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THE BREEDING ECOLOGY OF THE RED-WINGED BLACKBIRD (AGELAIUS PHOENICEUS) IN EASTERN INTERIOR ALASKA

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(*AGELAIUS PHOENICEUS*)
IN EASTERN INTERIOR ALASKA

A

THESIS

presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December, 1983

THE BREEDING ECOLOGY OF THE RED-WINGED BLACKBIRD

(AGELAIUS PHOENICEUS)

IN EASTERN INTERIOR ALASKA

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ABSTRACT

Red-winged Blackbirds (Agelaius phoeniceus) reach the northwest edge of their breeding distribution in eastern interior Alaska. Breeding phenology was more synchronous, eggs were larger, rate of weight increase was faster, and both clutch size and female reproductive success were higher for this population in comparison with populations further south. The lack of difference in the rate of tarsometatarsus increase in conjunction with the faster weight increase suggest that the observed weight increase and female reproductive success are environmental responses to good foraging conditions during the nestling period. Larger eggs and clutches may also be due to environmental responses. The high female reproductive success in light of the lack of predation, the apparently good foraging conditions and a very different harem size distribution in comparison to a Washington State study is taken as evidence that females choose males predominantly on the basis of territory quality.

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I am indebted to all of my office mates in 412 Irving for providing the proper atmosphere required for the analysis and writing portion of this study. Philip Martin, Brian Cooper, and Matt Ayres critically reviewed ideas presented to them. Dr. MacLean is again to be thanked for the number of times he provided vital sustenance to these discussions.

Thanks are extended to Julius Sam of Northway who allowed me to study the birds at Julius, Andrew, and Tractor Trail Lakes; and to Ted Inman and Stan Williams for helping me obtain equipment for this study. Finally, special thanks are due to Amy Reges for drafting the figures in this thesis.

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INTRODUCTION

The Red-winged Blackbird (redwing), *Agelaius phoeniceus*, has been one of the most intensively studied passerine birds in North America. Its breeding range extends from the tropics of northern Costa Rica to the subarctic taiga forests of Canada and eastern interior Alaska (Orians, 1980). During breeding season redwings are usually found associated with cattail (*Typha*) or bulrush (*Scirpus*) marshes.

Redwings have a polygynous mating system which may best be termed resource defense polygyny (Emlen and Oring, 1977). Zero to twelve females (Orians, 1980) may nest on the territory defended by the male. The nests are normally built in the cattail or bulrush portions of the territory.

Krebs (1978) defined ecology as the "the scientific study of the interactions that determine the distribution and abundance of organisms". In this respect the information gathered over the last twenty years by numerous researchers has provided valuable insights into the factors which can influence the distribution and abundance of redwings. However, it is important to understand the significance of breeding adaptations at the edge of the range, since the breeding adaptations of populations in the more central portions of the range may be different. Although abundance of many species decreases near the edge of their distribution, this need not be the case. In order to understand whether individual fitness and population abundance are low or high near the margins of distribution it is important to understand the underlying factors which affect the ability of the organism to maintain itself and reproduce in its environment.

In recent years there has been a controversy over the basis of female choice of breeding sites in the redwing breeding system. Female choice may be based on territory quality, a male's genetic quality, and/or a male's future parental investment. In his classic paper on the evolution of polygyny in birds and mammals, Orians (1969) suggested that in the absence of male parental care polygyny could evolve in a [illegible] re females base their choice of mate on territory quality alone. In this system females pair bigamously when territory quality is such that the expected reproductive gains of the female are as good or better than if she were to mate monogamously. Weatherhead and Robertson (1979), on the other hand, proposed the "sexy son" hypothesis, under which females base their choice of mate on male genetic quality. According to this hypothesis males which put more effort into epigamic display and less into territory defense (intrasexual display) will leave sons which are more successful because they are better at attracting females than males which put more effort into territory defense. Although proficiency in territory defense and proficiency in attracting mates are not mutually exclusive, the controversy hinges on the importance of the role of territory quality in the evolution of polygyny in redwings.

The purpose of this study was to document the breeding ecology of redwings in eastern interior Alaska at what is probably the northern end of their breeding range in western North America. The information gathered has been used both to understand the significance of breeding adaptations at the edge of the range and to elucidate some aspects of the phenomenon of female choice in the mating system of redwings.

STUDY AREA

This study was conducted in the vicinity of Northway, Alaska (62 degrees 58' N,141 degrees 56' W). Northway is a village located in the Northway-Tanacross lowlands where the Chisana and Nabesna Rivers meet, to form the Tanana River. The average annual temperature in Northway is -5.5 degrees C and the average annual precipitation is 265 mm (National Weather Service).

The Northway-Tanacross lowlands consist of a discontinuous permafrost of gravel, loess, and sand deposited by alluvial streams and is overlain by a wet loam soil with a thick organic mat (Selkregg, 1976). The lowlands consist of a mosaic of terrestrial vegetation types dominated by open and closed black spruce coniferous forest (Viereck et al, 1981). About a third of the lowlands is covered by open water (Spindler and Kessel, 1977). Some of the major plant species and taxonomic groups of vegetation which occur in or around these ponds and lakes are Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), Dwarf Birch (*Betula glandulosa*), Labrador Tea (*Ledum* palustre groenlandicum), Bearberry (Arctostaphylus spp.), Fireweed (Epibolium angustifolium), Cottongrass (Eriophorum spp.), Tundra Rose (Potentilla fruticosa), Prickly Rose (Rosa acicularis), horsetails (Equisetum spp.), and various mosses and lichens.

Redwings breed along ponds and lakes in the Northway-Tanacross lowlands which support suitable stands of cattail (Typha latifolia) or bulrush (Scirpus validus). The presence of cattail or bulrush in the Northway-Tanacross lowlands is very patchy. A survey of all lakes and ponds within one-half km of the Chisana River for 50 km upstream of the Northway Junction bridge revealed that only one pond out of more than twenty-five ponds and lakes had cattail vegetation. None of these ponds or lakes had bulrush vegetation. Although the presence of cattail and bulrush is very patchy, there are several lakes in the vicinity of Northway which have suitable stands of cattail and support breeding redwings (Table 1, Figure 1). These lakes were chosen for study because they were close enough together that each could be visited at least once every four days. With the exception of Shashamund Lake, all of these lakes are contained within an area of 16.9 square km. Most of the lakes and ponds within this 16.9 square km area were checked for redwing activity, and only those listed in Table 1 were found to have breeding redwings. Shashamund Lake was only studied in 1981 due to lack of suitable transportation to that lake during the 1982 field season.

Table 1. Lakes and associated areas, number of breeding males, and number of breeding females in this study.

Lake	Approximate Area(ha)	1981 males	1981 females	1982 males	1982 females
Hudeac Lake	12.9	2	3	2	3
Pond Southeast Hudeac Lake	6.4	1	1	0	0
Lake at west end Northway	6.4	1	5	1	4
Tractor Trail Lake	12.9	1	3	1	1
Andrew Lake	25.7	3	6	4	8
Julius Lake	45.0	9	16	8	17
Shashamund Lake	36.7	7	12	--	--

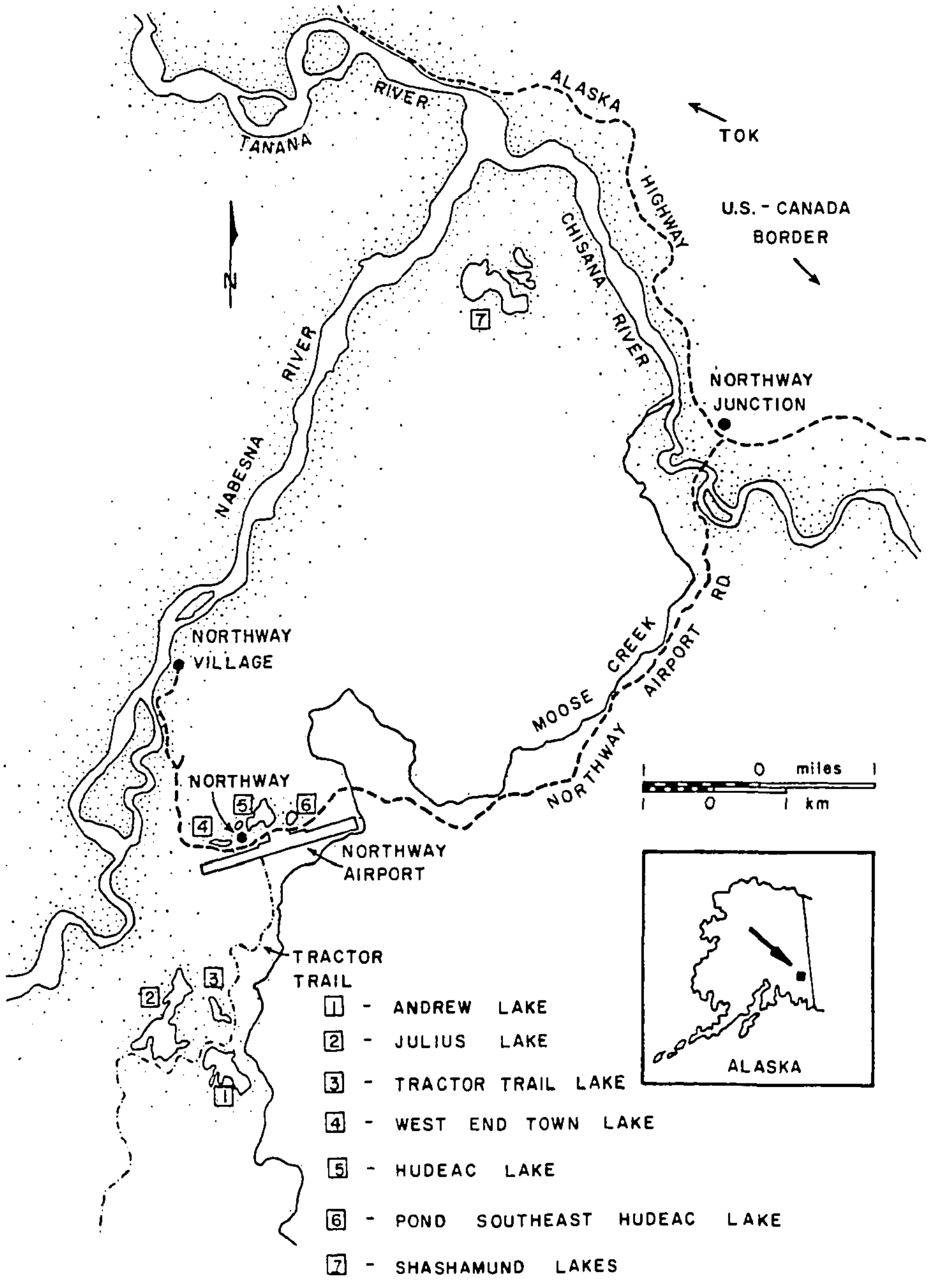

Figure 1. The Northway area with study lakes identified.

METHODS

Observations of the breeding area extended from 10 May to 7 July 1981, and from 11 May to 6 July 1982. Each male redwing that was discovered was observed to determine the extent of his territory by noting the area within which he reacted to a human intruder. Female activity on each male territory was also noted.

I began intensive and systematic searches for nests on 1 June 1981, and on 6 June 1982 until all male territories had been searched for nests. There were also additional searches for nests when it was suspected that additional nesting was occurring on a territory. As each nest was found measurements were made to characterize the nest site. These measurements included height of the nest above water, depth of the water below nest, density of cattails within a 0.3 m radius around the nest, highest cattail within a 0.3 m radius around the nest, distance from nest to shore, and distance from nest to open water.

I visited nests once every four days in 1981 and once every three days in 1982, except when this was prevented by adverse weather. Eggs were measured for length and maximum breadth and individually marked for identification. I also recorded whether the eggs in each clutch were warm or cold in order to determine if incubation had commenced. Nestlings in the nest were weighed at each visit with a 10, 50, or 100 gram Pesola scale depending on weight. Length of the right tarsometatarsus of each nestling was also measured using dial calipers.

Each nestling was individually marked on a combination of the left or right tibia or tarsometatarsus with a permanent marker (El Marko by Flair). I discovered that some females will remove banded young nestlings from the nest in an attempt to remove the band from the nest, so nestlings were not banded with U.S. Fish and Wildlife Service bands until I judged that fledging was imminent. Nestlings were assumed fledged if they were not present in the nest after eight days of age and had appeared healthy on the previous visit to the nest.

Egg volume was calculated as 0.524*length*breadth**2 (Preston, 1974). The weight and tarsometarsus length at day 1 is defined as any measurement of these parameters taken within 24 hours of hatching. I used the total number of first nesting attempts in order to calculate clutch size per nest, number of eggs hatched per nest, and number of young fledged per nest. Thus renesting has not been incorporated into these parameters.

Tests of statistical difference were performed according to Zar

(1974), Conover (1981), and Biomedical Computer Program (BMDP) statistical software. Unless otherwise specified, each null hypothesis was rejected if the test statistic exceeded the critical value of 0.05.

RESULTS

1. Breeding Phenology

A male redwing was present at the east end of Hudeac Lake in Northway when I arrived on the afternoon of May 10, 1981. The ice on Hudeac Lake was breaking up at this time. This male was feeding intensively at the edge of a mat of vegetation exposed by the melting ice. I observed this male's feeding activities from a nearby stand of cattails. There was no apparent defense illicited by my intrusion into the cattails, so I judged that this male had recently arrived in the Northway area. These same cattails were defended by a male redwing at 3:30 a.m. the next morning. The first female redwing was seen at Hudeac Lake on May 17, 1981.

In 1982 observations at the breeding areas commenced on May 11. The first male redwing was spotted on Julius Lake the evening of May 14 when it was covered with ice. Some margins of this lake were open and may have provided feeding sites for arriving males. The first female redwing was spotted at Hudeac Lake on the morning of May 22,

1982. The ice on the study lakes at this time was breaking up.

Figure 2 compares the phenology of clutch initiation, hatching, and fledging in 1981 and 1982. Median dates of clutch initiation, hatching, and fledging were May 29, June 13, and June 25 in 1981; corresponding dates were two to three days later in 1982. In 1981 there was no snow on the ground in May; however, in 1982 snow remained on the ground until May 8 (National Weather Service). Likewise lakes which were melting on May 10 in 1981 did not achieve an equivalent stage of melt off until around May 20 in 1982. Thus although breakup differed by about ten days, the breeding seasons seemed to be separated by only three days in the two years of this study.

In Figure 2 the cumulative frequency curves for 1981 and 1982 converge in the later half of each of the clutch initiation, hatching, and fledging subseasons. In 1981, 10% of the clutches were started by May 25 whereas in 1982 10% of the clutches were not initiated until May 28; these dates are 8 and 6 days, respectively, after females were first observed on the study area. Likewise, the peak in nesting (Figure 3) was separated by two days (June 11 in 1981 and June 13 in 1982). However, in both 1981 and 1982 90% of the clutches were started by June 9. Thus although the breeding season in 1982 started two to three days later than in 1981, the 1982 breeding season terminated essentially on the same schedule as the 1981 breeding season. The central 80% (10%-90%) of nests were initiated in a 14 day period in 1981, and a 12 day period in 1982.

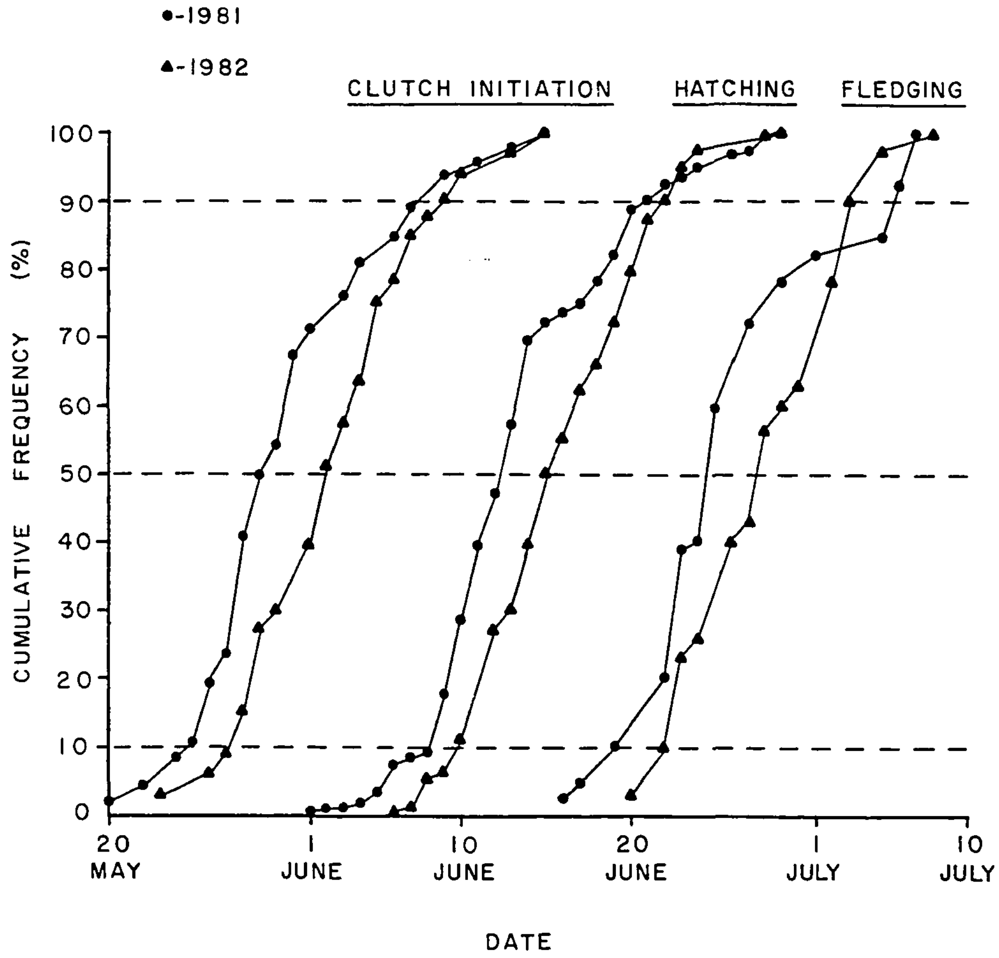

Figure 2. Cumulative frequency of clutch initiation, hatching, and fledging phenology for 1981 and 1982.

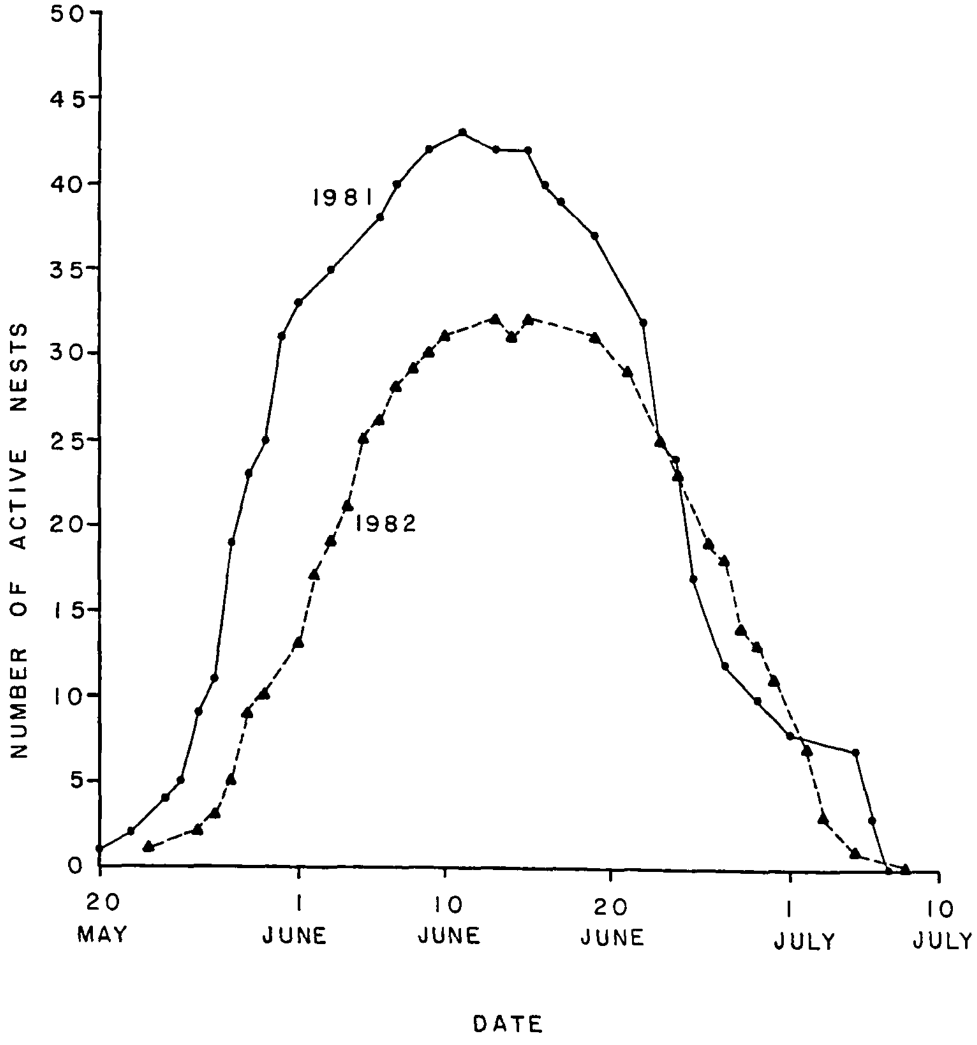

Figure 3. Number of active nests as a function of date in the breeding season. This figure excludes renesting attempts.

2. Egg Volume, Clutch Size, Number of Eggs Hatched per Nest, and Number of Nestlings Fledged per Nest

Table 2 compares the results for mean egg length, breadth, and volume for 1981, 1982, and both years combined. Egg volume, length, and breadth were all significantly larger in 1982 (Mann Whitney; Volume:$P=.0087$; Length, Breadth:$0<P<0.0001$).

The mean clutch size in 1981 and 1982 was 4.4 and 4.3 respectively. The mean clutch size for both years combined was 4.3. Table 3 shows the number of nests in each clutch size category for 1981, 1982, and both years combined. The modal clutch size in both years was 4.0.

The mean number of eggs hatched per nest in 1981 and 1982 was 3.9 and 3.6, respectively (3.8 for both years combined). In 1981 and 1982, 11.1% and 15.5%, respectively, of the eggs laid did not hatch (12.9% for both years combined). Table 4 shows the number of nests in each category of eggs hatched per nest for 1981, 1982, and both years combined.

Table 5a shows the number of nests in each nest termination category. In both 1981 and 1982 most of the nests fledged young. The mean number of nestlings fledged per nest in 1981 and 1982 was 3.4 and 3.5 respectively (3.4 for both years combined). In 1981 and 1982 12.8% and 4.2%, respectively, of the eggs hatched did not fledge (9.6% for both years combined). Table 5b shows the number of nests in each

Table 2. Egg Length, Breadth, and Volume

Year	N	Avg.Length-mm	Avg.Breadth-mm	Avg.Volume-cu.mm
1981	169	25.0 (±1.2)[a]	18.0 (±0.9)	4240 (±530)
1982	138	25.5 (±1.3)	18.4 (±0.6)	4510 (±410)

a. Number in parentheses indicate standard deviation

Table 3. Number of nests in each clutch size category and total number of nests and eggs.

Year	Clutch Size 1	2	3	4	5	6	Total Nests	Total Eggs	Eggs/ Nest
1981	1	1	3	24	18	0	45	198	4.4
1982	0	1	2	17	12	1	33	142	4.3
Total	1	2	5	41	30	1	78	340	4.3

Table 4. Number of nests in each category of eggs hatched per nest and total number of eggs hatched.

	Number of eggs hatched per nest							Total Nests	Total Nestlings	Nestlings/ nest
	0	1	2	3	4	5	6			
1981	3	0	1	6	19	16	0	45	176	3.9
1982	2	0	2	10	10	8	1	33	120	3.6
Total	5	0	3	16	29	24	1	78	296	3.8

Table 5a. Number of Nests in each Nest Termination Category

Nest Termination Category	1981	1982
All Nestlings Fledged	29	28
Some Nestlings Fledged (Excluding Nests with young removed due to banding)	4	2
Some Nestlings Fledged (only nests with young removed due to banding)	7	0
All Nestlings died in the nest	1	1
Nest desertion (eggs still in nest)	2	2
All Nestlings removed from nest due to banding	2	0
Unknown	2	0

Table 5b. Number of nests in each category of number of young fledged per nest and the total number of young fledged.

Year	Number of young fledged per nest							Total Nests	Total Fledglings	Fledglings per nest
	0	1	2	3	4	5	6			
1981	5	0	2	7	16	8	0	38	129	3.4
1982	3	0	4	7	10	8	1	33	115	3.5
Total	8	0	6	14	26	16	1	71	244	3.4

category of young fledged per nest for 1981, 1982, and both years combined. Some of the nests which had nestlings evicted following banding in 1981 did fledge young. These nests are not included in Table 5b, although they are included in Table 5a as successfully fledged.

Table 6 shows hatching success (eggs hatched/eggs laid) and breeding success (nestlings fledged/eggs laid) as a function of clutch size. Hatching success and breeding success are equally high for different clutch sizes. Fledging success (nestlings fledged/eggs hatched) also is equally high across different initial brood sizes (Table 6). The strongest positive relationship in Table 6 is the one between number of young fledged and number of young hatched. If an egg hatched there was a high probability that the resulting nestling fledged. Thus, the nonmodal clutch size of five fledged more young per nest, on the average, than the modal clutch size of four. Average nestling weight at day seven was independent of number of young fledged per nest (Figure 4). Thus large broods fledged young of similar weight as small broods.

3. Growth Rates

Nestling weight as a function of age is depicted in Figure 5. Only the weights at day ten, during the fledging period, are significantly different between years (two sample t test, P=.01). Weight

Table 6. % hatching success, % fledgling success, and % breeding success as a function of either clutch size or number of eggs hatched per nest.

	Clutch size 1	2	3	4	5	6	Total
1981 Hatching Success	0(1)[a]	0(1)	100(2)	90(24)	99(16)	--	92(44)
1982 Hatching Success	--	100(1)	100(2)	84(17)	85(12)	100(1)	86(33)
Total Hatching Success	0(1)	50(2)	100(4)	87(41)	93(28)	100(1)	90(73)
1981 Breeding Success	0(1)	0(1)	100(2)	78(23)	93(11)	--	83(38)
1982 Breeding Success	--	100(1)	50(2)	81(17)	82(12)	100(1)	81(33)
Total Breeding Success	0(1)	50(2)	75(4)	79(40)	87(23)	100(1)	82(71)

	Number of eggs hatched per nest 1	2	3	4	5	6	Total
1981 Fledging Success	--	100(1)	83(6)	90(18)	94(10)	--	91(35)
1982 Fledging Success	--	100(2)	83(10)	100(10)	100(8)	100(1)	96(31)
Total Fledging Success	--	100(3)	83(16)	94(28)	97(18)	100(1)	93(66)

a. Number in parentheses indicate number of nests on which each statistic is based.

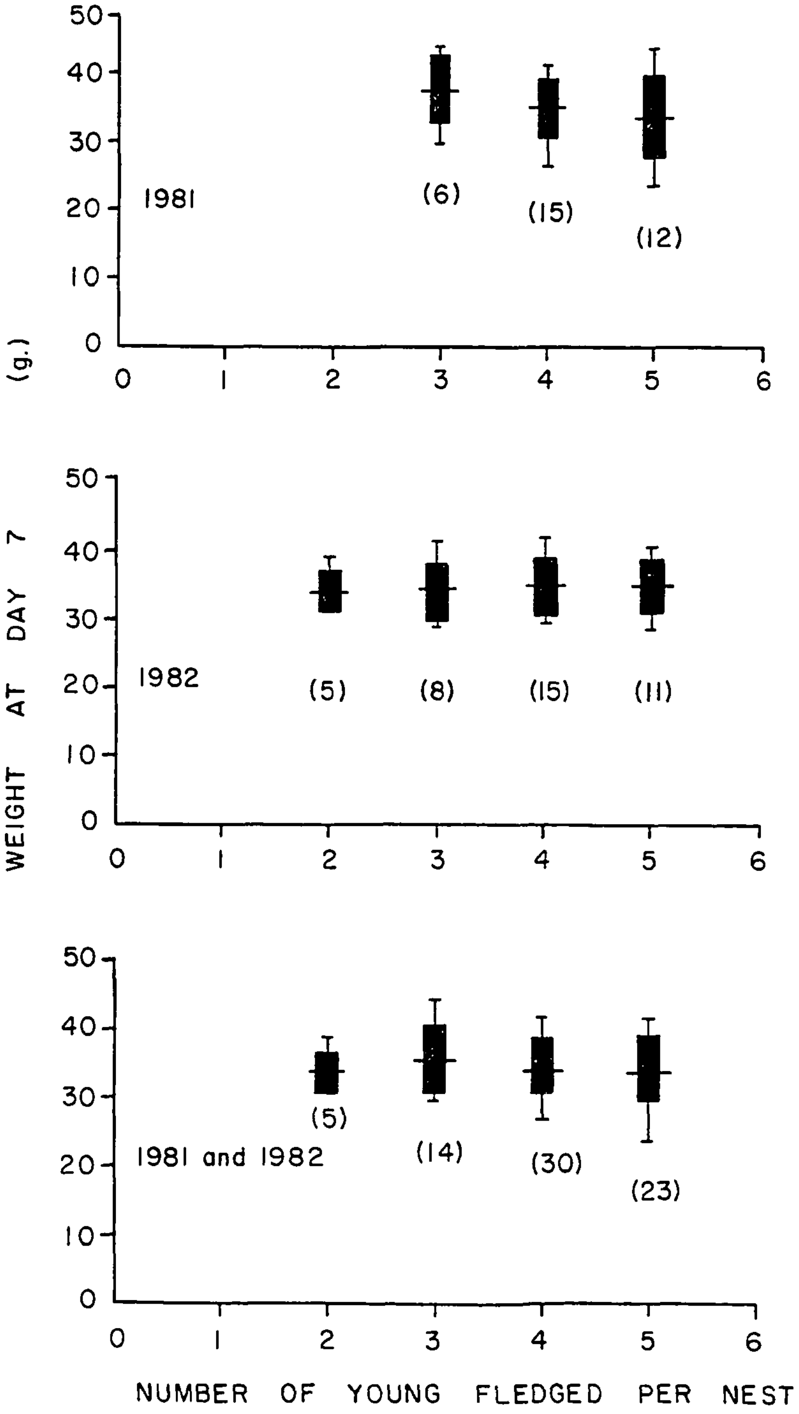

Figure 4. Growth as a function of the number of young fledged per nest. Numbers in parentheses indicate sample size. Mean, range, and standard deviation are indicated.

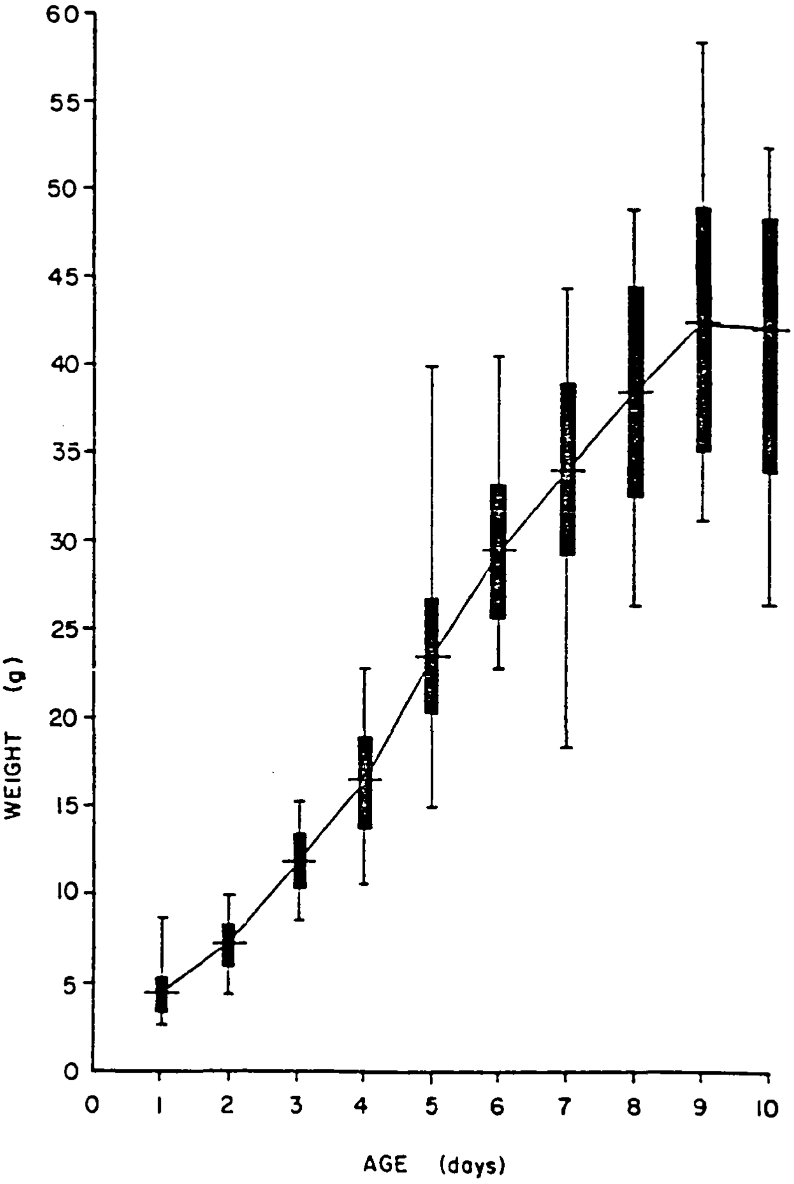

Figure 5. Nestling weight as a function of age (1981 and 1982). Mean, range, and standard deviation are indicated.

does not appear to be approaching an asymptote by the time of fledging. The relationship between tarsometatarsus lengths and age is depicted in Figure 6. Tarsometatarsus length does seem to be approaching an asymptote by the time of fledging.

4. Results Pertaining to Female Choice

Table 7 displays the number of territories in each harem size category for 1981, 1982, and both years combined. The mean harem size in 1981 and 1982 was 2.0 and 2.2 respectively. For both years combined the mean harem size was 2.1.

Table 8 compares 1981 and 1982 for the six nest site characteristics measured in this study. None of these six nest site characteristics differed significantly between 1981 and 1982. Spearman rank correlation coefficients were calculated for each of the nest site characteristics with the number of young fledged per nest for 1981, 1982, and both years combined. None of these correlations were significant. The number of young fledged per nest was also checked against each of the six nest site characteristics for the possibility of the existence of nonlinear relationships. No definable nonlinear relationships were found. Thus, within the range of nest sites chosen by females, there is no evidence that quality of the nest site affects reproductive success in the Northway population. However, two of the nests which failed in 1982 failed because they were built too close to

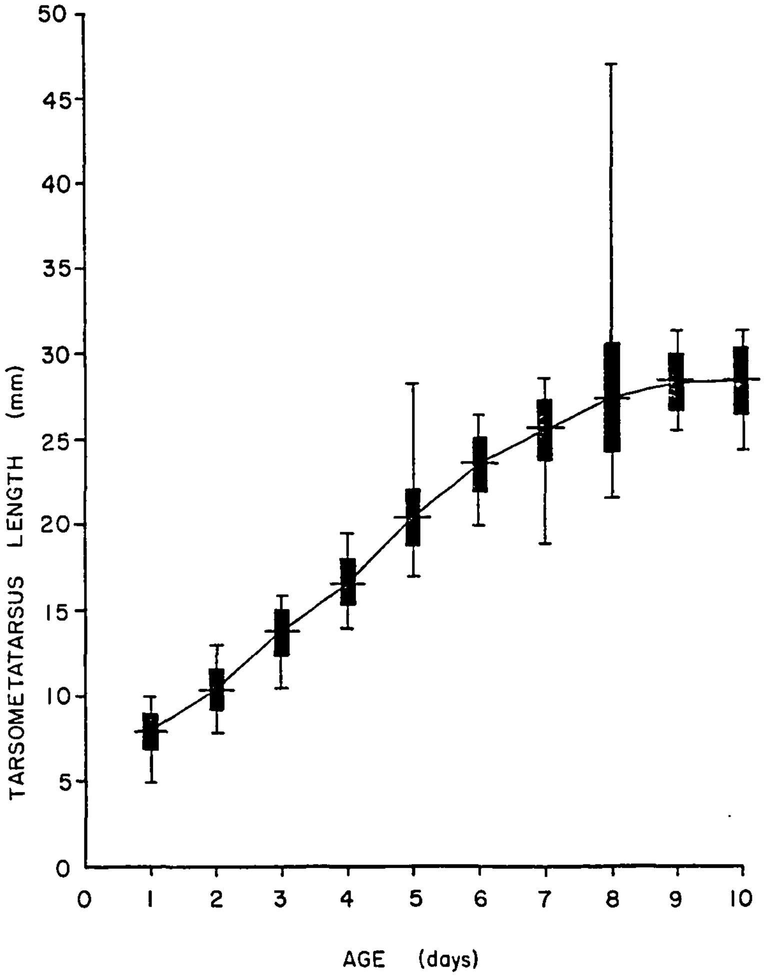

Figure 6. Tarsometatarsus length as a function of age (1981 and 1982). Mean, range, and standard deviation are indicated.

Table 7. Number of territories in each harem size category.

	Number of females per territory					Total Territories	Avg. Harem Size
	1	2	3	4	5		
1981	8	10	5	0	1	24	2.0
1982	4	7	1	3	0	15	2.2
Total	12	17	6	3	1	39	2.1

Table 8. Nest Site Characteristics

Year	HBN - cm	DBN - cm	HCT -cm	DCT - #	DNS - cm	DNOW - cm
1981	25 (±13)[a]	41 (±(18)	125 (±23)	15 (±4)	1236 (na)[b]	174 (na)
1982	21 (±14)	50 (±25)	124 (±27)	16 (±4)	967 (na)	217 (na)

HBN - Height from water level to bottom of nest.
DBN - Depth of water below nest.
HCT - Highest cattail in a circle 30 cm radius around nest.
DCT - Number of cattails in a circle 30 cm radius around nest.
DNS - Distance nest to shore.
DNOW - Distance nest to open water.

a. Number in parentheses indicate standard deviation.
b. Standard deviation no applicable because of highly skewed and/or kurtotic distribution.

water. In one of these nests the eggs became wet and cold, and in the other nest the nestlings became wet and died. The absence of any discernable relationship between nest site characteristics and breeding success may therefore be the result of the fact that very few nests failed in either year. The absence of predators, the good weather present during the nestling period in both years of the study, and the apparent abundance of food probably account for the high nest success.

Table 9 depicts the number of young fledged per nest as a function of harem size. In 1981 females in the modal harem size of two fledged more young from their nests on the average than females in other harem sizes. However, in 1982 females in harems of four fledged the most young per nest. For both years combined there is a general increase in number of young fledged per nest with increasing harem size except for harems of five (based on data from one harem). A Kruskal-Wallis test was performed to compare the mean number of young fledged per nest for harems of different sizes. No significant differences among these means were found (1981:$0.9<P<0.95$; 1982 and both years combined:$0.5<P<0.75$). On the basis of these data no pattern of the number of young fledged per nest as a function of harem size seems to exist.

In order to test if females with established nest sites might be temporarily despotic in time and therefore delay nest establishment by other females within the harem I performed an analysis originally used by Yasukawa and Searcy (1981). I first calculated the difference in

Table 9. Number of young fledged per nest as a function of harem size.

		Harem Size				
	Year	1	2	3	4	5
Female Reproductive Success	1981	3.0(7)[a]	3.6(13)	3.5(14)	--	3.0(4)
	1982	3.8 (4)	3.1(14)	3.3(3)	3.8(12)	--
	Total	3.3(11)	3.3(27)	3.5(17)	3.8(12)	3.0(4)

a. Number in parentheses indicate sample size in number of nests.

clutch initiation dates between each pair of nests. The interclutch initiation difference was then subdivided into two categories: those differences that occurred only between harems and those differences that occurred only within harems. Thus two distributions of interclutch initiation differences were obtained. The cumulative frequency graphs of the within and between harem distributions of differences in clutch initiation dates for 1981, 1982, and both years combined are shown in Figure 7. Using the between harems distribution as the expected distribution, a Kolmogorov-Smirnov test was performed. The results of this test for 1981, 1982, and both years combined indicate that the difference between the distributions in each graph is not significant. On the basis of this analysis it cannot be concluded that despotic behavior between females influences the temporal pattern of nest establishment.

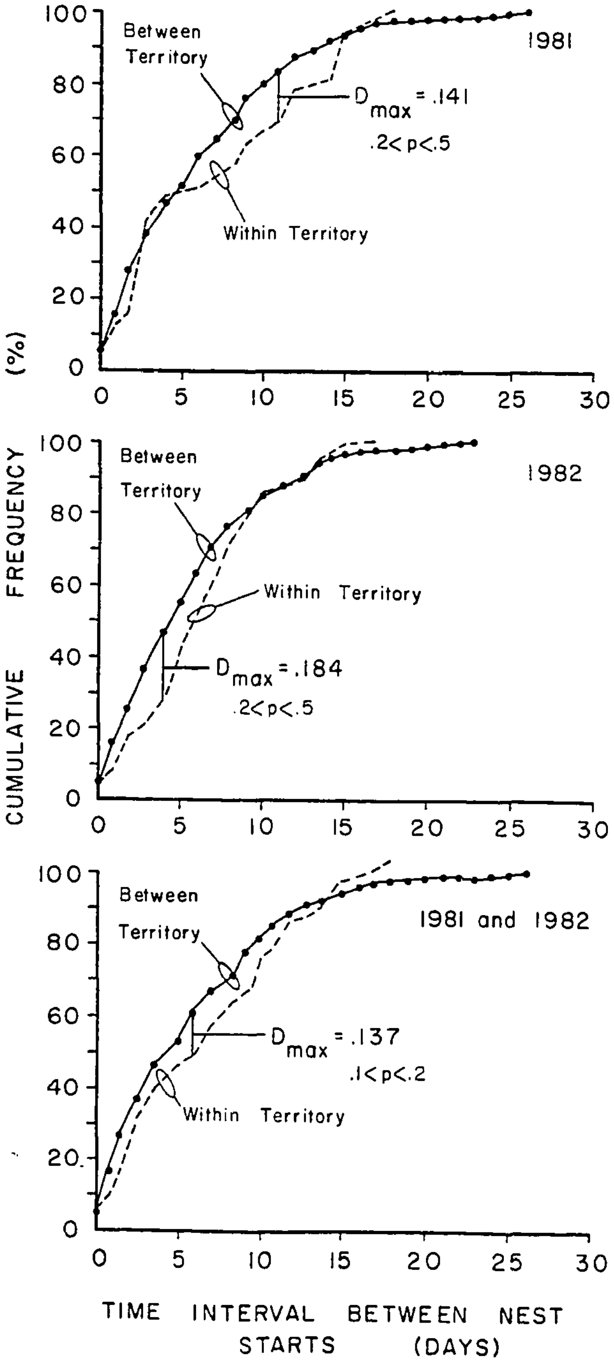

Figure 7. Cumulative frequency of the distributions of differences in clutch initiation for nest pairs between harems and nest pairs within harems.

DISCUSSION

1. The significance of breeding adaptations at the edge of the range

a. Adaptive Response vs. Environmental Response

The adaptive significance of life history parameters such as clutch size and development rates has been the focus of attention in ecology in recent years. Much of the literature has concerned comparisons of these parameters across species (for example see Lack, 1968; Ricklefs, 1968, 1973). However, the variance in these parameters that exists within a species probably provides the best opportunity for understanding the constraints responsible for these breeding adaptations. Therefore, comparisons of these parameters between different populations has the potential for identifying factors important in the evolution of breeding adaptations.

Given that a particular feature of breeding biology varies between two populations, it is not appropriate to assume that this difference has come about for adaptive reasons. Local environmental conditions may affect the expression of breeding adaptations. Thus differences in breeding parameters between populations can be classified as either adaptive responses or environmental responses of can have components of both. Adaptive responses, for the sake of this discussion, are therefore defined as phenotypic changes due entirely to a change in the genetic machinery responsible for the expression of a trait. Environmental responses, on the other hand, are defined as phenotypic changes that are entirely environmentally induced. Environmental responses therefore represent plasticity in the expression of a trait.

b. Breeding Phenology

Breeding Red-winged Blackbirds have probably evolved in marshes, although in recent times uplands have provided suitable breeding habitat (Robertson, 1972; Case and Hewitt, 1963; Albers, 1978; Joyner, 1978; Dolbeer, 1976; Stowers et al, 1968). Orians (1980) suggested that redwings are adapted to breeding in marshes where aquatic emergents such as Typha and Scirpus are present. The marshes provide a food source for both adults and young. In particular, emerging odonates (dragonflies and damselflies) are probably the most important food source (Orians, 1980). Odonates make the transition from an aquatic immature to a terrestrial adult by swimming towards the edge of the lake and emerging either on shore or on the stalk of an aquatic emergent plant. There they go through their final molt to the winged adult insect. During this final molt they are vulnerable because they must let their exoskeletons harden before they can become airborne. Thus the edge of the marsh provides a source of food for redwings during the time of year when odonates emerge from lakes and ponds.

Orians (1980) suggested that the redwing breeding season in eastern Washington is coupled to the pattern of odonate emergence. Although I have no quantitative data concerning odonate emergence in the Northway area, I did notice that odonates reached a peak in emergence somewhere between mid and late June. This corresponds with the period during which nestlings were present in the nest.

It is interesting to note that the peak in active nesting (Figure 3) is only separated by two days between 1981 and 1982, whereas the time of lake thaw is separated by about ten days. Therefore, the birds are not using lake thaw as a cue to time their nesting activity. It appears on the basis of my data that the birds are attempting to time their breeding with the average time of peak odonate emergence. However, other strategies of adaptive breeding phenology are also possible.

Table 10 compares the breeding phenology of several populations over the breeding range of the Red-winged Blackbird. The date at which the first clutch in the breeding population is initiated is later in Northway than any other locality except for a population in Mentor, Ohio (Bernstein, 1980) where the first egg laid occurred on May 23. This is comparable to the 1982 figure for this study.

There can be large year to year variation in the date at which the first clutch in a breeding population is initiated. Holm's (1973)

Table 10. Comparison of breeding phenology

Source	Location	Year	Date of First Clutch Initiation	Median date of Clutch Initiation	Date of Peak in Active Nests
This study	Northway, AK	1981	May 20	May 29	June 11
This study	Northway, AK	1982	May 23	June 2	June 13
Picman (1981a)	Delta, British Columbia	1976	April 15[a]	----	May 16
Picman (1981a)	Delta, British Columbia	1977	April 15[a]	----	May 7
Weatherhead and Robertson (1977)	Kingston, Ontario	Mid 1970's	May 7	----	----
Holm (1973)	Spokane, WA	1965	April 7[a]	----	----
Holm (1973)	Spokane, WA	1966	April 21	----	----
Holm (1973)	Spokane, WA	1967	May 11	----	----
Moulton (1981)	Aitkin, MN	1977	May 17	May 24	----
Crawford (1977)	Iowa	1972-74	May 19	----	----
Lenington (1982)	Chicago, IL	1974	May 8	----	----
Smith (1943)	Chicago, IL	1941	April 21	----	----
Goodard and Board (1967)	Oklahoma	early 1960's	April 20	----	----
Bernstein and McLean (1980)	Mentor, OH	1976	May 23	June 7	----
Dolbeer (1976)	Erie Co., OH	1973	April 30	May 30	May 14
Dolbeer (1976)	Erie Co., OH	1974	May 3	June 8	June 9
Case and Hewitt (1963)	Ithaca, NY	1960	May 1	----	----
Case and Hewitt (1963)	Ithaca, NY	1961	May 5	----	----
Robertson (1973a)	New Haven, CT	1968	May 3[a]	May 18-26	----
Robertson (1973a)	New Haven, CT	1969	May 4[a]	May 19-27	----
Robertson (1973a)	New Haven, CT	1970	May 6[a]	----	----
Caccamise (1976)	Ocean Co., NY	1973	May 17	----	June 11
Brown and Goertz (1978)	Louisiana	1963-75	April 7	----	May 15[a]

a. These dates were estimated from graphs.

study near Spokane, Washington over 3 years shows a range of nearly 5 weeks from April 7 to May 11 in the date on which the first clutch was initiated. Since the date of initiation of the first nest in a breeding population may not be a good indicator of the overall pattern of clutch initiation in the population and is sensitive to sample size, it is probably more appropriate to compare median clutch initiation dates.

In both years of this study the median clutch initiation date for first nestings was only 4 days later than the date at which 10% of the clutches were initiated. Except possibly for a study conducted by Moulton (1981) in Minnesota in which the median clutch initiation date and the date of first clutch initiation were separated by only seven days, the synchrony observed for the Northway population is the greatest observed for redwings in North America.

The median clutch initiation date for this study (Table 10) is not uniquely later than other localities. However, the median clutch initiation date is susceptible to inflation by clutch initiation due to renesting. Most renesting in redwings is a response to loss of a clutch or brood. In this study a very low percentage of females renested. It is my opinion that renesting data, when lumped with data for a female's first nesting attempt, will cloud the examination of breeding phenology since it is strongly influenced by the probability of loss of a first nest due to, for example, predation. This is particularly true in a short breeding season where double brooding (producing two successful nestings) is difficult. Thus, if one is to look at the adaptive features of breeding phenology, it is probably wise to exclude renesting. Most of the redwing studies do not do this.

The date at which the peak of active nesting is achieved is used in Table 10 because this date is less susceptible to inflation by renesting. The peaks of active nesting in this study (June 11, 1981 and June 13, 1982) are among the latest for all the studies listed. It is possible that the peak in odonate emergence is later in Northway than at localities further south. The peak emergence of odonates in eastern Washington occurs in the later half of June (Orians, 1980). This agrees with my observations for Northway. However, without insect emergence data for the Northway marshes and the other study sites in Table 10 it is difficult to make any conclusions as to the significance of the peak of active nesting at each locality.

c. Egg Size and Growth Rates

Table 11 compares the mean egg length, breadth, and volume found in this study with other studies that have reported these egg parameters. The largest values for all three of these parameters occurred in this study. Table 12 compares the weight:age relationship for this study with other studies that have examined this relationship in redwings. Since I have defined day 1 as any weight measurement taken within 24 hours of hatching, I have reassigned the data reported by several authors as day 0 to day 1 of my classification. Thus, it

Table 11. Comparison of egg length, breadth, and volume

Source	Location	Year	N	Avg.Length-mm	Avg.Breadth-mm	Avg.Volume-cu.mm
This Study	Northway, AK	1981-82	307	25.3 (±1.3)[a]	18.3 (±0.8)	4360 (±490)
Bent (1958)	U.S. National Museum	--	380	24.8	17.5	3980
Brown and Goertz (1978)	Louisiana	1963-75	303	23.6	17.4	3740
Crawford (1977)	Iowa	1972-74	310	24.3	17.6	3940

[a] Numbers in parentheses indicate standard deviation.

Table 12. Comparison of nestling weight (grams) at each day of the nestling period.

Source	This study	This study	Cronmiller and Thompson(1968)	Crawford (1972)	Dyer and Abramsky(1976)	Orians(1973)	Robertson (1973b)	Strehl(1978)	Williams(1940)
Location	Northway,AK	Northway,AK	Livingston Co., NY	Iowa	Ohio and Ontario	Taboga,Costa Rica	New Haven, CT	Union Co.,Il.	Logan Co.,OH
Year	1981	1982	1979	1972-74	--	1967	1968-70	1976	1940
Habitat	Marsh	Marsh	Marsh	Marsh	Marsh	Marsh	Marsh	Marsh	Marsh
Day 1	4.6(61)[a]	4.3(26)	4[b]	3.76(109)	4.5[b]		3.5[b]	3.52(137)	4.5[b]
2	7.4(41)	7.1(36)	10	5.93(85)	6.5		5	5.18(111)	5.5
3	11.7(47)	12.2(32)	13	9.07(87)	9.5		7.5	8.29(132)	7
4	16.8(37)	16.0(35)	17.5	13.11(66)	12.5		11	11.93(130)	11
5	23.6(42)	23.5(41)	23.5	17.50(59)	16.5		15	15.93(124)	16
6	29.2(44)	30.0(33)	28	22.46(50)	21	23	19.5	19.93(123)	21.5
7	34.7(37)	33.7(42)	31.5	26.62(39)	25	27	23.5	24.30(111)	26
8	38.0(31)	39.2(44)	35	30.00(31)	29.5		27	27.34(99)	28.5
9	40.9(27)	42.3(24)	38	32.5(24)	32		30	29.28(99)	31.5
10	39.2(26)	44.8(15)		34.99(22)	35		32.4	31.28(67)	33.5

a. Numbers in parentheses indicate sample size
b. Values in this column were obtained from a graphical representation of the data

may be possible to differ by up to one day depending on how the researcher actually assigned weight measurements to his classification scheme. However, by fledging (day 9 and day 10) the nestlings in the Northway population are heavier than nestlings in the other studies even if a one day discrepency in classification is considered. Only Cronmiller (1980) showed similar magnitude in weight increase during the nestling period. Table 13 compares the results of tarsometatarsus lengths from this study with other studies that have examined this relationship in Red-winged Blackbirds. Robertson's (1973b) data on tarsometatarsus lengths are very similar to my data except possibly for day 10 nestlings. Thus, it appears that the growth pattern in tarsometatarsus in the Northway population is similar to that observed in more southerly populations of redwings.

The larger egg size and the faster weight gain observed for this population may be indicative of phenotypic release in the expression of these traits due to environmental conditions. It is possible that females lay both larger and more eggs in response to good foraging conditions in the egg laying period. This agrees with the observation that there was a significant increase in egg size in 1982, though in both years average egg size was larger than that found in other studies (Table 11). Also, the lack of a significant difference in the weight:age relationship between years suggests that weight gain is decoupled from initial egg size. It is also possible that egg size may be dependent on female body weight. Power (1970) found that 92% of the geographical variation in female body weight is attributable to

Table 13. Comparison of tarsometatersus length (mm) at each day of the nestling period.

Source	This study	Robertson(1973b)	Williams(1940)
Location	Northway, AK	New Haven, CT	Logan Co., OH
Year	1981-82	1968-70	1940
Habitat	Marsh	Marsh	Marsh
Day 1	8.1(86)[a]	8.5[b]	
2	10.5 (76)	10	
3	13.8 (81)	12	
4	16.6 (70)	16	
5	20.6 (82)	19	
6	23.6 (79)	22.5	
7	25.5 (79)	25.75	
8	27.4 (74)	28	
9	28.3 (51)	29.5	27.41
10	28.6 (41)	31	

a. Numbers in parentheses indicate sample size.
b. Values in this column were obtained from a graphical representation of the data.

variation in isophane, a measure that is primarily based on latitude. Thus, the larger egg size found for the Northway population may be due to females being larger in comparison to females in populations further south.

If food were superabundant during the nestling period it is possible that the rate of weight gain is the maximum attainable for redwings. The observation that nestlings in different size broods are the same weight at day 7 (Figure 4) also suggests that nestlings in the two years of this study are growing as fast as possible. Only Cronmiller and Thompson (1980) have reported the relationship between growth and brood size. Since in their study experimentally enlarged broods fledged lighter young than control broods, it is not possible to determine if the fast rate of weight gain observed for the Northway population is an adaptive response. The similarity between the pattern of growth for tarsometatarsus in this population and that observed by Robertson (1973b) and the dissimilarity in the weight:age relationship, particularly in comparison to that observed by Roberston (1973b), may be due to a tighter genetic control over bone growth. Surely there is more potential for plasticity in weight change during the nestling period than there is for tarsometatarsus change. Thus, the fast rate of weight gain may be an environmental response due to good foraging conditions during the nestling period.

d. Clutch Size

Clutch size in birds has probably been the most examined life history character of any taxonomic group (Lack, 1968; Cody, 1966; Williams, 1966; Ricklefs, 1977; Perrins, 1977; Skutch, 1949; Hussell, 1972). Lack's hypothesis (Lack, 1968) states that clutch size in altricial birds has been adjusted evolutionarily to the maximum number of young that can be fed and subsequently survive to reproduce. More recently Jones and Ward (1976) have provided evidence that some birds may be physiologically limited in the amount of eggs they can lay. The number of eggs laid may therefore depend on the condition of the female at the onset of egg laying as well as on the rate of depletion of body reserves during the period of egg laying. For example, in Red-billed Quelea (Quelea quelea) the female lays eggs until a minimum threshold in body condition is reached (Jones and Ward, 1976).

Table 14 lists several studies that have considered clutch size, the number of eggs hatched per nest, and the number of young fledged per nest in the Red-winged Blackbird. These three parameters were calculated on the basis of active nests, i.e., nests that have had at least on egg laid in them.

The average clutch size in this study is higher than that found in other studies. If there is a tendency to adjust clutch size to body condition then the adaptive clutch size in most redwing populations may be larger than the realized modal clutch size. In this case the higher clutch size found in this study may be the result of

Table 14. A comparison of clutch size, number of eggs hatched

Source	Location
This study	Northway, AK
This study	Northway, AK
Miller (1968)	Saskatoon, Saskatchewan
Picman (1980a)	Delta, British Columbia
Rigby (1982)	Williamstown Lk, New Brunswick
Rigby (1982)	Maritimes Region, Canada
Weatherhead & Robertson (1977)	Kingston, Ontario
Holm (1973)	Spokane, WA
Orians (1961)	Colusa & Yuba Co., CA
Moulton (1981)	Aitkin, MN
Blakely (1976)	Iowa City, IA
Crawford (1977)	Iowa
Lennington (1982)	Chicago, IL
Smith (1943)	Chicago, IL
Perkins (1928)	Indianapolis, IN
Holcomb (1971)	Fremont, NB
Goodard and Board (1967)	Oklahoma
Bernstein and McLean (1980)	Mentor, OH
Dolbeer (1976)	Erie Co., OH
Francis (1975)	Erie Co., OH
Holcomb and Twiest (1968)	Toledo, OH
Williams (1940)	Logan Co., OH
Cromiller and Thompson (1980)	Livingston Co., NY
Case and Hewitt (1963)	Ithaca, NY
Robertson (1972)	New Haven, CT
Brenner (1966)	Centre Co., PA
Wood (1928)	Harrisburg, PA
Caccamise (1976)	Ocean Co., NJ
Meanley and Webb (1963)	Chesapeake Bay, MD and DE
Brown and Goertz (1978)	Louisiana
Orians (1973)	Taboga, Costa Rica

per nest, egg mortality, number of nestlings fledged per nest, and nestling mortality.

Year	Clutch Size	Number of Eggs hatched per nest	Egg Mortality	Number of nestlings fledged per nest	Nestling Mortality	Egg and Nestling Mortality
1981	4.4	3.9	11.0%	3.4	12.8%	22.8%
1982	4.3	3.6	15.5%	3.5	4.2%	19.0%
1966	3.76	2.37	37.0%	1.33	44%	64.6%
1976-77	3.41	--	--	0.54	--	84.2%
1976	3.4	1.87	45.0%	1.12	40.2%	67.1%
--	3.7	--	--	--	--	--
1974-75	3.61	--	--	--	--	--
1966-67	3.58	--	--	0.99	--	72.1%
1959-60	3.69	--	--	--	--	--
--	3.7	--	--	1.2	--	67.6%
1973	3.52	--	--	--	--	--
1972-74	3.67	--	--	1.05	--	71.4%
1974, 1978	3.60	--	--	1.54	--	57.2%
1941	3.28	2.43	25.7%	1.96	14.6%	40.2%
1927-28	3.6	3.17	12.0%	2.04	35.6%	43.3%
1966	3.7	--	--	--	--	
early 1960's	3.4	1.35	60.1%	0.81	40.0%	76.2%
1976	2.4	--	--	--	--	--
1973-74	3.38	--	--	1.3	--	61.5%
1969-73	3.69	2.40	35.0%	1.33	44.6%	64.0%
1964-65	3.50	--	--	0.82		76.6%
1940	3.4	--	--	1.57	--	53.8%
1977	3.4	1.80	46.9%	--	--	--
1960-61	--	--	--	0.91	--	--
1968-70	3.25	2.13	34.3%	1.33	37.8%	59.1%
1960-64	3.20	2.12	33.8%	1.55	26.9%	51.6%
1928	3.9	3.3	15.4%	2.1	18.2%	46.2%
1973	3.03	1.94	35.8%	1.19	38.6%	60.7%
1958-61	3.30	--	--	--	--	--
1963-75	3.82	2.87	24.9%	0.83	71.1%	78.3%
1967	2.67	--	--	--	--	--

females being in very good condition at the time of egg laying and/or a low rate of depletion of body reserves during egg laying.

Alternatively, the possibility exists that the adaptive clutch size in most redwing populations is the modal clutch size. If there is a genetic basis for the tendency to lay a certain number of eggs in a clutch, then there may be directional selection towards a larger clutch size in the Northway population since the nonmodal clutch of five is more productive than the modal clutch of four in terms of young fledged per nest (Table 6). As noted earlier, nestlings fledged at comparable weights in both nests which fledged four and nests which fledged five (Figure 4). If nestling survival to reproduction is strongly dependent on weight at fledging, then these results support the view that the nonmodal clutch of five leads to greater female reproductive success than the modal clutch of four in the Northway population, at least in the two years of study. However, since females feed fledglings after they leave the nest, it may be that the ability of females to feed fledglings conveys an advantage to clutches and subsequent broods of four. In this case it would be expected that stabilizing selection will maintain the modal clutch size.

e. Female Reproductive Success

Female reproductive success was calculated as the number of young fledged per active nest (Table 14). Ideally it would be best to calculate female reproductive success as the number of young fledged per reproductively active female in the breeding population. However, this requires a well banded populaton, a luxury not available to most studies. Using the number of active nests is not an entirely accurate way to calculate female reproductive success since female redwings can renest when they lose a clutch and brood, and at some locations can raise two or three broods in a breeding season. However, many researchers report female reproductive success as the number of young fledged per nest that fledged young. This can lead to obviously inflated results such as those reported by Meanley and Webb (1963) who report an average female reproductive success of 4.2 nestlings fledged per nest when the average clutch size reported by that study was 3.3 eggs per nest.

Using the number of young fledged per active nest, one can arrive at a conservative estimate of female reproductive success. For the purpose of comparison, I recalculated the number of young fledged per nest reported by many authors so that it conforms more nearly with my method of calculating female reproductive success. Both the number of eggs hatched per nest and the number of young fledged per nest in this study are very much higher than those reported by the various other studies over the geographical range of the Red-winged Blackbird.

There are several reasons for these results. First, predation was virtually non-existent. In other studies predation has been the major reason for nesting failure (Robertson, 1972; Caccamise, 1976; Holm, 1973; Robertson, 1973a; Shipley, 1979; Moulton, 1981; Rigby, 1982; Young, 1963; Orians, 1973; Miller, 1968). Various snakes

(Robertson, 1972; Shipley, 1979; Facemire and Fretwell, 1980; Orians, 1973; Miller, 1968) and raccoons (Procyon lotor) (Blakely, 1976; Moulton, 1981; Robertson, 1972; Shipley, 1979) are the predators most commonly cited, neither of which occur in eastern interior Alaska. Mink (Mustela vison), which do occur in the Northway area, have been suggested by Shipley (1979) as a potential redwing nest predator. Apparently they either occur in low density or have a different pattern of habitat use in comparison to redwings, so that they are not a serious nest predation threat. Muskrats (Ondatra zibethicus) were very common on Julius and Shashamund lakes in both years of this study. Both Bent (1958) and Miller (1968) have suggested that they are potential predators on redwing nests. Since there was no predation in this study I agree with Robertson (1972) that muskrats are an unlikely predator.

At Northway, there is probably no significant interspecific competition for nests sites and food. Picman (1977, 1980a, 1980b) showed that Long-billed Marsh Wrens (Cistothornus palustrus) compete with redwings for nest sites in the coastal marshes of British Columbia. These wrens have been known to peck eggs and nestlings, and probably restrict redwings to less dense portions of a cattail stand. Short-billed marsh wrens (Cistothorus platensis) have also been shown to peck redwing eggs when experimentally presented with redwing nests (Picman and Picman, 1980). Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) can compete with redwings for territories and are successful at restricting redwings to areas of emergent vegetation that are less productive in terms of odonate emergence (Orians and Willson, 1964; Miller, 1968; Orians, 1966; Orians, 1980). It has also been suggested that grackles (*Quiscalus quisula* and *Quiscalus mexicanus*) affect nest site selection by redwing females (Wiens, 1965; Lenington, 1982; Rutledge and Chandler, 1979). I found only one nest built by a bird other than a redwing that used cattails as the support vegetation. This nest was built by a pair of Rusty Blackbirds (*Euphagus carolinus*). Rusty Blackbirds are common in the Northway area; however, I only observed 2 to 3 pairs of breeding Rusty Blackbirds on the larger study lakes, so I do not consider them to be serious competitors for nest sites. Interspecific competition for food, if it occurs, was not documented. However, I feel that the success with which females raise broods of five to fledging indicates that food was not limiting during the nestling period. No starvation was found among nestlings in either year of this study.

In both years of this study the weather during the nestling period was warm and sunny. One brood was lost in July of 1981, late in the nestling period, due to 3 continuous days of heavy rain. In general weather did not adversely affect nesting success for most of the population that year.

f. Population Status

It might be expected that since redwings are so good at fledging young in the Northway area in comparison to more southern locations, that the population in eastern interior Alaska might be growing. If this is the case, then either a range extension or an increased density of breeding females may result. Particularly if the limits of available breeding habitat correspond with the limits of the breeding range, population increase can only result in an increased density of breeding females in the Northway area. The number of both males and females in the two years of this study was similar both for the population as a whole and for most of the study lakes (Table 1). Thus, the only data available do not support the idea that breeding densities are increasing in the Northway area. There has also been no documentation of a breeding range extension to the north or west of the Northway-Tanacross lowlands. However, redwings have been sighted in the cattails at Smith Lake adjacent to the University of Alaska at Fairbanks, 400 km west of the study area. A male and female redwing were sighted for several days in late May and early June of 1979, and a female redwing was sighted in mid-May of 1980 (Dan Gibson, University of Alaska Museum, pers. comm.). Whether these birds are indicative of range extension or merely migrated past the boundary of the realizeable breeding range is not clear. Even the initial documentation of redwings (Kessel, 1966) in the Northway-Tanacross lowlands about 40 km west of the study site may have been merely the documentation of an overlooked population rather than of a recently established population in that area.

If the population of redwings in Northway is not growing, then there must be other factors offsetting the high number of young fledged per nest. The ability of females to feed fledglings could constrain the number of young surviving to reproduction, such that a replacement rate of approximately 1.0 is realized for this population. The cost of migration may also be greater for this population. Although there have been no recoveries of the 293 birds I banded, Dolbeer (1978) has information which suggests that redwings which breed in eastern interior Alaska may be wintering near the Gulf Coast of Louisiana and Texas. If this is true, then the migration distance for redwings in eastern interior Alaska is probably the longest of any population of redwings. Therefore, migratory mortality may be a factor which could keep this population from growing.

There is no information available on the year to year cohesiveness of this population. If mortality is very high due to, for example, migration costs or fledging mortality, such that this population is not replacing itself, then birds breeding in this population may be a mosaic of birds from other populations. In this case the Northway population would be considered a sink, and the origins of the breeding birds the sources. However, in this situation it might be expected that there would be year to year variability in the number of birds attempting to breed in the Northway area since it is likely that there is year to year variability in production at the sources. My data do not support this notion, and thus I feel that the redwings in the Northway area are a cohesive population. Banding studies are needed to resolve this issue.

Even if the number of young fledged per nest is indicative of the number surviving to reproduction, the two years of this study could be on the high end of a distribution of female reproductive success. Thus it may be that on the average the population is merely replacing itself. A two year data base is not sufficient to resolve this question.

g. Conclusions concerning breeding adaptations

Breeding phenology seems to be more synchronous in the Northway population than in other populations. If there is a coupling of the timing of nesting to the peak in odonate emergence, this greater synchrony may be a response to greater synchrony in odonate emergence. Alternatively, if the predictability of odonate emergence is low, this synchrony may result because redwings are timing their nesting to coincide with an average date of odonate emergence. Since no emergence data on odonates were collected in this study it is not possible to evalute these hypotheses.

I believe that the larger egg size in the Northway population is the result of good foraging conditions during the period of egg laying. It could also be the result of females being in good condition at the time of egg laying. However, even if migration costs are high for this population, there is evidence for Red-billed Quelea that females who lose clutches can recover in a short period of time to lay a replacement clutch (Jones and Ward, 1976). If the larger egg size was due entirely to an adaptive response then the significant difference observed between 1981 and 1982 should not have occurred.

The lack of interpopulation differences in the growth of tarsometatarsus during the nestling period suggests that neither an environmental nor an adaptive response has occurred in tarsometatarsus growth. It is expected that an adaptive response in the weight:age relationship should be coupled to an adaptive response in tarsometatarsus growth. The most likely force selecting for faster growth rates during the nestling period in an open nesting passerine species would be intensified predation such that nestlings fledge at similar body size in a shorter period of time. Since no predation was noted in the Northway marshes I can think of no other factor that would select for faster growth rates. Thus the fast growth rate in terms of weight in the Northway population is interpreted as an environmental response to local conditions. Greater food availability during the nestling period is probably the factor responsible for this environmental response.

Though redwing clutch size is larger in Northway than in other locations, it is not yet appropriate to attribute this to an adaptive response. The ability of females with clutches of five to fledge more young than females with clutches of four may be due to a superabundance of food during the nestling period. However, Haukioja (1970) showed in Reed Buntings, _Emberiza schoeniclus_, that though there is no brood size dependent starvation or growth during the nestling period, that there is brood size dependent mortality among fledglings until the time of independence. The data are not available in this study to address this point. The larger clutch size in this population may be due to an increased ability of females to lay eggs. Again this could be the result of females being in good condition at the onset of egg laying. However, if migration costs are substantial then large clutch size may be attributable to an abundance of food which allows a slow rate of depletion of body reserves during egg laying. Thus, it is not clear whether large clutch size for the Northway redwings is an adaptive response or an environmental response.

The success with which females can fledge young suggests that this population may be growing. However, it is possible that several factors such as migratory costs, winter mortality, or fledgling mortality may result in a replacement rate of approximately 1.0. Although breeding densities are consistent from year to year, without information on available habitat beyond the edge of the range it is difficult to determine if range extension is occurring.

2. The interpretation of female choice at the edge of the range

a. Territory Quality

Searcy and Yasukawa (1983) suggested that female redwings can base their choice of mate on territory quality, male parental investment, or on a male's genetic quality. Territories can vary in their ability to provide food for the female and the nestlings (Orians, 1980). However, redwings do not rely entirely on the territory for food (Orians, 1980). This does not mean that territories are not important sources of food, because travel time costs can be kept to a minimum if foraging occurs on the territory. In this study I observed that females did forage off the territory as well as on the territory, but, I have no data concerning the relative amounts of foraging that occurred on and off the territory.

Territories may also vary in their ability to shield the nest from predators, cowbird parasitism, and adverse physical conditions. Thus, it is expected that females should base their choice of mate on the quality of potential nest sites that exist on the territory. Physical characteristics of nest sites might therefore illuminate territory attributes that are important preventing predation, cowbird parasitism, and destruction due to adverse physical conditionss. Table 15 compares the results of the means of some of the six nest site characteristics measured in this study with other studies that have also measured these same characteristics.

Nest height is quite variable across studies. Nests in shrubs tend to have higher placement than nests in aquatic emergent vegetation such as cattail, and therefore the only valid comparisons of my data in Table 15 may be with Bernstein (1980), Holcomb (1968), and Miller (1968). Since mean nest height placement is consistent from year to year in this study (two sample t test, P=0.2621), it seems that lower nest locations are used in the Northway population. The depth of water below the nest seems to be greater than that reported by the two other studies for which this type of data has been

Table 15. A comparison of nest site characteristics.

Source	Location	Year	Vegetation	HBN cm[a]	DBN cm
This study	Northway, AK	1981-82	*Typha*	23 (±14)[b]	45 (±22)
Bernstein and McLean (1980)	Mentor, OH	1976	*Typha*	57	--
Brown and Goertz (1978)	Louisiana	1963-75	Various	110	--
Caccamise (1977)	Ocean Co., NJ	1973	Various	126	--
Holcomb and Twiest (1968)	Toledo, OH	1964-65	*Typha* and grasses	55	--
Miller (1968)	Saskatchewan	1966	Various	23[c]	23
Ortego and Hamilton (1978)	Louisiana	1975	Various	126	--
Rutledge and Chandler (1979)	San Antonio, TX	1978	Various	83	34

HBN - Height from water level to bottom of nest
DBN - Depth of water below nest
a - Note that some studies may have measured nest height from water level to rim of nest (rim to bottom is 10-15 cm)
b - Numbers in parentheses indicate standard deviation
c - Author stated that he measured to rim of nest

recorded. However, comparing the means of these measurements is not an accurate way to assess the question of whether nest locations are different in the Northway population. Variance for a particular characteristic would help to determine if that characteristic is important in nest site selection since characteristics with large variances are probably unimportant. It is unfortunate that variances of nest site characteristics have not been reported in the literature.

Since nest success was so high in this study it is difficult to discern any patterns between nest placement and the number of young fledged per nesting attempt. Thus, if the nest site characteristics I measured are important in nest site selection, their meaning may be masked by the lack of nest predation in this study. The possibility also exists that the characteristics I measured are not the ones used by females in determining where to place a nest. Thus, the observed nest height placement and the depth of water below the nest may each be an artifact of other factors involved in nest site selection.

Females in the Northway population may base their choice of nest site on innate preferences that were evolutionarily established when the ancestral birds of this population occupied an area of the breeding range that did suffer appreciable nest predation. Particularly if this population is a sink, made up of a mosaic of birds from other populations which are sources, then the innate preferences for nest sites would likely exist in the Northway females. In any case, these innate preferences, if they exist, are probably not maladaptive since very little nest failure was observed in this population.

b. Male Parental Investment

Males can provide parental investment that is both shareable or nonshareable among females in the harem. One form of male parental investment that is usually not shareable is the feeding of young. Yasukawa (1981) observed that males in an Indiana population of redwings feed fledglings. However, this has not been observed for redwings breeding in western North America. In this study I never observed a male feeding either a nestling or a fledgling. Only in cases where there is a sufficient amount of asynchrony in nesting on a territory can this type of investment be provided sequentially to different broods so that feeding of one brood does not adversely affect feeding of another brood. Even if feeding of nestlings by males does occur in my study area, this investment is probably nonshareable because synchrony is so marked. Wittenberger (1980) has shown that in bigamous breeding situations in Bobolinks (Dolichonyx oryzivorus), there is more starvation in the broods of secondary females. This may be due to most of a male's parental investment going into feeding the young of the primary female. In this study I never observed a male feeding either a nestling or a fledgling.

One form of male parental investment that is shareable is the detection of potential predators. Male redwings warned the females of my approach to the nest, an indication that they do serve this function.

There are both benefits and costs for females living in a harem. If the benefits exceed the costs, then it is expected that females in the harem will show cooperative behavior, whereas if the opposite is true then females in the harem should show competitive behavior. Particularly if there is nonshareable male parental investment, such as feeding the young, then it is expected that females may behave competitively towards each other. In this study there was no significant difference in the time interval of nest starts between territories and the time interval of nest starts within territories (also see Yasukawa and Searcy, 1981).

I do not feel that the sample size in this study of the time intervals between nesting attempts within harems is large enough to adequately test the idea of temporal competition for nest sites within a harem. Even if temporal competition for nest sites was found, an interpretation could be made that it is advantageous for females joining a harem to delay nesting. Females could also preferentially join a harem with more advanced females in order to maximize temporal separation. Both of these behaviors could still imply that the harem is competitive, but that competition is not manifested through despotic behavior by established females. However, temporal separation could also arise if males have difficulty courting more than one female at a time.

Holm (1973) found that in a synchronous year (1967), harems of five and six females were under-represented in comparison to a more asynchronous year (1966). This was attributed to already established females in a harem preventing settling by unestablished females. The two years of my study appeared equally synchronous in terms of clutch initiation. Since harem size was not significantly different between years (Kruskal-Wallis contingency analysis, $.25<P<.5$) my study cannot test the idea that synchronous breeding leads to despotic behavior by females already established in a harem.

I feel that if the harem is competitive, it is likely that females attempting to settle on the territory close in time will be overdispersed in space. Seastedt and MacLean (1979) suggest that nest spacing in Lapland longspurs (Calcarius lapponicus) may be responsive to the potential for polygyny. However, Yasukawa and Searcy (1981) did not find overdispersion of nests in space when females nested within eight days of each other. There are no data available from this study to attempt to answer this question for the Northway population.

c. Male Genetic Quality

If females choose males on the basis of territory quality, and the territory quality distribution differs between locations, it is expected that the harem size distribution would also be different. However, if females choose males on the basis of genetic quality, as suggested by Weatherhead and Robertson (1979), a different harem size distribution would not be expected since the genetic variance in ability to attract females should not be very much different between populations. Table 16 compares the mean harem size found in this study with the mean harem sizes found in other studies. Although the harem size found in this study is at the low end of the distribution reported in Table 16, it is within the range reported by the other studies. The harem size may be low because the distribution of cattail patch size may be skewed toward small patches. I have no data on cattail patch size or male territory size in this study to compare with other studies. However, the harem size distribution in this study has an overabundance of small harems in comparison to a study of redwings in Washington State (Searcy and Yasukawa, 1983). Searcy and Yasukawa (1983) present data in which 34% of the 107 harems studied had more than five females. None of the harems in this study were larger than five. The mean harem size in the Washington study was 4.6 and the mean harem size in this study was 2.1, a significant difference (Kruskal-Wallis contingency analysis, $P<.001$).

d. Conclusions concerning Female Choice

The results of this study show that in the absense of severe predation female reproductive success can be very high. Since territories can vary in their ability to shield nests from predators and to provide access to food, females over most of the breeding range of the Red-winged Blackbird probably choose mates based predominantly on

Table 16. A comparison of mean harem size.

Source	Location	Year	Mean harem size
This study	Northway, AK	1981	2.0
This study	Northway, AK	1982	2.2
Picman (1980a)	Delta, British Columbia	1976-77	4.6
Weatherhead and Robertson (1977)	Kingston, Ontario	1974-75	2.8
Holm (1973)	Spokane, WA	1960-67	2.9
Orians (1980)	Columbia NWR, WA	1964-68	6.4
Orians (1980)	Western Washinton State	1963, 1965	4.3
Orians (1961)	East Park Reservoir, CA	1959-60	3.7
Orians (1961)	Haskell Ranch, CA	1959-60	2.8
Moulton (1981)	Aitkin, MN	1977	2.2
Nero (1956)	Madison, WI	1948-53	2.0
Blakely (1976)	Iowa City, IA	1973	2.7
Lenington (1982)	Chicago, IL	1974, 1978	5.6, 2.2
Smith (1943)	Orland, IL	1941	2.6
Goddard and Board (1967)	Oklahoma	early 1960's	2.0
Bernstein and McLean (1980)	Mentor, OH	1976	1.3, 2.0, 2.4
Dolbeer (1976)	Erie Co., OH	1973-74	4.3
Case and Hewitt (1963)	Ithaca, NY	1960-61	2.0
Brenner (1966)	Centre Co., PA	1960-64	1.3
Meanley and Webb (1963)	Chesapeake Bay, MD and DE	1958-61	1.9
Orians (1973)	Taboga, Costa Rica	1967	1.3, 3.7

territory quality. The effect of male parental investment is probably minimal due to the apparent lack of feeding young by males in the Northway population. The effect of male genetic quality in the sense that Weatherhead and Robertson (1979) proposed the "sexy son" hypothesis is probably also of little importance to female choice since there are observed differences in harem size distributions at different locations.

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