MALE CHARACTERISTICS AND PAIRING SUCCESS IN RED-WINGED BLACKBIRDS

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ABSTRACT.—As female Red-winged Blackbirds (*Agelaius phoeniceus*) in Washington populations choose mates mainly on the basis of territory quality, sexual selection should favor those characteristics that enhance a male redwing's ability to obtain and defend a good territory. In this study, correlations were sought between harem size and characteristics of male redwings that might be expected to contribute to the ability to compete for territory. Weak evidence is presented that large size, experience, good physiological condition, and the ability to devote a large proportion of daily activity to territory defense contribute to pairing success in some years. Even the significant correlations between success and male characteristics are weak, but strong correlations cannot be expected because (1) many different male characteristics probably contribute to competitive ability, none of which are of overwhelming importance; (2) males will not always make the optimal choice of territory, especially as their choice is constrained by extreme site fidelity; and (3) females will also fail to make optimal choices of territories and mates. *Received 14 August 1978, accepted 29 November 1978.*

SEXUAL selection involves either differential choice of mates by one sex or competition within a sex for the opportunity to mate with the other sex. In Red-winged Blackbirds (*Agelaius phoeniceus*) of Washington populations, female choice of breeding situation (Wittenberger 1976) is influenced mainly by territory quality rather than male quality (Searcy 1977, 1979a). Over 80% of copulations involve a female and the male on whose territory she is nesting (Emily Davies pers. comm.). Thus sexual selection must favor those traits that enhance success in competition between males for territories. Such selection would be expected to be very powerful in redwings, as males with good territories may have 10 or more mates, while males with poor territories have none, and breeding success per female does not decline as the number of females on a territory increases (Orians 1972, Holm 1973). This paper addresses the question: what characteristics in male Red-winged Blackbirds contribute to success in competition for territories?

Territoriality has been described as a system in which a territory owner is dominant over all conspecific individuals within a certain area (the territory), with the boundaries of the territory being the points at which dominance relations between neighbors reverse (Emlen 1957, Wiley 1973). The ability of a male to dominate other males in encounters should strongly influence both his ability to obtain a good territory when territories are initially established and his ability subsequently to defend his territory against neighbors and intruders.

Whether or not a given individual can dominate another is partly a function of how dominance is measured. Dominance can be measured either as priority of access to a limited resource (a competitive measure) or as the ability to make other individuals retreat or submit in aggressive encounters (an aggressive measure). Rankings in a hierarchy formed using a competitive measure are only imperfectly correlated with rankings formed using an aggressive measure, and often the correlations are quite weak (Syme 1974, Syme et al. 1974). Furthermore, rankings formed using competition for different rewards are not always identical (Van Kreveld 1974, Syme

1974). Therefore, we cannot assume that characteristics that contribute to dominance in one situation will necessarily contribute to dominance in another.

Size has been found to correlate with measures of dominance in species of many taxa, for example mammals (Barnett 1963, Schaller 1967, Bouissou 1972, Drickamer et al. 1973), lizards (Carpenter 1960, Rand 1967, Trivers 1972), and fish (Allee et al. 1948, Frey and Miller 1972, Gorlick 1976, Barlow and Ballin 1976). In birds, early studies with chickens (Murchison et al. 1935) and canaries (Shoemaker 1939) failed to find correlations between body size and dominance, but this failure may have been due to the small samples used. With larger samples, positive correlations between size and dominance were found in chickens (Collias 1943) and house finches (*Carpodacus mexicanus*) (Thompson 1960).

Aggressiveness may also contribute to dominance. Some studies have shown that dominant individuals participate in more aggressive encounters than subordinates (e.g. Carpenter 1960, Kikkawa 1961, Rose et al. 1971, Meese and Ewbank 1973, Eaton and Resko 1974, Spurr 1974). The explanation of these correlations could be either that individuals win encounters because they are constitutionally more aggressive or that those individuals who win encounters learn to be aggressive. More certain of interpretation are studies in which hormone implants or injections have been used to raise aggressiveness, and the increase in aggressiveness has resulted in a rise in dominance (e.g. Allee et al. 1939, Noble and Borne 1940, Boss 1943, Bennett 1940, Selinger and Bermant 1967, Crook and Butterfield 1968).

Age may contribute to dominance ability, presumably because experience in aggressive encounters increases the probability of winning further encounters. A confusing factor is that size, as well as experience, often increases with age. Evidence that dominance increases with age has been found in male sea elephants (*Mirounga angustirostris*) (Le Boeuf 1974), female pheasants (*Phasianus colchicus*) (Collias and Taber 1951), and White-bearded Manakins (*Manacus manacus*) (Lill 1974).

Plumage coloration or configuration correlates with dominance in some bird species, for example Harris' Sparrows (*Zonotrichia querula*) and White-throated Sparrows (*Zonotrichia albicollis*) (Rohwer 1975, Harrington 1973). Plumage is generally not thought to be a cause of high or low dominance but rather a signal of dominance status. Marler (1955, 1956), however, found that female chaffinches (*Fringilla coelebs*) dyed red to resemble males were able to dominate most normal females. Peek (1972) and Smith (1972) dyed epaulets of male redwings black, whereupon most of the experimental birds lost their territories, but this result may be due to a failure of species recognition rather than to a lowering of the dominance status signalled by the experimental birds.

The condition of an animal with respect to energy reserves might also affect dominance status. Condition would be more likely to be important in free-living animals than in captive ones fed *ad libitum,* and as most studies of dominance have been done with captive animals, it is not surprising that condition has seldom been considered as a factor affecting dominance. Collias (1943) found that presence or absence of molt, which strongly affects energy balance, was the most important factor determining the outcome of dominance encounters in chickens.

In the present study, I hypothesized that characteristics known to lead to high dominance rank in other species would be important in competition for territories in redwings. The following male attributes were hypothesized to affect success: (1) body size, measured as wing length and weight; (2) experience; (3) aggressiveness,

measured by display rates and reaction to a strange male; (4) size and color of epaulets; and (5) condition, measured as body weight per wing length cubed. In addition, I reasoned that the amount of time a male was able to expend in territory defense relative to other activities should influence his ability to get and defend a good territory. Therefore, I predicted (6) that the percentage of the day a male spent defending his territory would affect his success. To test these predictions, correlations were sought between characteristics of territory owners and the quality of their territories. Harem size, an estimate of the relative number of females settling on a territory, was used as a measure of territory quality.

STUDY AREA AND METHODS

Fieldwork for the study was done at the Turnbull National Wildlife Refuge in eastern Washington during the springs of 1974, 1975, and 1976. Redwings breed on the refuge in areas of cattails (*Typha latifolia*) and bulrushes (*Scirpus* sp.) along the margins of small lakes. Early each spring males were captured with decoy traps (Smith 1972), color banded, measured, and released.

Wing length was measured in 1974 as the chord of the wing, but in 1975 and 1976 the wing was flattened when measured because this procedure gave a more repeatable value. Two measurements of epaulet size were made: the distance from the bend of the wing to (1) the farthest extension of red plumage (length of red), and (2) the farthest extension of yellow plumage (length of yellow). The color of the red part of the epaulet was rated by comparison to Royal Horticultural Society color sheets and given a numerical score between 12 (orange) and 18 (vermillion).

Weights were measured with a 100-g spring scale. When weight of territorial males was regressed against day of capture, it was found that weight declined by 0.09 g per day in 1974 (Pearson's $r = -.327$, $P < .05$) and by 0.11 g per day in 1975 ($r = -.371$, $P < .05$). No significant decline was found in 1976. In the text, "weight" will refer to the actual weight at the time of measurement and "corrected weight" to the weight of the bird corrected back to the day the first individual was captured, using the assumption that each individual lost 0.09 g/day in 1974, 0.11 g/day in 1975, and 0 g/day in 1976.

Display rates were estimated by observing males for 30-min periods in 1974 and 1975 and 20-min periods in 1976 during the first 2 h after sunrise. Observations were made once in 1974 (8–29 May), once in 1976 (22 March–8 April), and three times in 1975 (25 March–11 April, 12 April–6 May, 26 May–3 June). In 1975 and 1976, time budgets of territorial males were estimated by visiting territories at 15-min intervals through 8-h periods in the middle of the day and noting the owners' activities. Time budgets were estimated once in 1976 (22 March–5 April) and at three stages of the 1975 season (25 March–11 April, 7–24 May, 4–28 June).

At the time of each capture, the number of minutes from the time the decoy was placed on the territory to the time the territory owner landed on the trap was noted. The inverse of this quantity, "the speed of response to a decoy male," was used as a measure of aggressiveness.

Harem sizes were calculated as the number of females needed to account for the nesting activity on a territory. It was assumed on the basis of previous observations (Orians unpubl. obs.) that a female would wait 7 days to renest if her first nest was destroyed and 20 days (including time spent feeding fledglings) after her last young fledged if her first clutch was successful. Nests started late in the season were ascribed to a female who had nested earlier on the same territory whenever a long enough period intervened between the disappearance of all eggs or young from the first nest and the appearance of eggs in the second. Thus, my estimate of the number of females settling on a territory is a minimal one, because there are undoubtedly cases where the owner of the first nest failed to renest on the same territory and a new female moved in to start the second nest.

Correlations between male characteristics and harem size were calculated separately for each year, because average harem size varied greatly from year to year. Only adult males holding territory during the nesting periods of each season were used in the analysis.

RESULTS

Two measurements of size were used: wing length and weight. For all 3 yr, the Spearman rank correlation coefficients between weight and harem size are positive, and in 1 yr the correlation is significant ($P < .05$, Table 1). Weight is a crude

TABLE 1. Correlation between harem size and morphological measurements. Tabled values are r_s, Spearman rank correlation coefficients; * denotes significance at the 0.05 level.

Year	n	Weight	Wing length	Length of red	Length of yellow	Color	Condition
1974	42	.300*	−.210	−.153	.112	.084	.306*
1975	34	.116	.073	.197	−.092	−.308	−.062
1976	41	.215	.319*	.122	.194	.263*	−.226

measure of size, because weight fluctuates greatly within individuals according to the amount of fat they have stored. Wing length is usually considered the most reliable measure of size in birds (Hamilton 1961, James 1970), and the correlation between wing length and harem size varies from positive to negative, with only the correlation for 1976 being significantly greater than 0 ($P < .05$, Table 1).

Table 1 also gives the correlations between epaulet measurements and harem size. Neither length of red nor length of yellow correlated significantly with harem size in any year. There was a significant positive correlation between epaulet color and harem size in 1976 (the redder the epaulet, the greater the male's harem size), but there was an even larger negative correlation in 1975. It seems that neither epaulet size nor color is a reliable signal of dominance status, although epaulet color may be correlated with some trait that contributes to success in some years and not others. In fact, there is a suggestion that epaulets become redder with age. In 1975, the epaulets of 15 experienced males (known to have bred in 1974) received an average color rating of 17.07, while 27 inexperienced males (caught for the first time in 1975) had an average rating of 16.78; the difference is nearly significant ($P = 0.08$ according to a one-tailed Mann-Whitney U test). The 16.83 average of 24 experienced males in 1976, however, was only slightly greater than the 16.76 average of 17 inexperienced males ($P > .10$).

As weight should be approximately a function of the cube of a linear dimension, physical condition was measured as weight per wing length cubed. This is a measure of how fat a bird is for its size. The correlation between condition and harem size varied from positive to negative (Table 1), with a significant positive correlation in only 1 yr (1974).

Correlations between display rates and harem size are given in Table 2, along with the dates at which the observations were made. The three display rate measures used are: (1) number of songs given during the observation period (song number), (2) number of flight displays given during the observation period (flight displays), and (3) songs given per minute while the male was actually on his territory (song rate). The three significant correlations (all positive) are between song number and harem size in 1974, flight displays and harem size in 1974, and song number and harem size in the third round of observations in 1975. The fact that all the significant correlations come from observations made late in the breeding season, when most females were already settled on their territories, suggests that males are stimulated to display by the presence of females on their territories (or by the presence of males trying to approach these females) rather than that males get a good territory and a large harem because they display more or are more aggressive.

In testing for a correlation between speed of response to a decoy male and harem size, only males with no prior experience with the decoy trap were used. Even though a year intervened between their experiences with the trap, males who had

TABLE 2. Correlations between harem size and display rates. Tabled values are r_s, Spearman rank correlation coefficients; * denotes significance at the 0.05 level.

Date	n	Song number	Song rate	Flight displays
1974				
8 May–29 May	34	.367*	−.147	.342*
1975				
25 March–11 April	17	−.341	−.269	.050
12 April–6 May	34	.176	.161	.182
26 May–3 June	31	.301*	.263	.041
1976				
22 March–8 April	36	−.115	−.115	.069

been trapped before took significantly longer to respond to the decoy than did naive birds (Mann-Whitney U test, $P < .025$ for the 1975 sample of 10 experienced and 17 naive birds; $P < .001$ for the 1976 sample of 17 experienced and 17 naive birds). Within the sample of naive birds for 1975, there was no significant correlation between speed of response and harem size ($r_s = -.096$, $P > .05$), nor was there a significant correlation for the 1976 sample ($r_s = -.228$, $P > .05$).

For the first observation period (25 March–11 April) in 1975, there was a significant positive correlation between harem size and percentage of the day males spent guarding their territories ($r_s = .456$, $n = 33$, $P < .01$), but there was not a significant correlation in either the 7–24 May ($r_s = -.036$, $n = 34$, $P > .05$) or the 4–28 June period ($r_s = -.009$, $n = 29$, $P > .05$). For the one observation period in 1976 (22 March–5 April), the correlation was again not significant ($r_s = -.098$, $n = 33$, $P > .05$). As with display rates, the one significant correlation presents a problem of cause and effect. It is possible that males that are able to spend a greater than average percentage of their time on territory defense, perhaps because they have greater energy reserves or are more efficient foragers, are therefore able to get and keep good territories. Alternatively, it may be that males that obtain good territories initially must spend more time in defense because of greater intruder pressure, this extra expenditure being worthwhile because of the greater payoffs of successful defense of good territories as compared to bad. The former explanation seems more likely in this case, because the significant correlation came from a set of observations made early in the season when foraging on the territory would have been least profitable and energy stress greatest, but I cannot disprove the alternative.

To test whether experience contributes to success, I compared the harem sizes of experienced males (known to have bred in at least one previous year) with the harem sizes of inexperienced males (caught for the first time in the year in question and thus believed to be breeding for the first time). In 1976, the 6.73 average harem size of 26 experienced males was significantly greater than the 4.59 average of 17 inexperienced males ($P < .02$ according to a one-tailed Mann-Whitney U test); in 1975, however, the 3.56 average harem size of 16 experienced males was actually less than the 4.62 average of 21 inexperienced males.

Another way of approaching the problem of the effect of experience on success is by comparing the success of adults and first-year males. First-year males can be recognized by their plumage and so constitute an identifiable group having less experience on average in territory defense than do adult males. No first-year males were observed holding territories in either 1974 or 1975, but in 1976 six first-year

TABLE 3. Results of multiple regression analysis with harem size (HS) as the dependent variable. The independent variables were wing length, weight, color (of epaulet), length of red, length of yellow, and (for 1975 and 1976) age. A stepwise regression procedure was used (Nie et al. 1975). The t shown is for the test of the null hypothesis, $b = 0$, against the alternative $b > 0$, where b is the regression coefficient for the last variable entered.

Year	Variable	n	r	Equation	t	P
1974	1. Condition	42	.290	HS = $-6.34 + 2.43 \times 10^5$ (condition)	1.91	<.05
	2. Color	42	.371	HS = $-14.26 + 2.78 \times 10^5$ (condition) + 0.41 (color)	1.55	>.05
1975	1. Age	34	.262	HS = $7.40 - 1.39$ (age)	1.54	>.05
1976	1. Wing length	41	.306	HS = $-42.23 + 0.37$ (wing length)	2.00	<.05
	2. Age	41	.353	HS = $-38.51 + 0.32$ (wing length) + 0.71 (age)	1.16	>.05

male territory owners were observed and their harem sizes estimated. These 6 first-year males had a lower success than the adults, their average harem size being 2.33 versus 5.88 for 43 banded adults ($P < .01$ according to a Mann-Whitney U test). Unfortunately, the first-year males differed from adults in more than their average level of experience. The average wing length of the 5 first-year territory owners that were measured was 125.0, significantly less than the 131.3 average of 41 adult territory owners ($t = 5.02$, $P < .01$). The juveniles also had smaller, more orange epaulets, as would be expected. On the other hand, the average weight of these first-year males (69.7 g) was not significantly less than that of the adults (71.2 g, $t = .980$, $P > .05$). The first-year males' condition, as measured by weight divided by wing length cubed, was, if anything, better than that of the adults (3.5 × 10^{-5} g/mm^3 for the first-years versus 3.17 × 10^{-5} for the adults). The 4 first-year males for which information is available were at least as aggressive toward a decoy male as were 17 naive adults, landing on the trap in an average of 4.75 min versus an average 5.92 min for the adults. Thus, the lower success of first-year males compared to adults can be explained by the lower average experience of first-year males, their smaller wing lengths, or their more subdued plumage, but not by weight, aggressiveness, or condition.

The data on adult males were subjected to a multiple regression analysis. I hoped that this technique would reveal correlations between male characteristics and harem size that were obscured by other correlations, and that more of the variance in harem size would be explained by the male characteristics than in the single variable, nonparametric correlations. The caution must be stated, however, that there is no way of testing whether the data meet the assumption of multivariate normality. In this analysis, only those characteristics were used for which the maximum sample size had been obtained in each year. These were wing length, corrected weight, condition, color of epaulet, length of red, and length of yellow. In addition, age was used in 1975 and 1976. For 1975, those males caught in 1974 were classified as 3 yr old, and those first caught in 1975 were classified as 2. For 1976, those caught in 1974 were classified as 4, those first caught in 1975 as 3, and those first caught in 1976 as 2. The data were entered in an SPSS stepwise multiple regression program (Nie et al. 1975).

The results are given in Table 3. The multiple regression analysis was not successful in revealing hidden correlations nor in explaining a greater amount of the variance in harem size. In 2 yr, only one variable entered the regression equation

TABLE 4. Harem sizes of males that switched territories between years. First-year harem size is the harem size actually observed in the year before the male switched territories. Hypothetical harem size is the harem size the male would have obtained if he had held the second year's territory in the previous year.

Male	First-year harem size	Hypothetical harem size	Difference
Y_{13}	1	3	+2
W_8	0	2	+2
W_{12}	3	6	+3

with a slope significantly greater than 0 at the 0.05 level—condition in 1974 and wing length in 1976. In 1975, no variable entered the regression equation with a slope significantly greater than 0, and, in fact, the first variable to enter (age) had a slope with the opposite sign from that predicted.

DISCUSSION

Few of the correlations between harem size and the factors predicted to be associated with inter-male competitive ability were significant, and even these were weak. If many factors do contribute to competitive ability, we should not expect strong correlations between any one factor and success. Furthermore, males cannot be perfect in assessing and ranking the available territories, nor can females be perfect in ranking the breeding situations available to them. Errors in both kinds of choices will tend to lower the correlation between male competitive ability and success. Nevertheless, if a hypothesis predicts that a certain characteristic be correlated with harem size, and only 1 correlation in 3 (for example) is significantly greater than 0, this is, at best, weak evidence for the hypothesis.

Cases where a predicted correlation between competitive success and a male characteristic is found in one year and not others may be explained in any of three ways. First, the correlation that was found is spurious and does not really indicate a relationship between the characteristic and competitive ability. Second, the relationship is real and existed all 3 yr, but error in the system was great enough to have obscured it 2 yr in 3. Or third, environmental conditions changed from year to year so that the relationship actually existed one year and not the others. There are reasons for suspecting that the latter two explanations may hold for some of the characteristics examined, but the first explanation must be kept in mind also.

Changing environmental conditions may explain the data on body size. Two measures of body size were considered, wing length and weight, and each showed a weak but significant correlation with harem size 1 yr in 3. One hypothesis that explains this situation is that large size is of itself helpful in dominance encounters, but that in some years there is a counterbalancing disadvantage to large size because larger birds have less energy left, after satisfying their maintenance requirements, to expend on territory defense. In good years, when food is plentiful and temperatures mild, energy is not a problem, and large birds retain an overall advantage in competition for territory, but when food availability is low, and energy costs are high because of bad weather, large birds lose their advantage (Searcy 1977, 1979b).

Error introduced by the site fidelity of male redwings may explain why male success did not increase with age in each year. Experienced males had larger harem sizes than inexperienced males in 1976 but not in 1975. Most returning males reclaimed

the territories they had held in the previous year. Ten of the 14 males observed in both 1974 and 1975 had territories in 1975 that at least overlapped their 1974 territories, and 24 of 25 males observed in both 1975 and 1976 had territories in 1976 that at least overlapped their 1975 territories. Even if an extra year of experience does increase the competitive ability of a male, this may not result in an increase in his relative success if he returns to his old territory instead of moving to a better one. If a male returns to his old territory, his only method of increasing his relative success is to expand his boundaries. As territory size does not correlate with harem size in Washington populations (Holm 1973), expansion must be less effective in increasing success than would be shifting to better quality habitat.

Why does a returning male reclaim his old territory instead of taking a new one? One possibility is that the old territories of returning males are generally of better quality than territories vacant due to the nonreturn of their previous owners. This possibility was tested by comparing the harem sizes of males who returned to the same territories to the harem sizes of males who were not seen the subsequent year. The 10 males who held the same territories in 1974 and 1975 actually had, in 1974, *smaller* harems (1.40) on average than the 25 males who did not return (2.60). The 21 males who held the same territories in 1975 and 1976 did have larger harems on average in 1975 than the 16 males who did not return (4.67 vs. 3.75), but the difference was not significant ($P > .20$). Another possible explanation is that males lack reliable cues to recognize good breeding habitat in early February, when they set up territories, so they return to their former territories, which they know are at least somewhat suitable. Weighing against this hypothesis is the observation that during the study four males reclaimed territories on which not a single female had nested the previous year. A third hypothesis is that knowledge of, for example, the location of foraging sites or sites safe from predators makes a familiar area more valuable than an otherwise comparable area. Further, it may be that males retain site dominance from year to year, perhaps because knowledge of an area makes it easier to defend. The fact that such a high proportion of returning males were *able* to reclaim their old territories implies that they do retain some measure of site dominance. Yasukawa (1979) has found that redwing males are, on average, more successful in obtaining a breeding territory for the first time if they have had experience in the same area in a previous year.

If it is in general advantageous for a male to reclaim his old territory, why do a small number of males shift territories between years? The logical hypothesis is that a male moves if he finds an area that is more attractive to females than his old territory and that is without its previous owner. This hypothesis was tested by considering those males that shifted between years and determining how many females the area that each held in the second year had attracted during the previous year compared to their own previous year's territory. Nesting data were available for both areas for only three of the five males who switched territories. All three did move to a territory that had a higher success in the first year than had their own territory (Table 4), but the trend was not significant due to the small sample size. All five males who switched could have had knowledge of the amount of female activity on the area to which they subsequently moved, as the new territories were all on the same lakes as the old, and the maximum distance a male moved was only 500 m, the average being 250 m. Males could easily have surveyed areas this close to their own territories during foraging trips. Many of the males who reclaimed their old territories, however, could also have found better territories nearby without their

old owners. Why one group shifted territories and the other did not is still unexplained.

Site fidelity creates a problem for all the predicted correlations between male characteristics and harem size. If redwing males were distributed so that the male with the greatest competitive ability got the best territory (and biggest harem), the male with the second greatest competitive ability got the second best territory, etc., then most of the variance in success could be explained by differences in characteristics that determine competitive ability. On the other hand, if males usually return to the territory they held the previous year, and males holding territory for the first time are largely relegated to territories that happen to be vacant due to deaths of the previous owners, then much of the variance in success will be explained by past abilities, past deaths, and changes in territory quality between years, in other words, by the history of the area. The greater the proportion of the variance in success explained by history, the less can be explained by differences in male characteristics. Female choice of mate and territory may be constrained by similar factors, so that females also fail at times to make optimal choices. Errors made by females would also lower the correlation between male competitive ability and success.

One might be tempted to conclude from these results that sexual selection in male redwings is a weaker evolutionary force than expected. It is true that a large part of the variance in pairing success appears to be unexplained by male characteristics, at least the ones examined in this study, and there is good reason to believe that a great deal of the variance can be explained by historical accident rather than male quality. Almost every selective force, however, must be obscured by chance events; this is obviously true, for example, of mortality due to predation and disease. Because the end product of evolution is the consequence of balancing selective forces, and most, if not all, selective forces are weakened by random events, sexual selection could still have had a large effect on the evolution of male Red-winged Blackbirds.

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