These data indicate postfledging parental feeding of young for at least 21 days in the Sooty Tern and 100 days in the Brown Noddy on Manana Island. Juveniles of both species spend some time at sea during these periods, and may be gaining experience necessary for the efficient capture of prey. These conclusions are consistent with the hypothesis of Ashmole and Tovar (1968) that prolonged parental care of young will occur in those species of birds whose feeding behavior requires a high degree of "skill." However, only the information on the Brown Noddy strongly corroborates the hypothesis.

This paper is based upon my doctoral dissertation submitted to the University of Hawaii. I thank Andrew J. Berger for guidance and criticism during this study. R. E. Ricklefs and W. B. Robertson commented helpfully upon the manuscript. The Hawaii State Division of Fish and Game kindly granted me permission to work on Manana. This study was supported by the Department of Zoology of the University of Hawaii, an NSF Graduate Fellowship, and a Mount Holyoke College Faculty Grant.

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SUCCESSIVE POLYGYNY IN UPLAND NESTING REDWINGED BLACKBIRDS

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Recent studies (Holm 1973, Zimmerman 1966, Verner 1964) and theoretical considerations (Orians 1969) of the polygynous mating system in birds have stressed its adaptive value in environments where the quality of males' territories differs sufficiently to affect the reproductive success of females. Particularly of interest in understanding the evolution and maintenance of polygyny are the behavioral aspects of nest site selection and the significance of such factors as the temporal pattern of nesting and the social conventions within the mating system. The importance of such behavioral and social considerations has been demonstrated, for example, in the polygynous mating system in the yellow-bellied marmot (*Marmota flaviventris*; Downhower and Armitage 1971).

Polygyny is common among Redwinged Blackbirds (*Agelaius phoeniceus*) nesting in marshes. No published information is available on the extent to which it occurs in other habitats, although many birds nest in cultivated fields, early successional areas and fields of forage crops (Bent 1958, Case and Hewitt 1963, Stowers et al. 1963, Robertson 1972). Surveys in 1957–1958 in Illinois, for example, indicated that although summer population densities were higher in marshes, most nesting occurred in hayfields (Graber and Graber 1963). The ability to utilize a variety of habitats for breeding suggests that nesting behavior of Redwinged Blackbirds is readily adaptable to different environments; studies of its breeding biology should therefore include such upland habitats and not be confined to marsh populations.

I recorded the nesting phenology of a group of Redwinged Blackbirds in an upland habitat and studied their behavior in an attempt to determine the social basis for polygynous matings. In this paper I will report instances of successive polygyny and propose a possible adaptive basis for this pattern of nesting. Information on nesting success and male territory size of these blackbirds will also be presented.

STUDY AREA

The study was made on an area of 3.2 ha. of early successional vegetation within the city limits of Iowa City, Iowa. The study area is bounded on the west by the Iowa River and on other sides by a wooded area, a housing development and the city park, an area of mown grass. Territories furthest from the river were located on undeveloped housing lots. Vegetation on the area was varied, depending on the recent history of each site. The density and phenology of vegetation ranged from grasses (Kentucky bluegrass, *Poa pratensis*, and reed canary grass, *Phalaris arundinacea*) to thick stands of goldenrod (*Solidago* spp.) and mixed clumps of forbs (daisy fleabane, *Erigeron annuus*; white sweet clover, *Melilotus alba*; dock, *Rumex crispus*; and coneflower, *Rudbeckia laciniata*). In some areas there were scattered clumps of saplings (cottonwood, *Populus deltoides*, and honey locust, *Gleditsia triacanthos*). Oak (*Quercus* spp.) and mulberry trees (*Morus alba*) occurred in the portion of the study area that paralleled the river.

The river bank dropped sharply so that a shallow area for foraging was not available. However, a storm water channel that ran through part of the study area to the river was frequently used by feeding birds. A pond outside the study area, in the park, was also used at times.

METHODS

Systematic observations were begun on June 1, 1973, by which time all but two territories had been set up, so that no observations were made on their initial establishment. I visited each nest daily from the date of its discovery. These observations did not appear to affect nesting success but may have caused a few

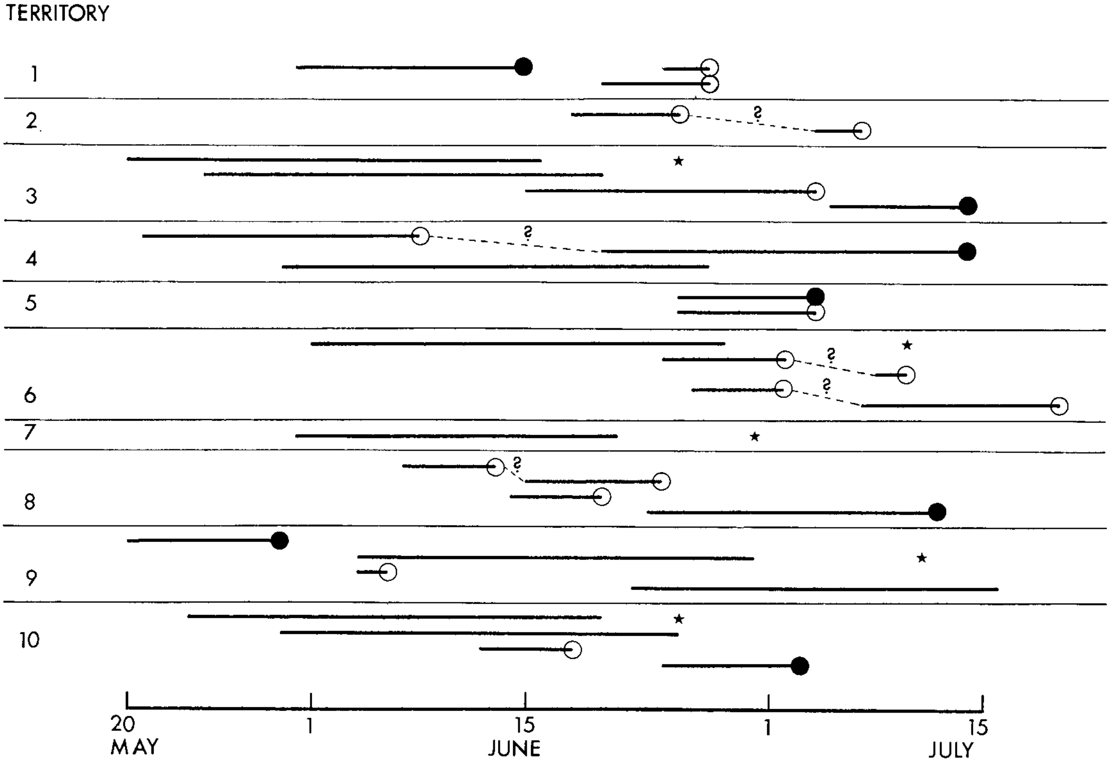

FIGURE 1. Nesting activity on the study area. Solid lines indicate the interval from nest construction to fledging. Circles indicate destruction or abandonment of the nest; solid circles indicate female was also killed. Star indicates time at which fledglings left the study area, where this is known. Dashed lines indicate possible renesting by the same female.

birds early in nesting to abandon their nests. Allen (1914) found that the presence of an observer near a nest early in the season was often sufficient disturbance to cause a nesting female to desert her nest. I mapped territories initially by approaching the nesting area and observing the area defended by a resident male against the intruding observer. More precise determination was later made by observing intraspecific territorial behavior of each male.

Since there were never more than two territories across the width of the study area at any point, I could observe with binoculars from outside the area without interfering with the birds' activities. Although birds were not marked it was usually possible to recognize individuals by their behavior and territorial defense.

RESULTS

The number of females nesting in a territory ranged from one to four (table 1). In some cases females probably renested, although this could not be determined with certainty since they were not marked. Where renesting seemed probable, the minimum number of nesting females possible is given. Marsh-nesting females are reported to range from one to six per male (Linsdale 1938, Orians 1961, Holm 1973), although Nero (1956) and Case and Hewitt (1963) observed a maximum of only three females per male. Males continued to mate with additional females as the nesting season progressed. Of the eight territories in which two or more females nested, only one male acquired more than a single female at the beginning of the breeding season. In other territories there was a hiatus of 4–20 days before a second female began nesting (fig. 1). Nesting females have been observed to have individual territories within a male's territory and aggressively to repel other females (Nero and Emlen 1961, Nero 1956, Case and Hewitt 1963, Orians 1973). I anticipated therefore that territorial behavior of nesting females would be an important factor in determining the number of females nesting on a territory at any one time. However, I saw no evidence of aggressive behavior among females, although observations were not made on the behavior of the earliest females, who nested in May. When not involved in brooding or feeding young, females nesting

TABLE 1. Number of females nesting in territories, and territory characteristics.

Territory	Min. no. ♀♀	Size (m²)	No. successful nests	Vegetation
1	3	700	0	Scattered forbs
2	1	1,300	0	Dense forbs
3	4	1,200	2	Dense forbs
4	2	1,200	1	Dense forbs
5	2	1,400	0	Scattered forbs
6	3	1,100	1	Dense forbs
7	1	3,600	1	Scattered forbs
8	3	5,600	0	Dense forbs
9	4	6,400	2	Grassy
10	4	9,600	2	Grassy

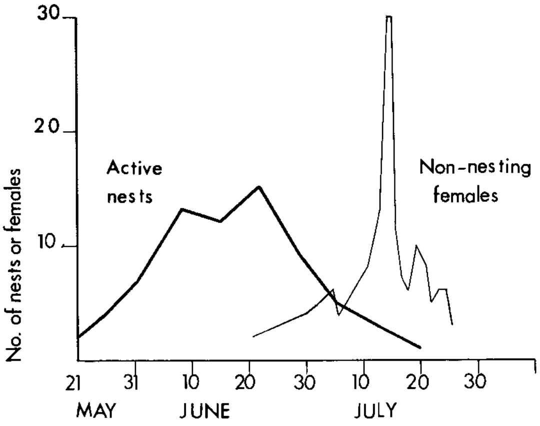

FIGURE 2. Size of non-nesting female group in relation to nesting activity.

TABLE 2. Reported sizes of Red-winged Blackbird territories (m^2) in marshes and uplands.

I. Marshes and ponds.

	Range	Mean(s)	Source
1.	243–4,533	688	Case and Hewitt 1963
2.	47–1,321	332 419 561 603	Holm 1973
3.	487–1,932	1,101	Orians 1973
	1,022–4,343	2,361	
4.	——	364[a]	Goddard and Board 1967
5.	124– 583	330	Nero 1956
6.	——	659	Orians 1961
	——	797	
	——	1,275	
	——	1,500	
	——	1,847	

II. Upland

	Range	Mean	Source
1.	121–4,006	2,185	Case and Hewitt 1963
2.	700–9,600	3,210	This study

[a] Estimated from data given.

More than one mean is given when data were available from different areas or years.

on the same territory were frequently observed foraging together at ground level on the territory. Such group social behavior was also seen when a female nested on a territory where other females were already nesting. For a few days before the new nest was constructed, the female was generally observed on the territory. In one instance, two females nested less than one meter apart, and on another occasion I saw two females from the same territory together collecting nesting materials and constructing nests near each other. From June 20 until the end of the nesting season, a group consisting only of females who were not nesting was also regularly seen on the study area (fig. 2). These are referred to as "non-nesting females" to avoid the implication that they did not breed elsewhere during the nesting season. During the day this group moved from one territory to another and was frequently observed perching quietly with a nesting female or foraging with her at ground level among dense clumps of forbs.

Females not currently nesting differed markedly in their behavior from nesting birds. They gave characteristic soft, short calls easily distinguished from those of nesting females. This call is apparently the same as the soft "check" or "prit" call that Nero (1956) described for arriving females at the onset of the breeding season. When non-nesting females were approached by an observer, they readily took flight and left the area. Nesting females, in contrast, made loud scolding calls and approached within 2–3 m of the observer in the defense of their nest. The breeding status of the group of non-nesting females described is unclear since none were captured for examination; however they did not appear to have juvenile plumage. Possibly they were females who had either nested early or unsuccessfully elsewhere. It is clear that these birds could not have been nesting on the study area, since on July 14 and 15 the group numbered 30 females, and only three nests were active at that time.

Territories. Territories ranged from 700 to 9,600 m^2 and were generally larger than reported sizes of territories in marshes (table 2). They remained sharply defined and only two changes were observed during the nesting season. On June 17 a male set up a territory (territory 2) by successfully defending an area that had been part of territory 7, and on June 22 territory 5 was set up on an area that had been part of territory 6. In both cases, nesting began within a few days of the appearance of a new territory.

Except where separated by a road or a narrow strip of mown lawn, territories were contiguous and were confined to areas not adjacent to the housing development. An adjoining area of 0.8 ha., not included in the study area, which bordered on the housing development and which provided poor cover for nesting, was not utilized. However, one male established a territory in that area early in the nesting season but apparently left after being unsuccessful in attracting any females.

Nesting success. Nest success, defined as the proportion of active nests which fledged at least one young, was 34.6%. The mean clutch size (excluding incomplete clutches) was 3.52 (±0.13 S.E.M.; N = 22). Of the 19 nests destroyed (i.e., which were not abandoned and did not fledge young), seven were destroyed when vegetation supporting the nests collapsed, often associated with winds and storms. Nine failures were due to predation and three to unknown causes. In four cases, there was evidence (tracks or scat) that raccoons, (*Procyon lotor*), were responsible. Seven nesting females were killed on or near their nests, and there were indications that four of these were killed by raccoons. Nest success was highest among those nests constructed early in the breeding season. Of the nine nests begun in the latter half of May, six were successful, while only three of the 23 nests begun in June or July were successful. Similarly, of the females killed, one was killed in May, one in June and five in July, when only 11 females were still nesting.

DISCUSSION

Among species where successive polygyny occurs, the staggered breeding of females may avoid problems of attracting predators to territories with a large number of nests and of overloading foraging areas. Verner (1964) has also suggested that it is of value among species in which the male must assist at some stage in the nesting period of individual females. In this situation, females may be expected to delay nesting until they can obtain help from the male. Males assist in feeding the young in a number of species where successive polygyny has been observed, including the Pied Flycatcher (*Muscicapa hypoleuca*; von Haartman 1951), the Long-billed Marsh Wren (*Telmatodytes palustris*; Verner 1964), the Ipswich Sparrow (*Passerculus sandwichensis princeps*; McLaren 1972) and the Dipper (*Cinclus mexicanus*; Price and Bock 1973). In the Dickcissel (*Spiza americana*), however, where successive polygyny has been observed the male does not assist his mates (Zimmerman 1966). In my study also, male Redwinged Blackbirds took no active role in care of the young beyond defending the nest, and females nesting in the same territory often overlapped extensively in their breeding periods. In fact, some females have been observed to nest in the same territory within a day or less of each other (Allen 1914, Nero 1956, Payne 1969, Orians 1973 and this study). Thus restrictions on the availability of the male cannot account for the cases of successive polygyny observed in this study. Since I never saw territorial behavior of nesting females towards other females, it seems unlikely that this prevented any females from nesting earlier in the season. Orians (1973) reached a similar conclusion, in a study of Redwinged Blackbirds nesting in tropical marshes. I therefore propose an alternative basis for the observed nesting pattern.

Older, more experienced females tend to nest early and form monogamous pair bonds, while younger females nest later and then mate with already-mated males. Evidence for this may be summarized as follows: In a study of the reproductive physiology of blackbirds breeding in California, Payne (1969) found that ovaries of yearling females develop slightly later than do those of older females. Allen (1914) described the arrival of resident adult females about April 10–May 1 and a later arrival of resident immature (though not sexually immature) females about May 10–June 11. Case and Hewitt (1963) also described delayed nesting of immature female Redwinged Blackbirds. This study suggests that polygynous pair bonds are most commonly formed after additional females arrive since with one exception, initially only one female nested in each territory. Holm (1973) also reported that females nesting early in the season did not settle in one or two territories but were fairly evenly distributed over the marsh and Allen (1914) suggested that many of the polygynous matings observed in his study occurred after the arrival of the group of resident immature females. If females who nest early each occupy a good quality territory, only the less suitable unoccupied territories will remain for females arriving later. This pattern of nesting will lower the polygyny threshold (Orians 1969) by decreasing the expected fitness of those later females who form monogamous pair bonds relative to those that nest in territories already occupied by earlier females.

Since predation is consistently the single most important source of mortality for eggs and nestlings (see, for example, data from Robertson 1972, Young 1963, Holm 1973), then the level of predator activity is an important factor in determining the quality of a territory. In heterogeneous habitats where patterns of predator activity such as runways are not obvious, a nesting female may be an indication to later nesting females of the quality of the territory in relation to predator activity. Thus, if later nesting females are attracted by the presence of females already nesting, they may tend to nest in territories where predators are less active. In this way they can indirectly assess territorial quality through gregarious social behavior and this may be the basis for such behavior observed in this study.

Delayed nesting of younger females would be advantageous if they are more likely to choose a better quality territory in this manner than if they nested earlier and risked, through inexperience, choosing a poor quality territory solely on the basis of its physical characteristics. For delayed nesting to be favored, however, this advantage must outweigh the disadvantage of generally poorer nest success later in the season. Nest success was higher earlier in the breeding season in this study and that of Robertson (1973) and Smith (1943).

To the extent that this hypothesis can be generalized for other species, two predictions can be made: 1) The best time to begin nesting may depend on intrinsic characteristics of the female, such as age. In the case of the Bobolink (*Dolichonyx oryzivorus*), for example, Martin (1974) found that subsequent secondary females were younger than primary mates. 2) To the extent that the successful nesting of an earlier female is a good indicator of the suitability of a territory, there is an adaptive basis for inexperienced females being attracted to territories with nesting females. Thus, given territories with very similar physical characteristics, a territory in which a female nests successfully should be more likely to attract subsequent females.

I thank Hugh Dingle and members of the Behavioral Ecology Seminar group at the University of Iowa for helpful comments and suggestions, and Elata Woodyard, Bill Platt, Ann Blakley and R. Bodenweiser for their assistance.

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FOOD SUPPLY AND NEST TIMING OF BROAD-TAILED HUMMINGBIRDS IN THE ROCKY MOUNTAINS

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Natural selection may favor animals which synchronize their activities in such a way that peak demands for given resources correspond with peak supplies. With this in mind, Lack (The Natural Regulation of Animal Numbers, Oxford, Clarendon Press, 1954) and Perrins (Ibis 112:242, 1970) considered the synchronization of breeding seasons of birds to food abundance. Perrins recognized that reproduction must often begin as soon as food supplies allow, and well before they peak, so as to anticipate the energetic costs of brooding and feeding chicks, which exceed those of incubating eggs. Accurate timing relative to resources should be clearest where demand is high, for example among hummingbirds breeding in temperate zones (Stiles, Univ. California Publ. Zool. 97, 1972). Especially in high, cool mountains, seasonal food sources must support an intense metabolism of these small homeotherms (Calder, Ecology 54:127, 1973; Lasiewski and Dawson, Condor 69:13, 1967; Pearson, Condor 52:145, 1950).

Breeding Broad-tailed Hummingbirds (*Selasphorus platycercus*) in the vicinity of the Rocky Mountain Biological Laboratory (Gothic, Colorado; 2900 m elevation), devote an average of 11.3% of their time foraging for flower nectar, as opposed to only 1.2% fly-catching for insects (total 18 hr 18 min daylight time-budget observation of two males and one female; unpubl. data). Predominantly taken are nectars of four flowers: *Delphinium nelsoni* Greene, *D. barbeyi* Huth., *Ipomopsis aggregata* (Pursh) V. Grant, and *Castilleja miniata* Dougl. My intention is to demonstrate (1) that the start of hummingbird reproduction at Gothic corresponds in time and space with flowering of the earliest nectar source, *D. nelsoni*; (2) that peak brooding activity in Gothic nests corresponds well with the peak density of the other three main hummingbird food plants (as listed above); and (3) that the total duration of summertime flowering of the four main food plants is implicated as a force that compresses the initiation of nesting toward the earliest possible date, because reproductive success of "late nesters" may be depressed in occasional years.

In the summers of 1972 and 1973, I followed 23 and 12 Broad-tailed Hummingbird nests, respectively, in 50 ha of aspen and conifer forest around Gothic. Qualitative notes only were taken on the condition of flowering during the first summer. In 1973, I counted blossoms of the four main hummingbird plants within 34 2 m × 2 m plots placed throughout the study area.

Figures 1 and 2 indicate the timing of flowering and of incubation in nests successfully brought to fledge in 1972 and 1973 (represented by the number of nests in the first ten days of their incubation activity). First incubation in Gothic followed *D. nelsoni* blooming by about 12 days in 1972, and by 7 days in 1973. Observations of May, 1973, suggest that male hummingbirds were frequent pre-season visitors who assumed residence just as the first *D. nelsoni* appeared. Also, females were first detected in a daily census of forests just as *D. nelsoni* blossomed in 1973 (fig. 2).

Figures 1 and 2 also show the period of brooding activity in successful nests in 1972 and 1973 (represented by the number of nests in the first ten days after hatch, ten days being roughly half the hatch-fledge interval). This period covered about five weeks, during which three of the four main hummingbird plants flowered, and blossom counts peaked as well (1973 data only; fig. 2). This suggests a close fit of the costliest period of the nesting season with that of the highest flower abundance.

Nest location, in addition to nest timing, reflected the pattern of flower appearance around Gothic. *D. nelsoni* and *I. aggregata* grew mostly along interfaces