

## SOME ASPECTS OF THE BREEDING BIOLOGY OF RED-WINGED BLACKBIRDS IN ALASKA

A. DAVID MCGUIRE<sup>1</sup>

**ABSTRACT.**—Red-winged Blackbirds (*Agelaius phoeniceus*) reach the northern limits of their breeding range in eastern interior Alaska. Blackbird breeding phenology in Alaska is more synchronous, eggs are larger, nestlings grow more rapidly, and clutch-size and female reproductive success are higher than in populations farther south. The lack of a difference in the rate of tarsometatarsus increase in conjunction with the faster growth rate of nestlings suggests that the differences I found between this and more southerly populations are environmental responses to abundant food resources in the nestling period. Received 16 Jan. 1984, accepted 21 Oct. 1985.

The Red-winged Blackbird (*Agelaius phoeniceus*), one of the most intensively studied passerines in North America, has a polygynous mating system best termed resource-defense polygyny (Emlen and Oring 1977). From 0 to 12 females (Orians 1980) may nest on a territory defended by a male. During the breeding season redwings are usually associated with cattail (*Typha* spp.) or bulrush (*Scirpus* spp.) marshes (Orians 1980), but they can also be found in some upland habitats (Robertson 1972).

Red-winged Blackbirds breed from northern Costa Rica to the subarctic taiga forests of Canada and eastern interior Alaska (A.O.U. 1983). Studies of the Red-winged Blackbird in Alaska are important because aspects of the breeding biology of the species at the northern limits of its range may differ from those of populations farther south. This paper compares the breeding biology of a population of redwings in eastern interior Alaska to that of other populations farther south.

### STUDY AREA AND METHODS

The study was conducted near Northway, Alaska (62°58'N, 141°56'W), a village in the Northway-Tanacross lowlands where the Chisana and Nabesna rivers converge to form the Tanana River. Redwings breed in this area around ponds and lakes in stands of cattail (*Typha latifolia*) and bulrush (*Scirpus validus*). I checked 43 lakes and ponds for redwing activity, but only the 7 listed in Table 1 had breeding blackbirds.

I studied the biology of redwings from 10 May to 7 July 1981 and from 11 May to 6 July 1982. I began intensive and systematic searches for nests on 1 June 1981 and on 6 June 1982, and continued each year until all male territories had been searched for nests. Weather permitting, I visited nest sites at 4-day intervals in 1981 and every 3 days in 1982. Length and breadth of eggs were measured to the nearest 0.25 mm using Bel Art dial Type 6932 calipers. Each egg was individually marked for later identification. Nestlings in the

<sup>1</sup> Dept. Biology, Fisheries, and Wildlife, Univ. Alaska, Fairbanks, Alaska 99701.

TABLE 1  
LAKES AND NUMBERS OF BREEDING MALE AND FEMALE RED-WINGED BLACKBIRDS

Lake	Approximate area (ha)	1981		1982	
		Males	Females	Males	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	4	1	5
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	— <sup>a</sup>	—

<sup>a</sup> Not studied in 1982.

nest were weighed at each visit with a Pesola spring balance. Length of the right tarsometatarsus of each nestling was measured to the nearest 0.25 mm.

Each nestling was individually marked with a black indelible ink pen on a combination of the left or right tibia and tarsometatarsus. Some females removed banded nestlings less than 6 days old from the nest, so nestlings were not banded until I judged that fledging was imminent (when young were 7–8 days old). Nestlings were assumed fledged if they were not present in the nest on or after 9 days of age and had appeared healthy on the previous visit to the nest.

Egg volume was calculated as  $0.524 \times \text{length} \times \text{breadth}^2$  (Preston 1968). The weight and length of tarsometatarsus on day one were considered as measurements taken within 24 h 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. Nests from which females removed banded nestlings (9 nests in 1981) were not used in calculations of breeding success, fledging success, number of young fledged per nest, or brood-size dependent growth rates.

Tests of statistical difference were performed according to Zar (1974), Conover (1980), and Biomedical Computer Program (Dixon 1981) statistical software. Parametric statistics (e.g., two-sample *t*-tests) were employed if the data passed tests for normality. Otherwise, comparable nonparametric statistics (e.g., Mann-Whitney *U*-tests) were used in the analyses. Unless otherwise specified, each null hypothesis was rejected if the test statistic exceeded the value of  $P > 0.05$ .

## RESULTS

Two male Red-winged Blackbirds were present at the east end of Hudeac Lake on the afternoon of 10 May 1981 as ice was breaking up on the lake. I saw no female redwings during daily visits to ponds with cattails until 17 May 1981.

In 1982 observations at the breeding areas commenced on 11 May. The first male redwing was noted at Julius Lake late on 14 May when edges of the lake were ice-free. The first female appeared at Hudeac Lake

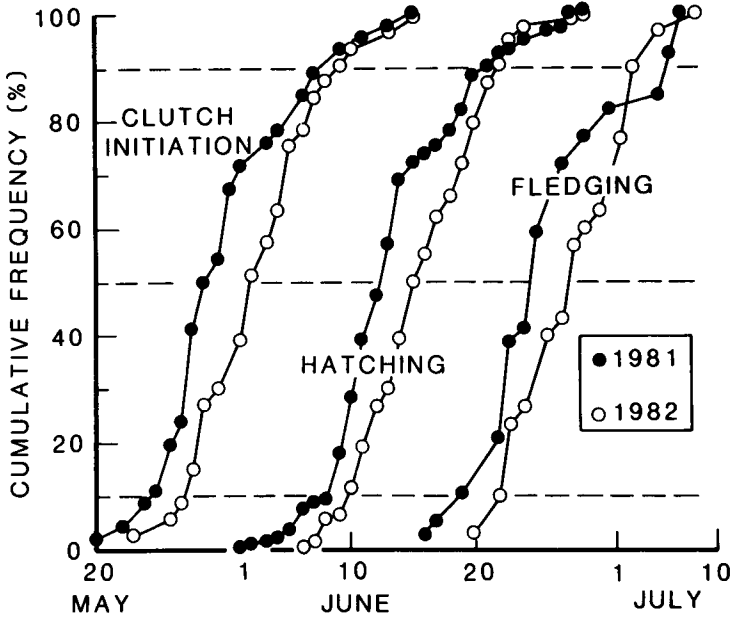


FIG. 1. Cumulative frequency of clutch initiation, hatching, and fledging phenology for 1981 and 1982.

on 22 May 1982, by which time the ice on the study lakes was breaking up.

In 1981 snow melted by 30 April, but in 1982 snow remained on the ground until 8 May (National Weather Service). Likewise, lakes which were melting on 10 May in 1981 did not achieve an equivalent stage of melt-off until around 20 May in 1982. Although ice breakup on the lakes differed by about 10 days, the breeding seasons seemed to be separated by only 3 days in the two years of this study (Fig. 1).

The phenological curves for 1981 and 1982 converge in the later half of each of the clutch initiation, hatching, and fledging sub-seasons (Fig. 1). The number of active nests peaked on 11 June in 1981 and 13 June in 1982 (Fig. 2); however, in both 1981 and 1982, 90% of the clutches were started by 9 June (Fig. 1).

Mean egg length was 25.0 mm in 1981 ( $N = 169$ ) and 25.5 mm in 1982 ( $N = 138$ ). Mean egg breadth was 18.0 mm in 1981 and 18.4 mm in 1982. Egg length, breadth, and volume were all significantly larger in 1982 (for length:  $U = 9635$ ,  $df = 1$ ,  $P = 0.0087$ ; for breadth:  $U = 8515$ ,  $df =$

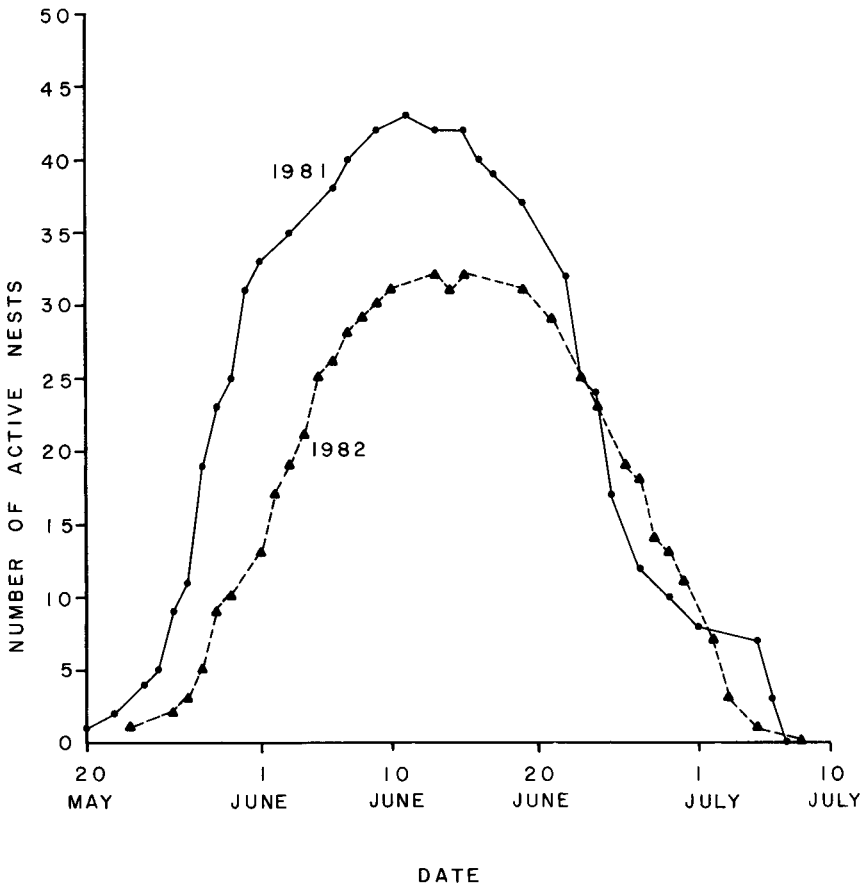


FIG. 2. Number of active nests as a function of date in the breeding season.

1,  $P < 0.0001$ ; for volume:  $U = 8488$ ,  $df = 1$ ,  $P < 0.0001$ ). Mean clutch-size was 4.4 eggs in 1981 ( $N = 37$ ) and 4.3 eggs in 1982 ( $N = 34$ ) ( $U = 576$ ,  $df = 1$ ,  $P = 0.4838$ ). Modal clutch-size in both years was 4 eggs. Mean number of eggs hatched per nest was 3.9 in 1981 and 3.6 in 1982 ( $U = 672$ ,  $df = 1$ ,  $P = 0.6032$ ). In 1981 and 1982, 11.1% and 15.5%, respectively, of the eggs laid did not hatch.

Mean number of nestlings fledged per nest was 3.4 in 1981 and 3.5 in 1982 ( $U = 616$ ,  $df = 1$ ,  $P = 0.8720$ ). In 1981 and 1982 12.8% and 4.2%, respectively, of the eggs hatched did not fledge. Percent hatching success and breeding success (nestlings fledged/eggs laid) were equally high for different clutch-sizes (Table 2). Fledging success (nestlings fledged/eggs

TABLE 2  
PERCENT HATCHING, FLEDGING, AND BREEDING SUCCESS BASED ON CLUTCH-SIZE AND  
NUMBER OF EGGS HATCHED PER NEST

	Clutch size						Total
	1	2	3	4	5	6	
<b>Hatching success</b>							
1981	0 (1) <sup>a</sup>	0 (1)	100 (2)	90 (24)	99 (16)	—	92 (44)
1982	—	100 (1)	100 (2)	84 (17)	85 (12)	100 (1)	86 (33)
Total	0 (1)	50 (2)	100 (4)	97 (41)	93 (28)	100 (1)	90 (77)
<b>Breeding success</b>							
1981	0 (1)	0 (1)	100 (2)	78 (23)	93 (11)	—	83 (38)
1982	—	100 (1)	50 (2)	81 (17)	82 (12)	100 (1)	81 (33)
Total	0 (1)	50 (2)	75 (4)	79 (40)	87 (23)	100 (1)	82 (71)
	Number of eggs hatched per nest						Total
	2	3	4	5	6		
<b>Fledging success</b>							
1981		100 (1)	83 (6)	90 (18)	94 (10)	—	91 (35)
1982		100 (2)	83 (10)	100 (10)	100 (8)	100 (1)	96 (31)
Total		100 (3)	83 (16)	94 (28)	97 (18)	100 (1)	93 (66)

<sup>a</sup> % (number of nests).

hatched) also was equally high across different initial brood sizes. Ninety-three percent of the chicks that hatched fledged, and more young fledged from nests of the nonmodal clutch-size of five than from the modal clutch-size of four.

Average nestling weight at day seven was independent of number of young fledged per nest (Fig. 3). Thus large and small broods fledged young of similar weight. Weight did not appear to be at an asymptote at the time of fledging (Fig. 4).

#### DISCUSSION

The adaptive significance of life history parameters such as clutch-size and development rates has been the focus of much attention in recent years. Most of the literature on life history parameters has concerned comparisons across species (e.g., Lack 1968; Ricklefs 1968, 1973). However, understanding the variability of these parameters within a species is essential to understanding their adaptive basis.

Except possibly for redwings breeding in Minnesota (Moulton 1981), in which the median clutch initiation date and the date of first clutch initiation were separated by only 7 days, the synchrony observed for the

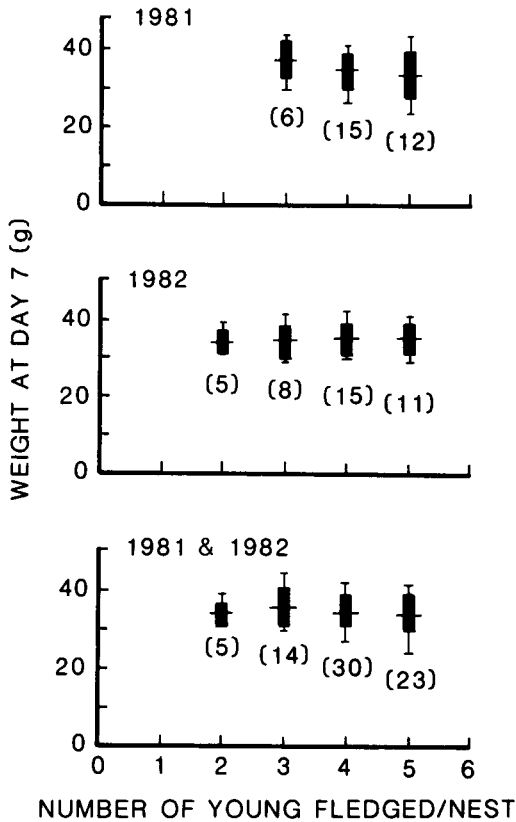


FIG. 3. Growth as a function of the number of young fledged per nest. Numbers in parentheses indicate sample size. Mean, range, and standard deviation are indicated.

Northway population (9 days between first clutch initiation and median clutch initiation) is greater than that observed for other populations in North America. This synchrony may be a result of the synchronous emergence of insects imposed by the short subarctic summer (see Kaufmann 1971).

Mean egg length, breadth, and volume found in this study are larger than those found by other studies (Bent 1958, Crawford 1977, Brown and Goertz 1978). The larger egg size observed for this population may be due to environmental factors. It is possible that females lay both larger and more eggs in response to good foraging conditions in the egg-laying period. Alternatively, larger eggs may be due to larger female body weight. Power (1970) found that 92% of the geographical variation in female

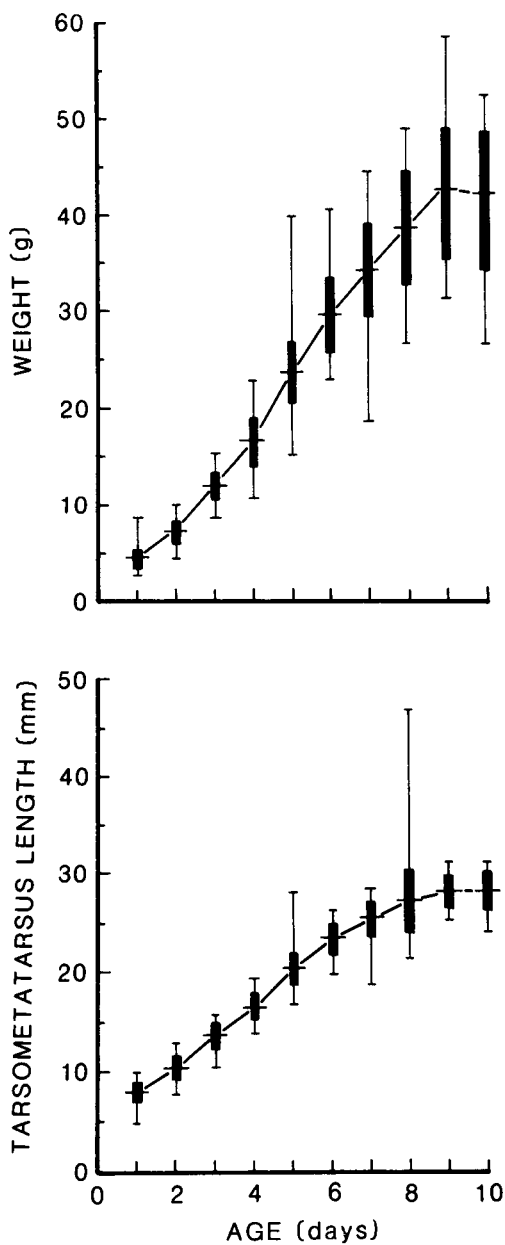


FIG. 4. Nestling weight and tarsometatarsus length as a function of age (1981 and 1982). Mean, range, and standard deviation are indicated.

redwing body weight was attributable to a measure based primarily on latitude.

At fledging (days 9 and 10) the nestlings in the Northway population were heavier than nestlings in the other studies (Williams 1940, Payne 1969, Robertson 1973, Dyer and Abramsky 1976, Crawford 1977, Strehl 1978, Cronmiller and Thompson 1980, Fiala 1981, Fiala and Congdon 1983). Only Cronmiller and Thompson (1980), working on a New York population of redwings, showed a similar magnitude in weight increases during the nestling period. If food were especially abundant during the nestling period, nestlings could gain weight at the maximum possible rate. The observation that nestlings in different size broods are the same weight at day 7 (Fig. 3) suggests that nestlings in the two years of this study gained weight at a rate that is near the physiological maximum. Robertson's (1973) data on tarsometatarsus lengths closely resemble my data, suggesting that growth of tarsometatarsi may be independent of breeding location.

The average clutch size of birds in the Northway population is higher than that found in other studies of Red-winged Blackbirds (e.g., Wood 1928, Orians 1961, Holcomb and Twiest 1968, Miller 1968, Payne 1969, Holcomb 1971, Holm 1973, Blakely 1976, Francis 1976, Crawford 1977, Weatherhead and Robertson 1977, Brown and Goertz 1978, Moulton 1981, Lenington 1982, Rigby 1982). This agrees with Lack's (1968) observation that intraspecific clutch size in passerines increases with latitude. It is not clear, however, if larger clutches reflect a genetic difference between this population and populations farther south, or whether females could be laying larger clutches because of good foraging conditions prior to and during egg laying.

In my study, both hatching success and fledging success are much higher than those reported in other studies over the range of the Red-winged Blackbird (e.g., Perkins 1928, Wood 1928, Smith 1943, Brenner 1966, Goddard and Board 1967, Miller 1968, Robertson 1972, Caccamise 1976, Francis 1976, Brown and Goertz 1978, Payne 1979, Rigby 1982). Lack of predation, low interspecific competition, abundant food, and mostly warm sunny weather during the nestling period in both years of my study may, in part, account for the high nesting success.

#### ACKNOWLEDGMENTS

This study was conducted in conjunction with a Master of Science degree program in biology at the University of Alaska at Fairbanks. I would like to thank all members of my advisory committee for promptly and critically reviewing drafts of the corresponding thesis (McGuire 1983). Particularly, I would like to thank E. C. Murphy, who suggested this



research, and S. F. MacLean, Jr., who initially stimulated my interest in evolution and ecology.

## LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American Birds, Sixth ed. Am. Ornithol. Union, Washington, DC.
- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and their allies. U.S. Natl. Mus. Bull. 211.
- BLAKELY, N. R. 1976. Successive polygyny in upland nesting Red-winged Blackbirds. *Condor* 78:129-133.
- BRENNER, F. J. 1966. The influence of drought on reproduction in a breeding population of Red-winged Blackbirds. *Am. Midl. Nat.* 76:201-210.
- BROWN, B. T. AND J. W. GOERTZ. 1978. Reproduction and nest site selection by Red-winged Blackbirds in north Louisiana. *Wilson Bull.* 90:261-270.
- CACCAMISE, D. F. 1976. Nesting mortality in the Red-winged Blackbird. *Auk* 93:517-534.
- CONOVER, W. J. 1980. Practical nonparametric statistics. Wiley and Sons, New York, New York.
- CRAWFORD, R. D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. *Wilson Bull.* 89:73-80.
- CRONMILLER, J. R. AND C. F. THOMPSON. 1980. Experimental manipulation of brood size in Red-winged Blackbirds. *Auk* 97:559-565.
- DIXON, W. J. (ED.). 1981. BMDP biomedical computer programs. Univ. Calif. Press, Berkeley, California.
- DYER, M. I. AND Z. ABRAMSKY. 1976. Examination of Red-winged Blackbird nestling growth rates using the logistic model: a case for r and k selection? *Proc. Bird Control Seminar* 7:121-125.
- EMLEN, S. T. AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- FIALA, K. L. 1981. Reproductive cost and the sex ratio in Red-winged Blackbirds. Pp. 198-216 *in* Natural selection and social behavior (R. Alexander and D. Tinkle, eds.). Chiron Press, New York, New York.
- AND J. D. CONGDON. 1983. Energetic consequences of sexual size dimorphism in nestling Red-winged Blackbirds. *Ecology* 64:642-647.
- FRANCIS, W. J. 1976. Clutch size and nesting success in Red-winged Blackbirds. *Auk* 92: 815-817.
- GODDARD, S. V. AND V. V. BOARD. 1967. Reproductive success of Red-winged Blackbirds in north central Oklahoma. *Wilson Bull.* 79:283-289.
- HOLCOMB, L. C. 1971. Nest building and egg laying by Red-winged Blackbirds in response to artificial manipulations. *Auk* 88:30-34.
- AND G. TWIEST. 1968. Ecological factors affecting nest building in Red-winged Blackbirds. *Bird Banding* 39:14-21.
- HOLM, C. H. 1973. Breeding sex ratios, territoriality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Ecology* 54:356-365.
- KAUFMANN, T. 1971. Biology and ecology of *Melanoplus borealis* (Orthoptera: Acrididae) in Fairbanks, Alaska with special reference to feeding habits. *Mich. Entomol.* 4:3-13.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.
- LENINGTON, S. 1982. Competition between Red-winged Blackbirds and Common Grackles. *Wilson Bull.* 94:90-93.

- McGUIRE, A. D. 1983. The breeding ecology of the Red-winged Blackbird (*Agelaius phoeniceus*) in eastern interior Alaska. M.S. thesis. Univ. Alaska, Fairbanks, Alaska.
- MILLER, R. S. 1968. Conditions of competition between redwings and Yellow-headed Blackbirds. *J. Anim. Ecol.* 37:43-62.
- MOULTON, D. W. 1981. Reproductive rate and reneating of Red-winged Blackbirds in Minnesota. *Wilson Bull.* 93:119-121.
- ORIAN, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. *Ecol. Monogr.* 31:285-312.
- . 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, New Jersey.
- PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. *Univ. Calif. Publ. Zool.* 90.
- . 1979. Sexual selection and intersexual differences in variance of breeding success. *Am. Nat.* 114:447-452.
- PERKINS, S. E. 1928. City park nests of Red-winged Blackbirds. *Bird Lore* 30:393-94.
- POWER, D. M. 1970. Geographic variation of Red-winged Blackbirds in central North America. *Univ. Kansas Publ. Mus. Nat. Hist.* 19:1-83.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419-451.
- . 1973. Patterns of growth in birds, II: Growth rate and mode of development. *Ibis* 117:531-534.
- RIGBY, M. D. 1982. Clutch-size and pre fledging survival in Red-winged Blackbirds at Williamstown Lake, New Brunswick. *Wilson Bull.* 94:569-571.
- ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. *Can. J. Zool.* 50:247-263.
- . 1973. Optimal niche space of the Red-winged Blackbird. III. Growth rate and food of nestlings in marsh and upland habitat. *Wilson Bull.* 85:209-222.
- SMITH, H. M. 1943. Size of breeding populations in relation to egg-laying and reproductive success in the eastern redwing (*Agelaius phoeniceus phoeniceus*). *Ecology* 24:183-207.
- STREHL, C. 1978. Asynchrony of hatching in Red-winged Blackbirds and survival in late and early hatching birds. *Wilson Bull.* 90:653-655.
- WEATHERHEAD, P. J. AND R. J. ROBERTSON. 1977. Harem size, territory quality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Can. J. Zool.* 55:1261-1267.
- WILLIAMS, J. F. 1940. The sex ratio in nestling eastern redwings. *Wilson Bull.* 52:267-277.
- WOOD, M. 1928. Mortality of young Red-winged Blackbirds. *Bird Lore* 30:262.
- ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.