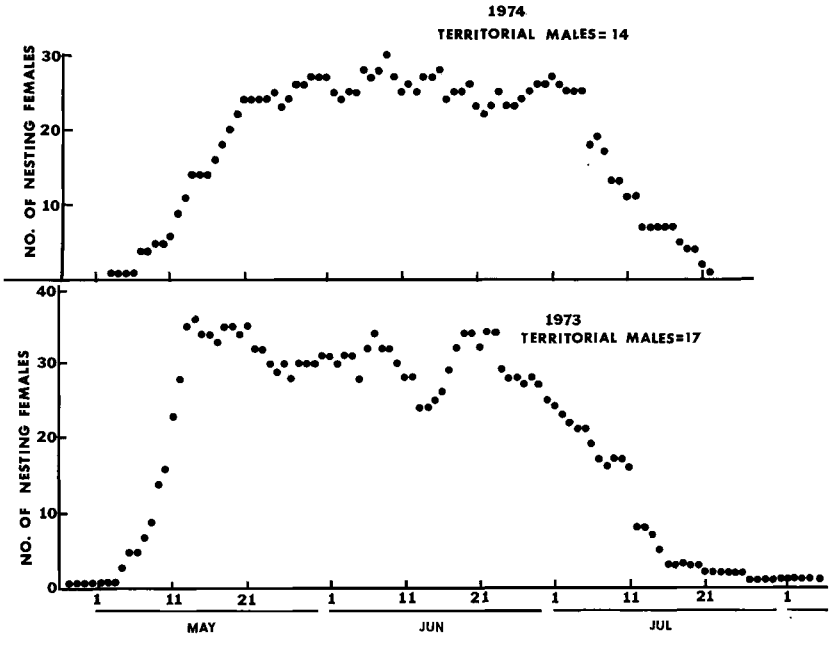

Fig. 2. Number of nesting females in Mason Field, 1973 and 1974. A nesting female is any female building a nest, laying or incubating eggs, or feeding nestlings.

territories in Mason Field in 1973, of which 17 were known to renest. Thus these 68 females accounted for 85 of the 105 active nests. The additional 20 active nests were destroyed by predators or abandoned before the females could be banded. Undoubtedly some of these 20 nests belonged to females tagged later while renesting, and some belonged to females in addition to the known population of 68.

A total of 64 nesting females was banded on the 14 territories in 1974, of which 10 were known to renest, accounting for 74 of the 81 active nests. As in 1973, the remaining nests (seven) belonged either to females banded later while renesting in Mason Field or to females in addition to the known population of 64.

Nesting females per territory.—The number of females nesting in Mason Field remained rather constant from mid-May through early July each year, ranging from 24 to 36 (mean 31.3) in 1973 and from 22 to 30 (mean 25.9) in 1974 (Fig. 2). Thus on any one day an average of 1.84 and 1.85 females was nesting per territory from mid-May through early July in 1973 and 1974, respectively.

The banding data showed clearly that although the female nesting

TABLE 1
NUMBER OF MALE TERRITORIES AND NESTING FEMALE RED-WINGED BLACKBIRDS IN MASON FIELD, 1973 AND 1974[1]

Year	No. of male territories	Minimum no. of nesting females for year	Maximum no. of nesting females for year	Maximum no. of nesting females on one day	Total active nests for year
1973	17	68 (4.00)	88 (5.18)	36 (2.12)	105 (6.18)
1974	14	64 (4.57)	71 (5.07)	30 (2.14)	81 (5.79)

[1] Values in parentheses represent average number of nesting females or nests per territory.

population remained numerically stable during each nesting season, there were turnovers in individuals nesting. About twice as many females nested over an entire nesting season (68 in 1973, 64 in 1974) as were present on any one day. Thus the minimum ratio of nesting females to male territories for the entire nesting season was 4.0 in 1973 and 4.6 in 1974 (Table 1).

The influx of females initiating their first nest in Mason Field was generally evenly distributed over the main part of the nesting season in 1974 (Fig. 3). A similar figure for 1973 is not presented because of the large number (20) of nests that were terminated before the females associated with them were banded. As I do not know how many of these females subsequently renested and were banded, it is impossible to say with certainty when many of the females banded during the last part of

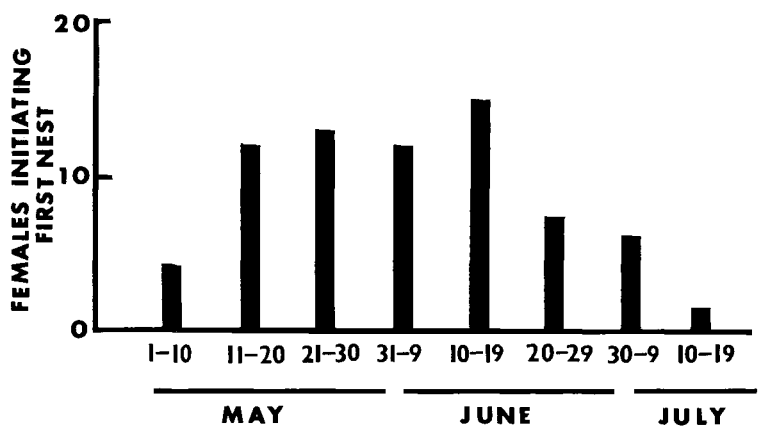

Fig. 3. Number of females initiating first nest in Mason Field during successive 10-day periods, 1 May–19 July 1974.

TABLE 2
RENESTING OF RED-WINGED BLACKBIRDS IN MASON FIELD, 1973 AND 1974[1]

Year	Minimum no. of females renesting in Mason Field	Number of renests	Minimum percentage of females renesting in Mason Field	Av. no. of days from end of nest to first egg of next known nest[2]	Av. distance (m) between successive nest sites[2]
1973	16	17	24	9.7 (4–30)	38 (8–95)
1974	9	10	14	12.1 (4–29)	40 (10–85)
TOTALS	25	27	19	10.6 (4–30)	39 (8–95)

[1] These values do not include any initial nesting or renesting that occurred off Mason Field.
[2] Range of values given in parentheses.

the 1973 nesting season first nested. The influx of nesting females in 1973 probably followed a pattern similar to that in 1974, as other characteristics of the female populations were similar (Fig. 2, Table 1).

The relation between age of female and time of nesting was investigated in 1974 to see if late-nesting females were predominantly 1-year-old birds. Aging by covert color, I classified 9 of 28 females (32%) that initiated nesting during the first half of the nesting season (before 8 June) as second-year birds compared with 4 of 11 (36%) during the last half. Thus age did not appear important in determining when a bird nested.

Renesting.—During 1973 and 1974, 25 of the 132 banded females (19%) are known to have renested (Table 2); 23 females renested at least once and 2 females renested at least twice. Of the 27 renests, 24 followed unsuccessful nesting attempts and 3 followed successful attempts. Two females in 1973 produced double broods. Females whose nests were destroyed in late May had the greatest probability of renesting, with the probability declining thereafter (Fig. 4). None of the 10 banded females whose nests were destroyed before 21 May renested.

Females switched territories in 3 of the 27 renesting attempts, and one banded female that abandoned her nest in Mason Field on 1 June 1973 was seen feeding fledglings 220 m north of the field on 18 July. She was the only banded female found renesting outside Mason Field in several searches made during late June-July in suitable nesting habitat extending out about 300–400 m from the study tract.

Measuring precise rates of renesting is difficult because of the continual egress and ingress of nesting females during the 1973 and 1974 nesting seasons. The evidence presented above indicates that those females leaving a territory did not commonly renest in nearby territories, either in Mason Field or adjacent areas. Potentially of course, many of these females

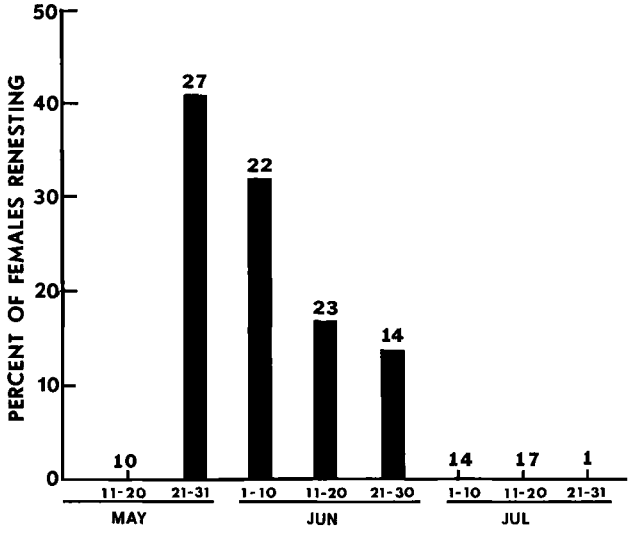

Fig. 4. Percentage of females that renested in relation to time of termination of previous nest in Mason Field, 1973 and 1974. The value above each bar is number of females that terminated nesting during that time period.

could have renested farther away, and many later nesting females could have nested elsewhere before nesting in Mason Field. For example in 1973 and 1974 at least 28 females had nested on and left Mason Field by 10 June. Based on the chronology of nesting (Fig. 1) and renesting (Fig. 4) in Mason Field, these females had ample time to renest elsewhere. Also the large number of females that entered Mason Field in the latter part of the nesting season (e.g. 29 after 9 June in 1974, see Fig. 3) had ample time to nest elsewhere earlier. Thus the true percentage of females that renested may be considerably higher than the values presented in Table 2.

Reproductive rate.—Clutch size averaged 3.38 (range 2–5, mode 3, N = 170) for 1973 and 1974 combined. A significant ($t = 4.8$, 168 df, $P < 0.001$) decrease in average clutch size occurred each year after the first week in June: average clutch size was 3.56 (mode 4) and 3.14 (mode 3) before and after 10 June, respectively.

Birds fledged in 1973 totaled 100 from 35 successful nests, and in 1974 totaled 70 from 23 successful nests (Table 3). The number of young fledged annually averaged 5.5 per territory and 13.3 per ha. Production varied widely among territories, ranging from 0 to 13 fledglings. The average number of young fledged annually per female was 1.3.

TABLE 3
NEST SUCCESS AND FLEDGING RATES FOR RED-WINGED BLACKBIRDS IN MASON FIELD, 1973 AND 1974

Year	Number of active nests	Percentage of nests successful	Young fledged/ territory	Young fledged/ hectare	Young fledged/ female
1973	105	33	5.9	15.4	1.5
1974	81	28	5.0	11.2	1.1
TOTALS	186	31	5.5	13.3	1.3

The average number of young fledged per active nest generally declined as the nesting season progressed (Fig. 5). Nests started during May averaged 1.0–1.4 fledglings compared with 0.3–0.5 fledglings for nests begun in late June-early July. This decline was due primarily to increased nest predation as the season progressed rather than to the decline in clutch size. The number of young fledged per successful nest remained rather constant, ranging from 2.8 to 3.1 for the seven time periods represented in Fig. 5.

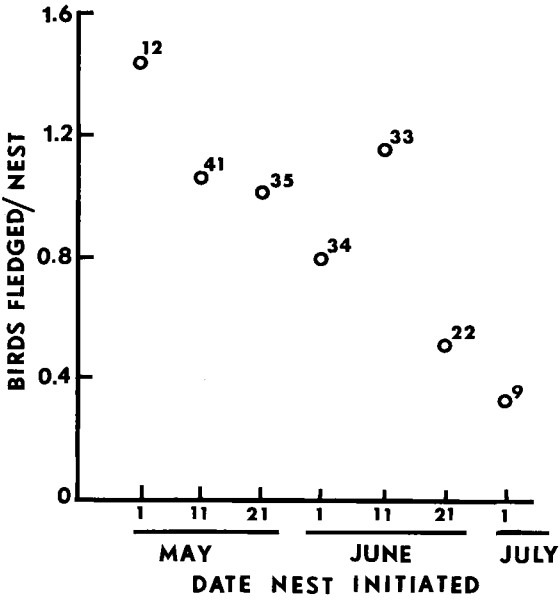

Fig. 5. Number of young fledged per active nest in relation to time of year nest was initiated. The value associated with each data point is number of active nests initiated during that time period.

Discussion

Human disturbance.—The use of nest traps in 1973 may have increased the susceptibility of nests to predation or made some females abandon their nests. Thus the turnover recorded in the female nesting population in 1973 possibly resulted, at least in part, from human disturbance. Still in 1974 when females were captured away from their nests and no human disturbance of nesting was evident, the turnover in nesting females was at least as extensive as in 1973, and as estimates of nesting success and fledging rates were actually higher in 1973 than in 1974 (Table 3), any human disturbance that may have occurred in 1973 does not appear important in the overall results.

Female movements.—Nero (1956) and Laux (1970: 42–44) found that female Red-wings were not particularly faithful to the same territory or territorial male from year to year, but both investigators felt that movement of females during a nesting season was slight. Three other studies indicate that such female movements do occur. Fankhauser (1964b), after banding early nesting females, recorded an influx of seven new nesting females after 21 June in a hayfield in Maryland. Jackson (1971) banded nesting females in central Ohio marshes and noted that there was sometimes an influx of new females into his study tracts, especially if he destroyed the nests of established birds. Haigh (1968: 50), although not working with banded birds, felt that new females were entering breeding populations of Red-wings late in the nesting season in marshes in Washington. My study supports these latter three findings and shows that the incidence of movements by females into and out of territories is substantial.

To estimate the sex ratio of Red-wings breeding in an area, investigators have traditionally tried to count either all females or all active nests present at one time during the peak of the nesting season and then divide this value by the number of male territories. This method is based on the assumption that the female population is sedentary during the nesting season. Estimates based on this method have generally ranged from 1.8 to 3.0 nesting females per male territory (Table 4).

I found that if the number of females nesting per territory is considered for the entire nesting season, this cumulative value is at least twice the value for any one point in time (Table 1). This difference may or may not be important, depending on the extent to which females nest in more than one territory. For example, in my study if virtually all the banded females nested and produced young only in Mason Field, then the female reproductive rates in Table 3 were indicative of annual reproductive rates for the nesting females. But if these females were commonly nesting and

TABLE 4
ESTIMATED RATIO OF NESTING FEMALES TO TERRITORIES FOR RED-WINGED BLACKBIRD POPULATIONS

Estimated av. no. of females nesting at one time per territory	Locality	Habitat	Reference
1.6	Oklahoma	Marsh	Goddard and Board (1967)
1.6–2.8	Illinois	Marsh	Smith (1943)
1.8–1.9	Ohio	Upland field	Present study
1.9	Maryland	Marsh	Meanley and Webb (1963)
1.9	New York	Upland field	Case and Hewitt (1963)
2.0	Wisconsin	Marsh	Nero (1956)
2.2	New York	Marsh	Case and Hewitt (1963)
2.7	California	Marsh	Collier (1968)
2.7–3.0	Washington	Marsh	Holm (1973)
2.8–3.7	California	Marsh	Orians (1961)
3.3	Michigan	Marsh	Laux (1970)

producing young elsewhere as well, the actual female reproductive rates would be higher than what I measured.

The fact that the number of females nesting at any one time during most of the nesting season remained rather constant and well below the total number that annually nested in Mason Field (Fig. 2) suggests that territorial males and/or nesting females regulated the nesting density at some upper limit or carrying capacity of the territories. The total number of females nesting in the territories was maximized by a temporal spacing of nest attempts by different females. Even if such a regulatory mechanism did occur, the central question would remain unanswered: (1) Did most females nest during the first part of the nesting season and then start switching territories, or (2) was there a surplus of breeding females that forced some females to delay nesting until the latter part of the nesting season? Jackson (1971: 104–105) presented some rather tenuous data supporting the idea of a surplus female population. Holcomb (1974) presented more substantial data indicating the converse.

I recorded four incidences of territory switching by females. Also, the low reproductive output per female on Mason Field compared with typical values for other passerine species (Henny 1972) suggests that these females fledged at least some additional young outside Mason Field. Thus I hypothesize that females were commonly switching territories (perhaps going substantial distances) and renesting rather than that a surplus female population delayed nesting until the latter part of the nesting season.

Reproductive success: upland and marsh habitats.—The number of young fledged per territory in the upland habitat of Mason Field was as high as or higher than all but one of the estimates for marsh habitats

TABLE 5
ESTIMATED NUMBER OF YOUNG ANNUALLY FLEDGED PER RED-WINGED BLACKBIRD TERRITORY

Estimated number of young fledged per territory	Locality	Habitat	Reference
2.6–3.7	Washington	Marsh	Holm (1973)
3.9	Oklahoma	Marsh	Goddard and Board (1967)
3.5–6.0	New York	Marsh	Case and Hewitt (1963)
5.7	Wisconsin	Marsh	Beer and Tibbitts (1950)
5.0–5.9	Ohio	Upland field	Present study
8.1	Maryland	Marsh	Meanley and Webb (1963)

reported by other investigators (Table 5). Previous investigators (Case and Hewitt 1963; Robertson 1972, 1973a, 1973b) have inferred that reproductive success is lower for Red-wings in upland than marsh habitat. They have noted that such factors as the percentage of active nests that were successful, the number of young fledged per successful nest, and the average number of females nesting at one time per territory tended to be lower in upland than in marsh habitat. Robertson (1972, 1973a) extended this reasoning to say that Red-wings probably prefer marsh habitat over upland habitat for nesting because it is a more "optimal" breeding habitat.

The only true measure of reproductive success is the number of young fledged either per territory or per adult female per nesting season. I cannot answer the question for adult females at present, but the data in Table 5 indicate that, on the average, just as many fledglings will be produced in an upland territory as will be produced in a marsh territory. More renesting and perhaps more energy may be required per fledgling produced in upland than in marsh habitat, but using "young fledged per territory" as the criterion of reproductive success, the data are insufficient to show which habitat should be preferred or considered inherently better for Red-wing nesting.

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SUMMARY

In 1973 and 1974 I examined the temporal spacing of nesting by female Red-winged Blackbirds in upland habitat in northern Ohio. Reproductive and renesting rates also were estimated.

Territorial behavior began in early April, and nesting occurred from early May to early August. The peak of nesting was from mid-May through early July and most young were fledged from early June to mid-July.

From mid-May through June the ratio of nesting females to male territories remained quite stable, averaging about 1.9:1.0, but new females constantly moved into territories and nested as previously established females finished nesting and left, and for the entire nesting season each year, an average of over 4.0 different females nested per territory. These data suggest that some social mechanism limits the number of nesting females at any one time to some "carrying capacity" of the territories. The total number of females nesting in the territories is maximized by a temporal spacing of nest attempts by different females.

A minimum of 19% of the females renested in the study area. I hypothesize that many of the other females were nesting elsewhere either before or after nesting in the territories on the study area. Four territory switches by females were recorded.

An average of 5.0–5.9 young were annually fledged per territory in this upland habitat, a reproductive rate within the range of estimations by other investigators for Red-wings breeding in traditional marsh-nesting habitat.

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