

BREEDING AND NONBREEDING SEASON MORTALITY OF TERRITORIAL MALE RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*)

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ABSTRACT.—The mortality of territorial male Red-winged Blackbirds (*Agelaius phoeniceus*) was determined in a banded population during the breeding seasons of 1973–1978. I used these data to test the hypothesis that sexual selection for characteristics that are advantageous in territory defense or mate acquisition, or both, occurs at the expense of survivorship. Observations of males that returned to the study area to reestablish territories, and of the tenures of these males on their territories, enabled me to partition annual mortality into components that estimate mortality during the nonbreeding and breeding seasons. The mean annual mortality of territorial male Red-wings was 52%, with 29% mortality occurring during the “nonbreeding” season (1 June to approximately 1 March) and 22% mortality occurring during the breeding season before 1 June. The effect of body size on survivorship was investigated by correlating male wing lengths measured in the third year of life with their ages at death. The correlation between wing length and survivorship was negative (-0.438) and statistically significant (one-tailed $P < 0.05$). I conclude that mortality during the breeding season is a potentially important selective force in this species, and that sexual selection may have occurred at the expense of survivorship. Sexual selection for large males appears to be opposed by survival selection for small males. Received 13 January 1986, accepted 15 July 1986.

DARWIN (1859, 1871) viewed natural and sexual selection as separate but complementary mechanisms of evolution. According to Darwin, natural selection favors adaptations that increase survival, while sexual selection favors adaptations that increase the ability to acquire mates but decrease survival. In contrast, contemporary evolutionary biologists consider both selection for increased survival (survival selection) and selection for increased mating ability (sexual selection) as components of natural selection (see Mayr 1972, Selander 1972). Sexual selection, however, is still thought to occur at the cost of decreased survival (e.g. Selander 1965, Searcy 1979, O’Donald 1980, Lande 1981, Searcy and Yasukawa 1981, Kirkpatrick 1982). Thus, when sexual selection produces sexual dimorphism, the larger and more conspicuous sex is presumed to pay a cost in higher mortality (see Andersson 1982, Searcy and Yasukawa 1983, Payne 1984). Survival selection therefore would act to limit the effects of sexual selection because it would favor smaller, less conspicuous individuals of the sexually selected sex. Although the opposition of sexual and survival selection has been presumed since Darwin (1859), there have been relatively few attempts to document the reduced survival that should accompany sexual selection.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a species in which sexual dimorphism is thought to be the product of sexual selection (see Searcy and Yasukawa 1983). Male Red-wings are larger and more conspicuous than are females (Nero 1956a, b; Orians and Christman 1968), and sexual selection is a potentially important evolutionary force because the variance in mating success is high (Payne 1979). However, although sexual selection is thought to act more strongly on male than on female Red-winged Blackbirds (Payne 1979), male and female Red-wing survivorship is virtually identical (Fankhauser 1971, Searcy and Yasukawa 1981). Thus, there is no evidence that males pay a cost in increased mortality. Furthermore, there is little evidence that larger male Red-winged Blackbirds suffer higher mortality than do smaller males (Searcy 1979, Johnson et al. 1980). These observations are inconsistent with the generally accepted view that sexual selection is primarily responsible for the sexual dimorphism in size, plumage, and behavior in Red-winged Blackbirds (see Searcy and Yasukawa 1983).

I tested the hypothesis that sexual selection has favored characteristics that enhance a male’s ability to acquire a territory or mates, but at the expense of his survival (Selander 1965, Searcy

1979). This sexual-selection hypothesis predicts that the mortality of males during the breeding season should represent a considerable portion of annual mortality because males pay a cost that results from their conspicuous and energetically expensive attempts to defend their territories and attract mates. I tested this prediction by partitioning the annual mortality of male Red-winged Blackbirds into components that estimate mortality in the breeding and nonbreeding seasons. The hypothesis also predicts that counter-balancing survival selection will favor small males. I tested this prediction by examining the relationship between size and survival of male Red-winged Blackbirds.

METHODS

I studied a breeding population of Red-winged Blackbirds at Yellowwood Lake, Yellowwood State Forest, Brown Co., Indiana. Males defended all available portions of emergent vegetation, as well as portions of adjacent campgrounds, at the north end of the lake. Descriptions of the study area have been published elsewhere (Yasukawa 1979, 1981).

All male Red-winged Blackbirds that both defended territories and acquired mates during the breeding seasons of 1973–1978 were captured in mist nets or potter traps and banded with U.S. Fish and Wildlife Service numbered aluminum bands and a unique combination of plastic color bands. The length of the flattened wing was measured for each captured male. Banded males were subsequently observed daily during their tenures on their territories in 1974–1977. These observations enabled me to determine whether each male returned to the study area in a subsequent breeding season, and when each male ceased to defend his territory, either because he quit his territory at the end of the breeding season or because he disappeared during the breeding season. A territorial male's permanent disappearance following his return to the study area and before 1 June was assumed to result from mortality rather than dispersal. This assumption was supported by my failure to discover males that disappeared in other nearby habitats that were suitable for nesting, and, with one exception, by the failure of these males to return to the study area in a subsequent breeding season.

In only one case did a male defend a territory in one year (1974), return to the study area in the next year and disappear before 1 June, and then reappear in another year (1976). In this exceptional case, the male did not simply disappear, but rather was forcibly evicted from his territory by another male (Yasukawa 1979). The evicted male then reclaimed his former territory when the usurper failed to return in the subsequent year. In contrast, many males that disappeared from their territories after 1 June re-

turned to the study area in the following breeding season. Therefore, disappearances after this date could not be assumed to represent mortality in all cases, and males that disappeared after 1 June and did not return to the study area in the following breeding season could have died either during the latter part of the breeding season or during the nonbreeding season.

Mortality was estimated by identifying the territorial male Red-winged Blackbirds on 1 June of each year, those that returned to the study area in the next breeding season, and those that subsequently disappeared before 1 June. A territorial male was defined as a male that defended a territory with at least one active nest. Annual mortality was estimated as the proportion of territorial males present on 1 June of one year that were not territorial on 1 June of the following year. Nonbreeding-season mortality was estimated as the proportion of territorial males present on 1 June of one year that failed to return to the study area in the following breeding season. Note that this period from 1 June to the beginning of the subsequent breeding season included the latter part of the actual breeding season, which continued into July in the study population. Breeding-season mortality was estimated as the proportion of territorial males present on 1 June of one year that returned to the study area and then disappeared before 1 June of the following year.

In addition to daily observations conducted in 1974–1977, the study area was visited for one week in late May 1978 to determine which males that were territorial on 1 June 1977 were still present in 1978. These data enabled me to estimate annual mortality for 1977–1978. I did not conduct daily observations in 1978, so I could not estimate the nonbreeding- and breeding-season components of mortality in that year.

In some cases, I obtained information on longevity of known-age birds. Males banded as young of the year, or as second-year birds (male Red-winged Blackbirds exhibit delayed plumage maturation), that subsequently acquired territories and were categorized as victims of nonbreeding- or breeding-season mortality were of known age when they died. To determine whether size affected survivorship in male Red-winged Blackbirds, I calculated a Spearman rank correlation coefficient of age at death and wing length measured for third-year birds (the first year in which males acquire the definitive, adult plumage). Statistical significance was accepted at the 0.05 level.

RESULTS

Overall, annual male Red-wing mortality was 52% (Table 1). An average of 0.43 of this annual mortality occurred during the breeding season before 1 June (i.e. breeding-season mortality = 22%; Table 1). This breeding-season mortality

TABLE 1. Mortality of territorial male Red-winged Blackbirds.

Year	n ^a	Mortality		
		Non-breeding season ^b	Breeding season ^c	Annual ^d
1974	30	26.7%	26.7%	53.3%
1975	22	18.2	13.6	31.8
1976	23	30.4	30.4	60.9
1977	28	39.3	17.9	57.1
1978	24	—	—	54.2
Mean	25	29.1	22.3	52.0

^a Number of males that were territorial on 1 June of the previous year.

^b Estimated as the percentage of *n* that failed to return to the study area in that year.

^c Estimated as the percentage of *n* that returned to the study area and then disappeared before 1 June of that year.

^d Estimated as the percentage of *n* that was not territorial on 1 June of that year.

is significantly higher than that expected (0.25) during a 3-month period (the median date on which males returned to the study area was 4 March), assuming that mortality occurs at a constant rate throughout the year ($\chi^2 = 9.56$, $P < 0.01$). The majority (78.3%) of the disappearances that I attributed to breeding-season mortality occurred after 1 April (Table 2), and 65.2% of the 23 males that disappeared during the breeding season had at least 2 years of previous breeding experience on the study area. Thus, there appears to be considerable male mortality during the breeding season. My estimates are probably conservative with respect to the sexual-selection hypothesis because the breeding season extends well beyond 1 June in this population. For example, 75% of the males that survived until 1 June were still defending territories on 1 July; some remained on their territories well into July. In addition, of the 17

males that disappeared between 1 June and 1 July, 8 did not return to the study area in the following breeding season. Although these 8 males were included in the category of non-breeding-season mortality, some could have died during the last portion of the breeding season (i.e. in June or early July). These results are therefore consistent with the hypothesis that sexual selection for characteristics of males that are advantageous in territory defense or mate acquisition, or both, is accompanied by considerable mortality during the breeding season.

Male Red-winged Blackbirds appeared to incur a cost in the form of reduced survivorship during the breeding season, but the magnitude of this cost varied from year to year. Breeding-season mortality varied from 14% in 1975 to 30% in 1976 (Table 1). Nonbreeding-season mortality varied from 18% in 1975 to 39% in 1977, and annual mortality varied from 32% in 1975 to 61% in 1976. Thus, the strength of counter-balancing survival selection, and even the season in which it exerts its effects, may vary from year to year.

The relationship between wing length and survivorship of known-age male Red-winged Blackbirds is shown in Fig. 1. As predicted by the sexual-selection hypothesis, the Spearman rank correlation coefficient was negative and statistically significant ($r = -0.438$, one-tailed $P < 0.05$). Thus, there is evidence that size-selective mortality favors small male Red-winged Blackbirds.

DISCUSSION

My estimate of annual mortality for territorial male Red-winged Blackbirds (52%) is similar to that published by Fankhauser (1971; 49%) and by Searcy and Yasukawa (1981; 46%). These authors based their estimates of annual mortality on band recoveries of known-age birds. In

TABLE 2. Breeding-season mortality of territorial male Red-winged Blackbirds.

Year	n ^a	Date last seen					
		March		April		May	
		1-15	16-31	1-15	16-30	1-15	16-31
1974	8	0%	12.5%	37.5%	25.0%	25.0%	0%
1975	3	0	0	66.7	33.0	0	0
1976	7	28.6	14.3	0	42.9	14.3	0
1977	5	0	20.0	40.0	40.0	0	0
Mean	6	8.7	13.0	30.4	34.8	13.0	0

^a Number of males that disappeared before 1 June.

contrast, I estimated annual mortality from return rates of territorial males. Both Nero (1956a) and Picman (1981) also observed returns of territorial male Red-winged Blackbirds, and they estimated annual mortality to be 45.1% (calculated from Nero 1956a: table 1) and 54%, respectively. Despite the differences in study sites and methods, the estimates are similar (compare, for example, Elder 1985 and references therein).

My estimates of mortality were based on the critical assumption that territorial male Red-winged Blackbirds are site faithful. An alternative explanation for disappearances before or during the breeding season is that males disperse to other locations. For example, Dolbeer (1982) estimated a mean dispersal distance of 31 km based on recoveries of after-hatching-year (AHY) male Red-wings. Although the use of both second-year (SY) and after-second-year (ASY) males overestimates dispersal by territorial males, and use of recovery data underestimates site fidelity, these results demonstrate that male Red-winged Blackbirds can disperse over considerable distances. Thus, my failure to observe missing males in nearby suitable habitats does not preclude the possibility of dispersal.

The site fidelity and dispersal of territorial male Red-winged Blackbirds have been studied in a banded population in Washington state (Beletsky and Orians in press). Based on returns of territorial males, Beletsky and Orians (in press) estimated annual mortality to be 48.3%; however, a portion of the nonreturning males were subsequently discovered on other territories. Although 26.9% of territorial males changed territories, 73.3% of these moved less than 200 m, and 33% moved to an adjacent territory. Movers were usually young males (60% were 2 or 3 years old), and 75% of them moved after only one year on a territory. Beletsky and Orians (in press) suggested that movers often may be inexperienced males that initially establish in poor areas before shifting to better territories in subsequent breeding seasons.

Although lack of site fidelity is a potential source of error in my estimates of mortality, I believe that the magnitude of the error is small. All the males that disappeared during the breeding season returned to their territories before their disappearances, so all demonstrated site fidelity. The vast majority did not disappear until after 1 April when females had

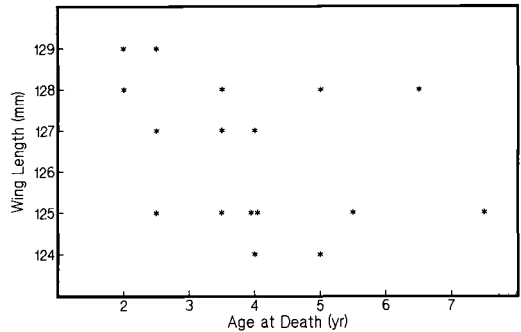


Fig. 1. Scattergram of age at death and wing length (mm) measured for third-year male Red-winged Blackbirds ($n = 17$).

already begun to settle on territories (see Nero 1956a, b). All of these males were previously experienced on the study area, and most had two or more years of experience. Older, experienced males have been shown to be the most site-faithful age-sex class of Red-winged Blackbirds (Beletsky and Orians in press). In several cases, because the males were site faithful, I was able to observe shifts in territory. In three cases males initially returned to their previous-year territories and then moved to adjacent, nonoverlapping territories. In a fourth case, a male returned to his territory, was subsequently evicted by a usurper, and then regained his original territory in the next year. Site fidelity thus seems well developed in the study population, especially among older, experienced males. It also seems unlikely that a dispersing male would find superior breeding habitat nearby because marshes are rare in the vicinity of the study area and a territorial male's ability to acquire information about sites away from the study area is probably limited (see Beletsky and Orians in press). It thus seems reasonable to assume that few surviving male Red-winged Blackbirds failed to return to their territories on the study area.

Estimates of annual mortality are available for many bird species, and these estimates have enabled ecologists to study a variety of topics, from population regulation to the evolution of life-history strategies. The recently renewed emphasis on sexual selection has underscored another important aspect of mortality. Survival selection is thought to oppose sexual selection because individuals that possess characteristics that are favored by sexual selection are presumed to suffer increased mortality (e.g. Selan-

der 1965). Mortality, then, is an important counter-selective force that acts to limit the effects of sexual selection. The many facets of mortality, however, suggest that estimates of annual mortality may obscure seasonal differences. In migratory bird species, seasonal differences in mortality are potentially great because the ecological circumstances and selection pressures of the breeding season can differ drastically from those of the nonbreeding season. Despite these potential differences, few studies have attempted to partition annual mortality into breeding-season and nonbreeding-season components.

Several authors (e.g. Lack 1954, Fretwell 1972, Wiens 1974) have emphasized the importance of mortality during the nonbreeding season, and have focused on the selection pressures that accompany this mortality. Despite the "widely held view that bird populations are primarily regulated by mortality outside the breeding season" (Krebs 1970: 324), however, only a few studies have specifically examined nonbreeding-season mortality (e.g. Selander 1965, Johnston et al. 1972, Johnson et al. 1980, Ketterson and Nolan 1982).

Red-winged Blackbirds appear to incur rather low mortality during the winter (Johnson et al. 1980), and my results suggest that even when the estimate of the nonbreeding season includes a portion of the breeding season and both spring and fall migration, the mortality of males is still low. In this regard the Red-winged Blackbird may be unusual.

While mortality during the nonbreeding season is of considerable importance in population regulation, breeding-season mortality could be of fundamental importance in the evolution of reproductive strategies via sexual selection. The evolution of (breeding season) territoriality, mating systems, and patterns of parental investment depend in part on the costs associated with alternative reproductive strategies (e.g. Brown 1964, Orians 1969, Trivers 1972). Mortality during the breeding season is an obvious parameter of these costs. Many ecologists suspect that these costs primarily involve nonbreeding-season mortality. For example, Selander (1965) thought sexual selection for large size in the Great-tailed Grackle (*Quiscalus mexicanus*) exposed males to increased risk of starvation and predation during the winter.

Contrary to the results of studies of other

territorial species of birds (e.g. see Nice 1937, 1943; Nolan 1978), male Red-winged Blackbirds seem to experience considerable mortality during the breeding season. Ultimately, this mortality probably results from the rigors of territory defense and the costs associated with large size and conspicuousness (see Searcy 1979; Yasukawa 1979, 1981). Territory defense is known to be time consuming and energetically expensive in Red-winged Blackbirds (Orians 1961, Searcy 1979), and much of the sexual dimorphism in size, plumage, and behavior in Red-wings appears to have evolved in response to intrasexual selection because large, conspicuous males have an advantage in territory acquisition and defense (see Searcy and Yasukawa 1983). Ultimately, the evolution of territoriality is thought to depend, in part, on the cost of territory defense (e.g. Brown 1964, Myers et al. 1979). Breeding-season mortality appears to be such a cost for male Red-winged Blackbirds.

Mortality during the breeding season could result from energy stress and starvation, predation, disease, parasitism, and other agents, but in Red-winged Blackbirds, energy stress and predation appear to be important sources of mortality. Male Red-wings expend considerable amounts of energy in territory defense and in other activities during the breeding season (Orians 1961), and they have been shown to lose mass as a result (Searcy 1979). This energy stress could lead to starvation, especially early in the breeding season when food is limited and weather conditions can be severe, and to susceptibility to disease and parasitism (see also Hamilton and Zuk 1982). Predation also appears to be an important source of breeding-season mortality. In 1976, when I observed the highest breeding-season mortality, I frequently sighted Cooper's Hawks (*Accipiter cooperii*) hunting on the study area, and on 14 April I observed an adult female Cooper's Hawk kill a territorial male Red-winged Blackbird. In addition, on two other territories in 1976 I found feathers and bands 1-2 days after the males had disappeared.

While our understanding of sexual selection has increased greatly in recent years (see Andersson 1982, Payne 1984 for recent reviews), almost all of the information available for birds has been gathered in an attempt to identify characteristics that are advantageous in intrasexual and intersexual selection. In contrast,

relatively little is known about the costs associated with the evolution of sexually selected characteristics, although most authors presume that such costs act to limit the response to sexual selection (see Searcy and Yasukawa 1983). Clearly, for the Red-winged Blackbird more information is needed on survival vs. sexual selection on females, and especially on breeding- and nonbreeding-season mortality of females. Perhaps information from continued, long-term studies will eventually produce useful data. A complete understanding of sexual selection for this and other species requires such information.

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100 Years Ago in The Auk



From "The Rediscovery of Bachman's Warbler, *Helminthophila bachmani* (Aud.), in the United States" by George N. Lawrence (1887, Auk 4: 36-37):

"No specimen of it [*Helminthophila bachmani*] has been obtained in the United States since the types discovered by Dr. Bachman in 1833, near Charleston, S. C., and described by Mr. Audubon. These are now in the National Museum at Washington. A search in the proper locality would probably result in finding more of this rare species, as was the case in Mr. Brewster's persistent pursuit of Swainson's Warbler. . . .

"As the coloring of this specimen was somewhat different from Mr. Audubon's plate, I wrote to Mr. Ridgway, pointing out wherein they differed, and requesting him to let me know whether the male (type) was accurately represented in the plate. He replied as follows: 'Your announcement of a specimen of Bachman's Warbler from Louisiana is a great

surprise to me, as it doubtless will be to ornithologists in general. Your bird corresponds in every particular with the male described and figured by Audubon, which is in our collection. The top of the head is dull ash gray, bordered anteriorly by a black band next to the yellow of the forehead, and the yellow of the face and underparts are of a dull yellow shade (oil yellow I would call it), exactly as you describe the specimen in your possession. Audubon's plate is very faulty in several particulars.'

"Mr. Galbraith [the collector] obtained only this specimen, and has no recollection of seeing another, but if he had—not knowing its desirability—he said, if a more highly plumaged bird had been in sight, it would have been shot in preference. . . ."