NESTING SYNCHRONY AND DISPERSION IN RED-WINGED BLACKBIRDS: IS THE HAREM COMPETITIVE OR COOPERATIVE?

KEN YASUKAWA[1] AND WILLIAM A. SEARCY

Rockefeller University Field Research Center, Tyrrel Road, Millbrook, New York 12545 USA

ABSTRACT.—Distributions of nesting attempts in time and space within territories of Red-winged Blackbirds were examined in order to test hypotheses about the costs and benefits to females of sharing territories and mates. In a Washington State population, the distribution of time intervals between nest starts on the same territories was identical to the distribution of time intervals between nest starts on different territories. In an Indiana population, short intervals between nest starts within territories were underrepresented, indicating that nests starts were overdispersed in time within territories. In both populations, there was no indication that nests started close together in time were either more or less likely to be nearest neighbors in space than expected by chance. These results support the hypothesis that females in the Indiana population suffer a net cost from sharing their mate's parental care. *Received 5 November 1980, accepted 17 March 1981.*

RED-WINGED Blackbirds (*Agelaius phoeniceus*) are polygynous, with up to 15 females nesting simultaneously within the territory of a single male (Orians 1961, Searcy 1979). In marshes, territories of male redwings are not large, and females mating with polygynous males must nest in close proximity to one another (Orians 1980). Thus, female Red-winged Blackbirds are subject to the costs and benefits associated with living in groups (see, for example, Horn 1968, Ward and Zahavi 1973, Alexander 1974, Zahavi 1974, Hoogland and Sherman 1976, Bertram 1978, and references therein). They are also subject to the potential costs of sharing a mate (Orians 1969). The balance of costs and benefits has important implications to theoretical models of the evolution of polygyny, determining whether the "competitive" or "cooperative" version of the polygyny threshold model applies to a given species (Orians 1969; Downhower and Armitage 1971; Elliott 1975; Altmann et al. 1977; Wittenberger 1979, 1980). Obviously, if individual females receive a net benefit from nesting on the same territory with other females, the evolution of polygyny is greatly facilitated. Conversely, if the proximity of other females imposes a cost, there must be greater differences in quality between territories and males to compensate a female for settling on the territory of an already-mated male. In this paper, we examine the distribution of nesting attempts in time and space within territories

---

[1] Present address: Department of Biology, Beloit College, Beloit, Wisconsin 53511 USA.

of Red-winged Blackbirds to test hypotheses about the costs and benefits of sharing territories and mates.

One potential cost of sharing a mate is a decrease in the parental care per young (Alexander 1974). Some forms of male parental care, such as providing a suitable territory and defending the nest against predators, can be shared among females, while others, such as provisioning young, are nonshareable (Orians 1980). The amount of nonshareable parental care provided by male Red-winged Blackbirds differs widely between populations. Male redwings in some populations (e.g. central California and eastern Washington State) expend little effort providing food for young (Orians 1961, Searcy 1979), while males in other populations (e.g. southern Indiana) make substantial contributions to feeding young, and this provisioning significantly increases nesting success (Patterson 1979). When males provide non-shareable parental care that affects female fitness, it may be advantageous for an early-nesting female to attempt to prevent or delay nesting by later-arriving females (Orians 1980). If early-nesting females enforce delays on subsequent females in order to garner a greater share of male parental care, then time intervals between nesting attempts within territories should be longer than those expected by chance. A pattern of overdispersion in time of nesting attempts within territories, however, could also result from avoidance behavior by later-arriving females seeking mates they will not have to share or from asynchrony enforced by the males.

Another potential cost of living in groups is increased competition for food (Alexander 1974). In Red-winged Blackbirds, the amount of food that females acquire on the territories of their mates varies substantially from region to region, presumably in response to the availability of food on and off the territory (Orians 1980). Where a female forages on her mate's territory, it may be advantageous for her to prevent or delay nesting by subsequent females in order to gain a greater share of the territory's food supply. If inter-female aggression reduces competition for food, we also expect longer time intervals between nesting attempts within territories than expected by chance. A second tactic for securing a competition-free food supply is to defend a portion of the male's territory. Nero (1956) states that female redwings defend such subterritories surrounding their nests. If females defend subterritories, then nesting attempts within a territory should be farther apart than expected by chance. Defense of subterritories becomes more difficult once incubation begins, however, because continued aggression would require neglect of eggs and young (Orians 1980). Thus, only nests started close together in time should be overdispersed in space. Again, overdispersion could be the product of avoidance behavior by later-arriving females or male aggressive behavior toward females attempting to nest close to one another in time or space, rather than aggressive defense by early-settling females.

The presence of other females might also be detrimental if nest predators are attracted to concentrations of nests, increasing the risk of predation per nest in densely occupied areas (Alexander 1974). Weatherhead and Robertson (1977) found that nest predation increased with density of nesting in an Ontario population of Red-winged Blackbirds, while Caccamise (1976) failed to find a relationship between predation and density in a New Jersey population. Where nest predation increases with density, overdispersion of nesting attempts in time and space within territories should be advantageous.

Another potential disadvantage of group nesting is that females might directly interfere with one another's nesting attempts. Female Long-billed Marsh Wrens (*Cistothorus palustris*) destroy eggs of conspecific females if given the opportunity (Picman 1977); however, there is no evidence of such mutual interference by female Red-winged Blackbirds. Such direct interference, if it exists, might also favor overdispersion of nests in both time and space.

Presence of conspecific females on the same territory is not necessarily detrimental. There can be benefits as well as costs associated with group living (Alexander 1974), and these benefits could outweigh the disadvantages in the Red-winged Blackbird. One potential benefit is that females could warn one another about predators and act together in defending themselves and their nests. Picman (1980) provided evidence that female redwings help protect one another's nests from marsh wren predation (see also Hoogland and Sherman 1976). In addition, a large enough concentration of nests might swamp some nest predators and thus lower the risk of predation per nest (see, for example, Tenaza 1971). Group vigilance and defense could also reduce other risks such as that of Brown-headed Cowbird (*Molothrus ater*) parasitism (Robertson and Norman 1977). Another potential benefit of group living is increased foraging efficiency. For example, female redwings could lead each other to favorable food sources (Ward and Zahavi 1973). If such benefits outweigh the costs of nesting near other females, then we expect the distribution of nesting attempts within territories to be underdispersed in time and space.

For any given habitat, the relative costs and benefits of group living will depend on the size and quality of the territory, the extent of parental care provided by the male, and the density of females nesting within the territory. Thus, the number of females attracted to a territory should reflect the quality of the total "breeding situation" confronting females (Wittenberger 1976). Further, harem size may also affect the relative costs and benefits of group living. For example, the costs of sharing a territory and mate may be low in small harems but high in large harems, or the costs of preventing or delaying nesting by later-arriving females may be prohibitive in small harems because the quality of the breeding situation is low. In either case, nesting attempts should be more dispersed in large harems than in small harems. If the benefits of group living outweigh the costs, however, then we might expect nesting attempts to be more synchronous in large than in small harems, because the best territories and males should quickly attract large harems, while poorer breeding situations should acquire females more slowly.

In this paper, we examine time intervals between nesting attempts of female Red-winged Blackbirds on the same territories and compare these to intervals between nesting attempts on different territories. If females influence the timing of each other's nesting attempts, this influence presumably diminishes rapidly with distance. Therefore, nesting attempts on one territory can be assumed to be approximately independent of the behavior of females occupying other territories. We also examine the frequency with which nests started close together in time on the same territory are nearest neighbors in space. We assume that a female is most likely to influence spacing of other nests started close to hers in time, both because those nests have the greatest beneficial or deleterious effects on the success of her own nest and because she has more time early in her nesting period to repel other females than she has during incubation and nestling periods.

<center>METHODS</center>

Nesting female Red-winged Blackbirds were studied at Turnbull National Wildlife Refuge, Spokane County, Washington (see Searcy 1979) and Yellowwood State Forest, Brown County, Indiana (see Ya-sukawa 1979). At both study sites, redwings nested in emergent vegetation dominated by cattails (*Typha latifolia*) and bulrushes (*Scirpus* spp.). At Yellowwood, bur reed (*Sparganium eurycarpum*) was also commonly used as a nesting substrate.

At Turnbull, nest data were obtained by searching for nests twice weekly during the nesting seasons of 1975 and 1976. At Yellowwood, searches were conducted three times each week during the 1975, 1976, and 1977 nesting seasons. Nests were marked with numbered tags tied to nearby vegetation, and their locations were plotted on study area maps. On each visit, we noted the contents of each nest, and from these data we subsequently constructed a nesting chronology for each territory. Territory boundaries were determined by plotting locations of male advertisement displays and boundary encounters.

Timing of nesting attempts.—We used the date on which a nest received its first egg to estimate the day on which a nesting attempt was initiated. First egg date was used because it can be determined accurately for any nest that survives until hatching, even if the nest was not found during the egg-laying period (Orians 1980). To determine whether nests within territories were initiated more or less synchro-nously than expected by chance, we calculated inter-nest intervals (number of days) for all combinations of two nests at a study area in a breeding season. We then compared intervals for pairs of nests placed within territories with those of pairs placed on different territories. The cumulative frequency distribu-tions for within- and between-territory intervals were compared using Kolmogorov-Smirnov tests for goodness of fit. The test statistic, d_{max}, is used to decide whether the maximum difference between observed and expected cumulative frequency distributions is statistically significant (Sokal and Rohlf 1969). Our analysis assumes that efforts to exclude other females will have a greater effect on subsequent nesting attempts on the same territory than on nesting attempts on other territories. The analysis also assumes that cooperative effects will be stronger among harem members than among females on different territories, because any benefits of synchronous nesting should decrease as distance between nests in-creases. Although nests on adjacent territories may be close to one another, the average distance overall between nests on different territories is much greater than the average distance between nests on the same territory.

The costs and benefits of nesting near another female may vary with stage of the nesting cycle, with status in the harem, or with size of the harem. Female Red-winged Blackbirds are thought to be most aggressive toward other females early in the breeding season, and primary females (those first to mate within a territory) who attempt to exclude unmated females are thought to have a more favorable cost/ benefit ratio for such behavior than lower-status females (Wittenberger 1979). To determine whether time of season or female status affects nesting synchrony, we calculated inter-nest intervals for nesting attempts initiated within 20, 40, 60, and 80 days of the earliest attempt in each population in each breeding season (see below). If proximity is most detrimental for early-nesting females, then nesting attempts within a territory should be least synchronous when analysis is restricted to the first 20 days of the nesting season. Analysis of longer periods should be less successful in demonstrating asynchrony within territories.

Restriction of analysis to shorter periods should also help control for possible error introduced by renesting. If individual females tend to renest on the same territory, this would disproportionately increase the number of long inter-nest intervals within territories. The amount of renesting occurring within a 20-day interval, however, should be near zero. Thus, the distribution of inter-nest intervals for the first 20 days of nesting can be considered to be free from the influence of renesting. Subsequent increases to 40, 60, and 80 days, while they incorporate effects of season and female status, may also reflect effects of renesting.

The cost/benefit ratio for attempts to exclude unmated females may also vary with quality of the breeding situation and therefore with harem size. To determine whether harem size affects nesting synchrony, we made separate comparisons of observed and expected inter-nest intervals for territories with less than, and greater than, average harem sizes.

Location of nesting attempts.—To determine whether synchronous nesting attempts within a territory tend to be separated in space, we examined relative locations within territories of pairs of nests that had inter-nest intervals of 8 days or less. We used 8 days as a criterion because this is approximately the interval between the start of nest construction and the start of incubation (Orians 1980). We calculated the proportion of nest pairs started within 8 days of one another on the same territory that were nearest neighbors in space, and we compared this observed proportion to that expected if nests were randomly
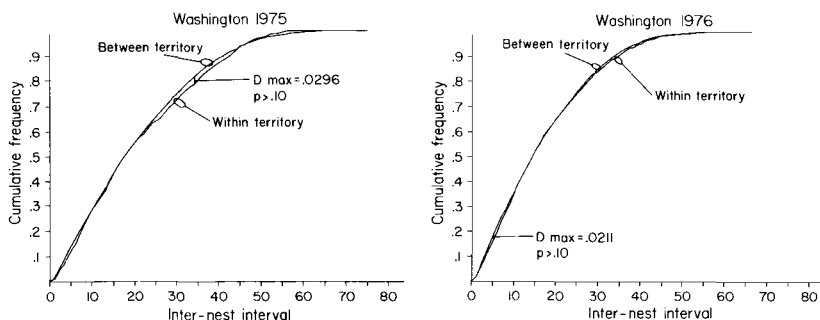
Fig. 1. Cumulative frequency distributions for within- and between-territory inter-nest intervals of Red-winged Blackbird nests at Turnbull National Wildlife Refuge, Washington State. Inter-nest intervals are number of days elapsing between first-egg dates for pairs of nests within a territory and on different territories. The within- and between-territory distributions are not significantly different statistically in either year according to Kolmogorov-Smirnov d_{max} tests.

placed within territories, using chi-square tests. We also performed the same type of analysis using only nearest neighbors of primary females in an effort to test for possible effects of time of season or female status on separation in space. If separation is most beneficial for early-nesting females, then primary females should be most likely to enforce separation of nesting attempts in space, or secondary females should be most likely to avoid nesting near primary females.

RESULTS

Inter-nest intervals calculated for all within- and between-territory pairs of nests at Turnbull in 1975 and 1976 yielded the cumulative frequency distributions shown in Fig. 1. Within- and between-territory cumulative distributions did not differ significantly in either year (1975: $n = 712$ within-territory intervals, $d_{max} = 0.03$, $P > 0.5$; 1976: $n = 1,425$ within-territory intervals, $d_{max} = 0.02$, $P > 0.5$). Limiting analysis to the first 20, 40, 60, or 80 days of the nesting season did not produce any significant differences in either year ($P > 0.05$ in all cases). In addition, separation of analysis into territories with large and small harems had little effect. There was some evidence that small harems were overdispersed in 1976, but this difference was not statistically significant at the 0.05 level ($n = 118$ within-territory intervals, $d_{max} = 0.12$, $P < 0.07$). All other comparisons were not statistically significant ($P > 0.1$ in all cases). In all comparisons, the within- and between-territory cumulative frequency distributions were very similar. Thus, there is no evidence that
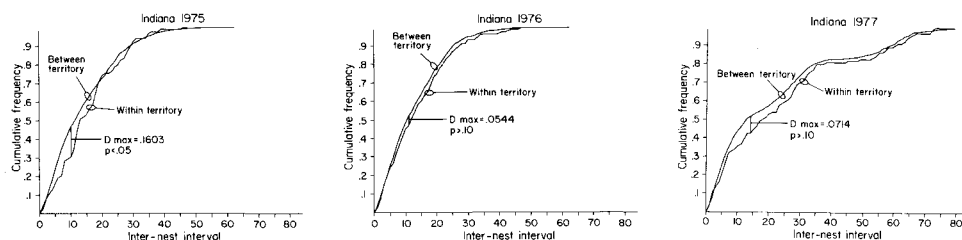

Fig. 2. Cumulative frequency distributions for within- and between-territory inter-nest intervals of Red-winged Blackbird nests at Yellowwood State Forest, Indiana. Inter-nest intervals as in Fig. 1. Kolmogorov-Smirnov d_{max} was statistically significant for 1975, but was not significant for 1976 or 1977.

TABLE 1. Observed and expected numbers of nearest neighbors for Red-winged Blackbird nests started within 8 days of one another on the same territory at Turnbull National Wildlife Refuge, Washington State.[a]

Year	Nests	Nearest	Non-nearest	χ^2
1975	All nests	21 (23.0)	77 (75.0)	0.23
	Primary nests	2 (3.8)	15 (13.2)	1.14
1976	All nests	64 (59.0)	182 (187.0)	0.50
	Primary nests	13 (13.0)	46 (46.0)	0.00

[a] See text for explanation. Primary = first nest constructed within a territory. Overall chi-square for all nests = 0.15, $P > 0.05$. Overall chi-square for primary nests = 0.25, $P > 0.05$. Expected values in parentheses.

female Red-winged Blackbirds at Turnbull National Wildlife Refuge nest asynchronously within territories.

Inter-nest intervals calculated for all nest pairs at Yellowwood in 1975, 1976, and 1977 yielded the cumulative frequency distributions shown in Fig. 2. In all 3 yr, short intervals were less common within territories than between territories, and there was a statistically significant difference in the cumulative frequency distributions in 1975 (1975: $n = 89$ within-territory intervals, $d_{max} = 0.16$, $P < 0.05$; 1976: $n = 136$ within-territory intervals, $d_{max} = 0.05$, $P > 0.5$; 1977: $n = 104$ within-territory intervals, $d_{max} = 0.07$, $P > 0.5$). Limiting analysis to 20-, 40-, and 60-day periods had little effect on these results. Within-territory nestings were consistently less synchronous than between-territory nestings, and these differences were significant in the 40- and 60-day analyses of 1975 nesting attempts, while all others were not significant ($P > 0.05$ in all cases). When territories were separated into those with large and small harems, none of the cumulative frequency distributions was significantly different ($P > 0.1$ in all cases). Thus, there is some evidence that female Red-winged Blackbirds at Yellowwood State Forest separate their nesting attempts in time when they nest together on one territory, but there is no evidence that nesting asynchrony declines as the nesting season advances or that harem size affects the degree of synchrony.

Tables 1 and 2 show the observed numbers of pairs of nests started on the same territories within 8 days of one another that were nearest neighbors in space for Turnbull and Yellowwood, respectively. The observed numbers were compared with those that would be expected if females nesting close in time on the same territory did not influence one another's nesting locations. The observed and expected numbers of nearest-neighbor pairs were very similar for all years in both

TABLE 2. Observed and expected numbers of nearest neighbors for Red-winged Blackbird nests started within 8 days of one another on the same territory at Yellowwood State Forest, Indiana.[a]

Year	Nests	Nearest	Non-nearest	χ^2
1975	All nests	9 (6.8)	34 (36.2)	0.85
	Primary nests	4 (2.7)	15 (16.3)	0.69
1976	All nests	10 (11.6)	42 (40.4)	0.27
	Primary nests	1 (2.8)	26 (24.2)	1.24
1977	All nests	7 (7.3)	40 (39.7)	0.01
	Primary nests	5 (4.3)	26 (26.7)	0.12

[a] See text for explanation. Primary = first nest constructed within a territory. Overall chi-square for all nests = 0.01, $P > 0.05$. Overall chi-square for primary nests = 0.00, $P > 0.05$. Expected values in parentheses.

study sites, and there were no significant differences according to chi-square tests ($P > 0.1$ in all cases).

Tables 1 and 2 also show the results for the analysis restricted to nests started within 8 days of the primary female on each territory. Once again, the observed numbers of nearest-neighbor pairs closely approximated the numbers expected assuming random placement of nests, and there were no significant differences according to chi-square tests ($P > 0.1$ in all cases). Thus, there is no evidence for spatial separation of nests started close together in time for either population.

DISCUSSION

For the Washington population, there was a nonsignificant tendency for small harems to be overdispersed in time in one year, but the distributions of time intervals between nesting attempts within territories closely approximated the between-territory distribution, and nests started close together in time on the same territory appeared to be randomly distributed with respect to each other in space. Thus, there is little evidence that female Red-winged Blackbirds in this population affect either the timing or the placement of nests of other females on the same territory. These results are consistent with those of a study of inter-nest intervals of female redwings from three populations in Washington State (Orians 1980). For the Indiana population, we again found no evidence that females influence the locations of other nests on the same territory, and there was no evidence that harem size affected nesting synchrony within a territory. There was some evidence, however, that female redwings can affect the timing of other nesting attempts. There were fewer short internest intervals within territories than expected by chance in all 3 yr of the Indiana study, and the within- and between-territory cumulative frequency distributions were significantly different in 1 yr. Thus, nesting attempts may have been overdispersed in time in the Indiana population.

Whether nest distributions appear clumped, random, or overdispersed in space probably depends on the spatial scale considered. Our data indicate that redwing nests are randomly distributed with respect to nests started close together in time on the same territory, but we have no doubt that if the scale was increased to entire marshes, we would find that nests are clumped. Clumping of nests on the scale of entire marshes is probably the result of underdispersion of food resources and/or nest sites (Orians 1980). Picman (1980) showed that redwing nests in British Columbia are clumped on such a scale, and he attributed this distribution to an advantage of cooperative defense against marsh wren predation. If cooperative defense promoted clumping of nests, however, we would expect clumping within territories as well as within marshes. Thus, our spatial data indicate that cooperative defense is not an important factor influencing nest dispersion in our populations. This result is consistent with our observation that marsh wren predation was not an important source of egg or nestling mortality in either population. Few marsh wrens nested on our study sites, and we found little evidence of mortality caused by marsh wrens.

One interpretation of the random distribution of nests found in Washington is that the costs and benefits of group living are slight or that the costs roughly cancel the benefits. If there is no appreciable net cost or benefit due to nesting in proximity to other females in time or space, then we would expect neither overdispersion nor underdispersion of nests. Another, equally plausible interpretation is that early-nesting females would receive sizeable net benefits from preventing or delaying nesting

by other females, but they are unable to invest the time and energy necessary to do so. We cannot discriminate between these two possibilities with our data. It is clear, however, that there is no net benefit of clumping nests in time and space within territories, as clumping should be easy to achieve behaviorally.

In contrast to our Washington results, there was some evidence of overdispersion of nesting attempts in time, though not in space, in Indiana. Overdispersion in time but not in space is predicted if (a) females are seeking to monopolize the male's parental care, or (b) females are trying to minimize competition for food without defending subterritories, or (c) males are enforcing asynchrony so that they can provision young of several females. Male-enforced asynchrony seems the least likely of these possibilities. We never observed any evidence of males forcing females to delay their nesting attempts, and Nero (1956) reports that male redwings often intervene in female disputes on behalf of the newly arriving females by attacking their original mates. Further, male Red-winged Blackbird reproductive success increases with increasing harem size (Holm 1973), but asynchronous nesting by a male's mates would probably reduce harem size (Verner 1964). Because the probability of attracting additional mates is relatively high, a male redwing would probably increase his fitness by investing his time in attempting to attract additional females rather than enforcing asynchronous nesting by his existing mates. Of the remaining alternatives, monopolization of male parental care seems more likely. This hypothesis is consistent with the difference between the time-interval distributions in Indiana and Washington. In Washington, male redwings provide little nonshareable parental care, so there is little advantage to females in monopolizing male parental care. In contrast, males in the Indiana population have been shown to provide important nonshareable parental care in the form of provisioning young (Patterson 1979), so there could be a net advantage to females who attempt to monopolize male parental care. Thus, our data favor the hypothesis that female redwings nest asynchronously within territories to minimize competition for male parental care.

Other lines of evidence also suggest that sharing a territory with other females is at times detrimental to the success of female Red-winged Blackbirds. Lenington (1980) found that female nesting success declined as harem size increased in populations of redwings in Illinois and New Jersey. In addition, female redwings are commonly observed to be aggressive toward one another during the breeding season. For example, females chase one another (Nero 1956) and attack caged females and stuffed females placed within the territories of their mates (O'Connor 1976, Yasukawa unpubl. data). Such behavior implies that the proximity of other females is somehow disadvantageous.

Although the costs and benefits of sharing a territory may depend on the number of females nesting within that territory, we found little evidence that the degree of nesting synchrony varies with harem size in our populations. Orians (1980) found some evidence that redwing inter-nest intervals tend to be shorter on territories that attracted more females than on those that attracted fewer females. We found a similar tendency in our Washington population, but the result was not statistically significant. If this trend is correct, it might mean that the costs of female aggressiveness are more important than the benefits (see Myers et al. 1979, Ewald et al. 1980), but further speculation would be premature.

These results have important implications for models of the evolution of polygyny.

According to the polygyny threshold model, polygyny occurs if unmated females that pair with already mated males providing superior breeding situations achieve higher fitness than females that choose bachelor males with inferior breeding situations (Verner 1964, Verner and Willson 1966, Orians 1969, Wittenberger 1976). This model can be divided into two subsets, depending on how the expected fitness of a newly mated female is influenced by the number of females her mate has already acquired (Altmann et al. 1977, Wittenberger 1979). In a competitive model, the presence of other females has a negative effect on a new female's expected success, and a female joins a harem only if the breeding situation is good enough to compensate her for the presence of other females (Orians 1969). In a cooperative model, the presence of other females is beneficial, at least up to some optimal harem size greater than one (Altmann et al. 1977). The cooperative model would predict clumping of nesting attempts, but we found no evidence of clumping within territories in either Washington or Indiana. The competitive model predicts overdispersion. We found some evidence of overdispersion in time in Indiana, but no evidence of overdispersion in Washington. Overdispersion may be beneficial to early-settling females in both populations, but such females may not always be able to impose delay or spacing on later-arriving females. Thus, our results are more consistent with the competitive than the cooperative version of the polygyny threshold model for the evolution of polygyny.

LITERATURE CITED

ALEXANDER, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5: 325–383.

ALTMANN, S. A., S. S. WAGNER, & S. LENINGTON. 1977. On the evolution of polygyny. Behav. Ecol. Sociobiol. 2: 397–410.

BERTRAM, B. C. R. 1978. Living in groups: predators and prey. Pp. 64–96 *in* Behavioural ecology (J. R. Krebs and N. B. Davies, Eds.). Sunderland, Massachusetts, Sinauer.

CACCAMISE, D. F. 1976. Nesting mortality in the Red-winged Blackbird. Auk 93: 517–534.

DOWNHOWER, J. F., & K. B. ARMITAGE. 1971. The yellow-bellied marmot and the evolution of polygamy. Amer. Natur. 105: 355–370.

ELLIOTT, P. F. 1975. Longevity and the evolution of polygamy. Amer. Natur. 109: 281–287.

EWALD, P. W., G. L. HUNT, & M. WARNER. 1980. Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. Ecology 61: 80–87.

HOLM, C. H. 1973. Breeding sex ratios, territoriality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). Ecology 54: 356–365.

HOOGLAND, J. L., & P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46: 33–58.

HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird *Euphagus cyanocephalus*. Ecology 49: 682–694.

LENINGTON, S. 1980. Female choice and polygyny in Redwinged Blackbirds. Anim. Behav. 28: 347–361.

MYERS, J. P., P. G. CONNORS, & F. A. PIANKA. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96: 551–561.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. II. Territoriality. Wilson Bull. 68: 129–150.

O'Connor, E. 1976. Response of female Red-winged and Brewer's blackbirds to the presence of intruding female conspecifics near their nests. Unpublished M.S. thesis, Seattle, Washington, Univ. Washington.

Orians, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr. 31: 285–312.

———. 1969. On the evolution of mating systems in birds and mammals. Amer. Natur. 103: 589–603.

———. 1980. Some adaptations of marsh-nesting blackbirds. Monogr. Popul. Biol. No. 14. Princeton, New Jersey, Princeton Univ. Press.

Patterson, C. B. 1979. Relative parental investment in the Red-winged Blackbird. Unpublished Ph.D. dissertation, Bloomington, Indiana, Indiana Univ.

Picman, J. 1977. Intraspecific nest destruction in the Long-billed Marsh Wren, *Telmatodytes palustris palustris*. Can. J. Zool. 55: 1997–2003.

———. 1980. Impact of marsh wrens on reproductive strategy of Red-winged Blackbirds. Can. J. Zool. 58: 337–350.

Robertson, R. J., & R. F. Norman. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55: 508–518.

Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds (*Agelaius phoeniceus*). Amer. Natur. 114: 77–100.

Sokal, R. R., & F. J. Rohlf. 1969. Biometry. San Francisco, W. H. Freeman.

Tenaza, R. 1971. Behavior and nesting success relative to nest location in Adelie Penguins (*Pygoscelis ageliae*). Condor 73: 81–92.

Verner, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Evolution 18: 252–261.

———, & M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143–147.

Ward, P., & A. Zahavi. 1973. The importance of certain assemblages of birds as 'information centers' for food-finding. Ibis 115: 517–534.

Weatherhead, P. J., & R. J. Robertson. 1977. Harem size, territory quality, and reproductive success in the Redwinged Blackbird (*Agelaius phoeniceus*). Can. J. Zool. 55: 1261–1267.

Wittenberger, J. F. 1976. The factors selecting for polygyny in altricial birds. Amer. Natur. 110: 779–799.

———. 1979. The evolution of mating systems in birds and mammals. Pp. 271–349 *in* Social behavior and communication (P. Marler and J. G. Vandenbergh, Eds.). New York, Plenum.

———. 1980. Group size and polygamy in social mammals. Amer. Natur. 115: 197–222.

Yasukawa, K. 1979. Territory establishment in Red-winged Blackbirds: importance of aggressive behavior and experience. Condor 81: 258–264.

Zahavi, A. 1974. Communal nesting by the Arabian Babbler: a case of individual selection. Ibis 116: 84–87.