

# DOMINANCE RELATIONSHIPS IN HAREMS OF FEMALE RED-WINGED BLACKBIRDS

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**ABSTRACT.**—We investigated the factors determining dominance in aggressive encounters between female Red-winged Blackbirds (*Agelaius phoeniceus*) resident on territories of single males. Three male territories were observed, with harems of 5, 5, and 3 females. Feeding platforms were placed on the territories to increase the sample of observable encounters between residents. Order of settlement on the territory was strongly related to dominance; in 19 of 23 dyads the earlier settler won the majority of encounters. Proximity to the nest at the encounter site was also related to dominance; in 30 of 45 dyads the female closer to her nest won the majority of interactions. The effect of proximity on dominance also was shown experimentally by moving the platforms from near one nest to near another, which caused the dominance relationships between the pairs of females to reverse. In a partial correlation analysis, both order of settlement and proximity to nest correlated independently with the percentage of encounters won within dyads. Size, age, and nesting stage were not related to dominance. Received 30 January 1987, accepted 18 September 1987.

RED-WINGED Blackbirds (*Agelaius phoeniceus*) are polygynous and territorial, with harems of up to 15 females (Searcy 1979a). Females resident in a harem are constrained to spend much of their time together on the same small area of habitat (usually 1,000–10,000 m<sup>2</sup>) for several weeks while nesting. Although some work has been done on the nature of a resident female Red-wing's relationship with nonresidents (Nero and Emlen 1951, LaPrade and Graves 1982, Yasukawa and Searcy 1982, Hurly and Robertson 1985), little attention has been paid to interactions among residents. We examined the factors determining dominance relationships within harems of Red-winged Blackbirds.

Interactions among female Red-winged Blackbirds during the breeding season are mainly aggressive. Resident females show overt aggression both toward nonresidents and toward other residents (Nero and Emlen 1951, Nero 1956a, Hurly and Robertson 1984, Searcy 1986). Females use a variety of aggressive displays (Nero 1956a, Orians and Christman 1968). Resident females will attack taxidermic mounts of female Red-wings that are placed close to their nests (LaPrade and Graves 1982, Yasukawa and Searcy 1982) and respond aggressively to playback of songs of conspecific females (Beltzky 1983a, b).

One possible structure for a primarily aggressive social organization is a system of territories, and it has often been suggested that

female Red-wings defend subterritories within the territories of their mates (Nero and Emlen 1951; Nero 1956b; Hurly and Robertson 1984, 1985). Hurly and Robertson (1984) concluded that female Red-wings were territorial because they contest the settlement of new females on the male's territory and because they show low overlap in use of space. Searcy (1986), however, found that low overlap among residents was due mainly to each resident concentrating her activity at her nest. When nest sites were disregarded, overlaps were actually greater than expected by chance. Searcy (1986) also found that overlaps in areas defended by advertisement and overt aggression were very high for pairs of females, about 10 times as high as for males. Searcy (1986) concluded that female Red-winged Blackbirds are not truly territorial.

If female Red-wings overlap widely in use of space within a male's territory, and most of their interactions are aggressive, then aggressive dominance is likely to be important in determining access to resources. It then becomes important to determine the factors that establish relative dominance between resident females. One possibility is that order of settlement on the male's territory determines dominance. Searcy (1986) found that resident females almost always dominated nonresidents (57 of 59 cases), and, in the small number of observed resident-resident encounters, earlier-settling females tended to dominate later-settling resi-

dents (12 of 15 cases). An advantage in aggressive encounters of earlier settlers in a harem would be analogous to the advantage of prior residency previously shown for flocks of captive (Guhl 1953, Yasukawa and Bick 1983) and free-living birds (Sabine 1959) and for territorial individuals in other taxa (e.g. Davies 1978, Wells 1978).

Another possibility is that relative dominance between two females is influenced by their proximity to their respective nests at the time of an encounter. Searcy (1986) found that female Red-wings are more aggressive close to their nests than farther away, and that the female closer to her nest won the majority of encounters between residents (9 of 13). An effect on dominance of proximity to a nest or core territory has been found in other species of birds (Brown 1963, Willis 1967).

A third possibility is that dominance is affected by stage of the nesting cycle. This possibility is suggested by LaPrade and Graves' (1982) demonstration of a correlation between breeding phase and level of aggressive response shown by female Red-wings to taxidermic mounts. Two final possibilities are that dominance is influenced by age or body size. Positive relationships between size and dominance are common in many taxa, for example frogs (Davies and Halliday 1978, Wells 1978, Howard and Kluge 1985, Robertson 1986), lizards (Tokarz 1985), fish (Gorlick 1976), and mammals (Bouissou 1972, Clutton-Brock et al. 1982). The relationship between size (measured by linear dimensions) and dominance is less consistent in birds; a positive correlation between the two has been found in some species (Searcy 1979b, Watt 1986) but not in others (Fugle et al. 1984, Arcese and Smith 1985, Robinson 1986). Dominance increases with age in some bird species (e.g. Lill 1974, Davies and Lundberg 1984, Arcese and Smith 1985). In captive flocks of male Red-wings, dominance increases with both age and size (Wiley and Harnett 1976, Searcy 1979b).

One problem with studying female-female interactions in harems is the low number of observable interactions, which makes it difficult to uncover statistically significant trends. During hundreds of hours of observation, Searcy (1986) recorded only 15 encounters between residents in which both participants could be identified individually (by color bands). By placing a feeding platform on each of the ex-

perimental territories, we attempted to increase both the number of interactions and the probability that we could observe the color bands of both participants.

#### METHODS

The study was conducted in a marsh along the shores of Pymatuning Reservoir near Linesville, Crawford Co., Pennsylvania. The primary vegetation in the marsh was cattails (*Typha latifolia*), with deciduous bushes and trees along the periphery. The site consisted of several peninsulas of cattails surrounded by open water with a depth of approximately 0.8–1.1 m. Observations were made in late April to mid-June, 1985 and 1986, between 0600 and 1200.

Most of the female Red-winged Blackbirds used in the study were color-banded soon after they settled on male territories. Territories were checked several times each week for nests, and new nests were flagged with small, numbered tags.

One feeding platform was placed on each experimental male territory, and its position was changed after approximately 75 observations were recorded. The platforms were placed to allow a clear view of the birds' color bands from 15–20 m away. The platforms were baited with small amounts of mixed seed (approximately 200 g) before each observation period. Bait was consumed quickly, so other than during the observation periods the platforms rarely contained food.

In 1985 one male territory was studied. This territory, W4, contained 5 females, four of which were color-banded. During the course of the study we observed no trespassing on platforms by banded females from territories of other males. Therefore, we feel justified in assigning all observations of an unbanded female on this platform to the one unbanded resident. In many cases this identification was confirmed by observations of the female returning to her nest. In 1986 we studied two male territories. R1 contained 5 females, 3 of which were color-banded. The two unbanded females were easily separable because one was missing a foot. On the last territory, Y1, there were 4 females, 3 of which were color-banded; the fourth, unbanded female never visited the platform.

The observer recorded data on all aggressive interactions in which there was a clear winner and loser and the identity of both females was unambiguously determined. Only interactions that took place on the platform were counted. In most interactions one female flew onto the platform, displacing a female that was already feeding; here the former was designated the winner. In other interactions both females were on the platform, and one threatened or physically attacked another and caused her to leave the platform; in this case the female remaining on the platform was designated the winner. In all cases, to be declared the winner of an encounter, a female had to have caused

the departure of a least one other female from the platform.

Dominance rank was calculated in two ways: by ranking females in terms of the ratio of interactions won to interactions lost and by determining the linear order that minimized the number of reversals (Brown 1975). For each female and platform location, we determined distance from the platform to the nest using a 30-m tape measure. Order of settlement was determined either (in 1985) by direct observation of settlement or (in 1986) by using first-egg dates and assuming that nesting order was similar to settlement order (see Searcy in press).

Relative ages were assigned based on the years of first capture of females. Many females on the study site were captured and banded in 1983, and most residents were captured each year from 1984 on. This method of assigning relative ages assumes that unbanded females are almost always 1-yr-olds breeding for the first time anywhere rather than older females moving from some other site; this assumption is supported by Picman's (1981) demonstration that more than 90% of surviving female Red-wings breed in successive years either on the same territory or on contiguous territories. Length of the flattened wing was used as a size measure.

RESULTS

*Dominance.*—The dominance hierarchies were almost entirely linear, i.e. there were few triangular relationships (Figs. 1-3). The hierarchies were clearly peck dominance hierarchies (Masure and Allee 1934) rather than peck right hierarchies (Schjelderup-Ebbe 1922), though the percentage of reversals was low.

Spearman rank correlations between ranks obtained by the Brown method and those based on won/lost ratios were all strongly positive, and varied between 0.90 and 1.00. Five of 8 correlations were significant at the 0.05 level.

*Order of settlement and dominance.*—Order of settlement on the territory may influence dominance. To analyze this possibility, we designated the females in each encounter as the "earlier" or "later" settler. On territory W4 the earlier settler won 121 of 157 (77%) encounters, on R1 the earlier settler won 174 of 263 (66%) encounters, and on Y1 the earlier settler won 29 of 40 (73%) encounters. Combining data from all three territories, earlier settlers were winners in 324 of 460 (70%) encounters.

The encounters between two members of one dyad cannot be considered independent, so it is not legitimate to perform Chi-square analysis on the raw encounter data. Instead, we deter-

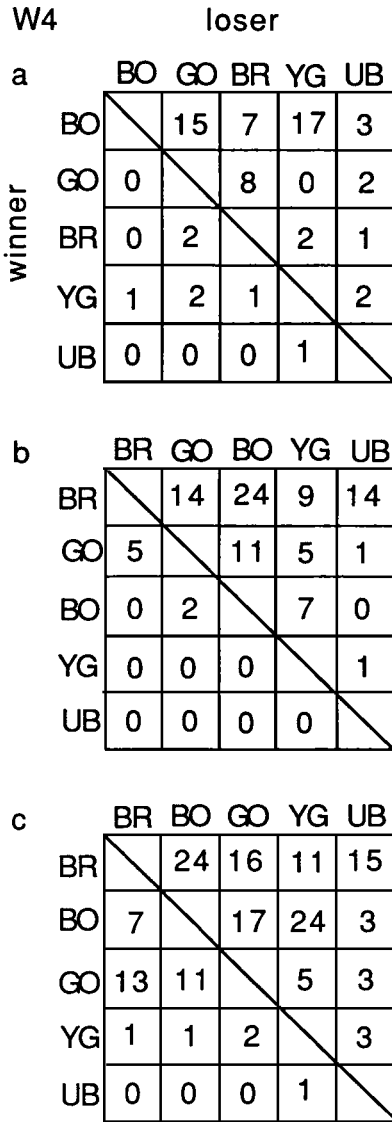


Fig. 1. Dominance matrices for female Red-winged Blackbirds resident on territory W4. The matrices show numbers of encounters won and lost for each dyad (a) at platform position 1, (b) at platform position 2, and (c) overall. Data are arranged to minimize the number of reversals.

mined for each dyad whether the earlier of the two females won the majority of the encounters in the overall matrices. Earlier settlers won the majority of encounters in 19 of 23 dyads; this is significantly more than expected by chance ( $\chi^2 = 9.78, P < 0.01$ ).

*Proximity to the nest and dominance.*—Another

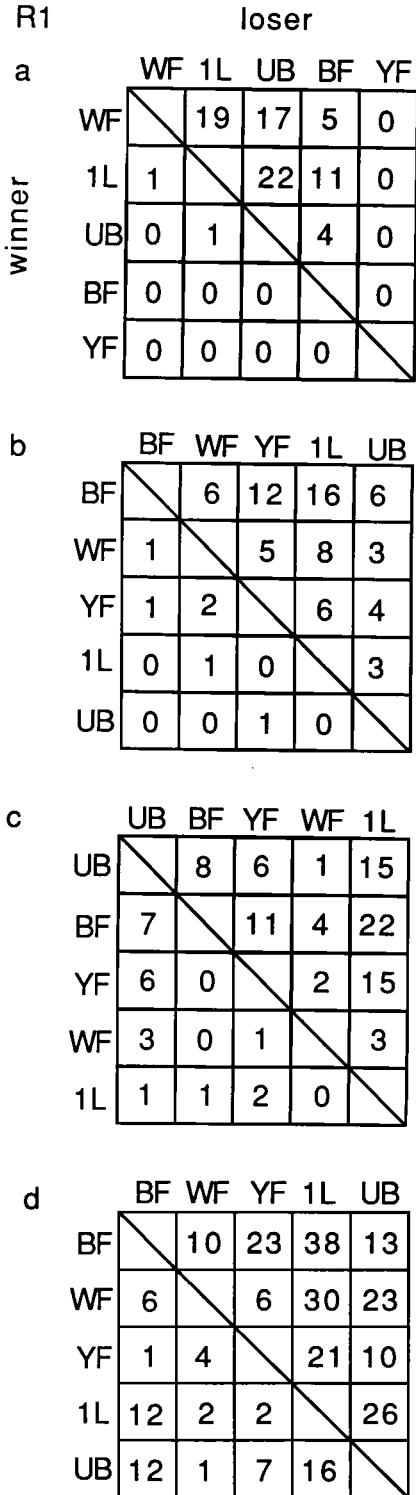


Fig. 2. Dominance matrices for female Red-winged Blackbirds resident on territory R1. The matrices show

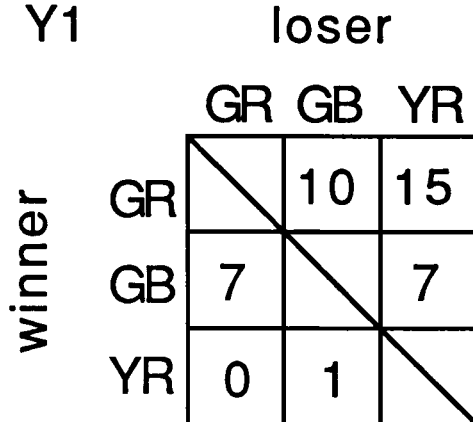


Fig. 3. Dominance matrix for female Red-winged Blackbirds resident on territory Y1. The matrix shows numbers of encounters won and lost for each dyad at the single platform position. Data are arranged to minimize the number of reversals.

factor that may influence dominance is the proximity of a female's nest to the site of the encounter. When the participants in each encounter were scored as to whether their nests were closer to the platform than their opponent's nest, closer females won 93% (129 of 138, excluding ties in proximity) of the interactions on territory W4, 57% (150 of 263) of the interactions on R1, and 35% (14 of 40) of the interactions on Y1. When all data were combined, closer females won 293 of 441 encounters (66%).

In analyzing the effect of proximity on dyads, each platform location was evaluated separately because relative proximity to nests often changed between platform locations. The female closer to her nest won the majority of encounters in 30 of 45 dyads (eliminating ties). This level was significantly more than expected by chance.

*Platform-moving experiments.*—To test whether proximity to the nest influences dominance independently of order of settlement or any other factor, we manipulated proximity by moving the feeding platform from close to one nest to close to a second, with the prediction that dominance would be reversed at the two

← numbers of encounters won and lost for each dyad (a) at platform position 1, (b) at platform position 2, (c) at platform position 3, and (d) overall. Data are arranged to minimize the number of reversals.

TABLE 1. Percentage of aggressive encounters won by female Red-winged Blackbirds in different stages of the nesting cycle.

| Territory | Stage 1        | Stage 2        | Stage 3        | Stage 4        | $\chi^2$ | <i>P</i> |
|-----------|----------------|----------------|----------------|----------------|----------|----------|
| W4        | 4%<br>(1/24)   | 36%<br>(33/91) | 77%<br>(68/88) | 0%<br>(0/1)    | 53.21    | 0.0001   |
| R1        | 65%<br>(15/23) | 12%<br>(2/16)  | 43%<br>(16/37) | 73%<br>(19/26) | 17.31    | 0.0006   |
| Y1        | None           | 14%<br>(1/7)   | 22%<br>(5/23)  | 82%<br>(23/28) | 22.49    | 0.0001   |

positions. On territory W4 the platform was close to the nest of female BO in its original position and close to the nests of females GO and BR in its second position. Female BO won 100% (15 of 15) of the encounters with GO at location 1 but only 15% (2 of 13) at location 2. The change in success was significant ( $\chi^2 = 20.90, P < 0.0001$ ). Female BO won 100% (7 of 7) of her interactions with BR at location 1 and 0% (0 of 24) at location 2. The change in success was again significant ( $\chi^2 = 31.00, P < 0.0001$ ).

On territory R1 the platform was first placed close to WF and 1L and then moved close to BF. The third position made the platform relatively distant from all the nesting females. Female WF won 100% (5 of 5) of her encounters with BF at location 1 and 14% (1 of 7) at location 2. The change in dominance was significant ( $\chi^2 = 8.57, P < 0.01$ ). Female 1L won 100% (11 of 11) of her encounters with BF at location 1 and 0% (0 of 16) at location 2. Again, the change in success was significant ( $\chi^2 = 27.00, P < 0.0001$ ).

*Nesting stage and dominance.*—We divided the nesting cycle into four stages: (1) preincubation, (2) incubation, (3) nestling, and (4) fledgling. A least-reversals matrix was created to compare the number of encounters won by each nesting stage. Encounters between two females in the same nesting stage were not counted.

On each territory there was a nonrandom association between percentage of victories and nesting stage. There was no consistent pattern, however, in which nesting stage was dominant (Table 1). Thus, the nonrandom pattern of wins probably results from confusion between nesting stage and some other variable, such as order of settlement or proximity to nest.

*Age and size.*—Prior experience with the male's territory may confer an advantage to breeding females, or dominance in general may increase with age. Any effect of age on dominance might be confused with an effect of order of settle-

ment, however, because earlier-settling females in other populations of Red-winged Blackbirds have been reported to be older. To test the effect of age, we computed Spearman correlations between ranks based on age and order of settlement. For the three experimental territories all the correlations were positive, but none was significant. For W4 the correlation was 0.300 ( $n = 5$ ), for R1 it was 0.650 ( $n = 5$ ), and for Y1 it was 0.875 ( $n = 3$ ).

Although age was not significantly correlated with order of settlement, there was still a possibility that age affected dominance independently. The older female in a dyad won the majority of encounters in just 12 of 20 dyads, which was not significantly more than expected by chance ( $\chi^2 = 0.80, P > 0.10$ ).

Using wing length as a measure of size, we found larger females won the majority of encounters in only 5 of 11 dyads; this is also not significantly different from chance ( $\chi^2 = 0.09, P > 0.10$ ).

*Partial correlation analysis.*—The only two factors with a significant relationship with dominance in the dyad analyses were order of settlement and proximity to the nest. The importance of proximity independent of other factors was substantiated by the platform-moving experiments. It remains possible, however, that order of settlement was associated with dominance only because of a relationship between settlement order and proximity to nest. We tested this possibility with a partial correlation analysis.

The variables used in the analysis were: (1) WON, the percentage of encounters won by a given bird within a given dyad, normalized using an arc-sin transformation; (2) DISTANCE, the number of meters by which the focal female's nest was closer (+) or farther (−) from the platform relative to the nest of the second female in the dyad; and (3) DATE, the number

TABLE 2. Simple and partial correlation coefficients for the relationships between WON, DISTANCE, and DATE.<sup>a</sup>

|                          | WON<br>vs.<br>DIS-<br>TANCE | WON<br>vs.<br>DATE | DIS-<br>TANCE<br>vs.<br>DATE |
|--------------------------|-----------------------------|--------------------|------------------------------|
| Simple correlations      | 0.515**<br>(46 df)          | 0.500**<br>(46 df) | 0.239<br>(46 df)             |
| Partial correlations     |                             |                    |                              |
| Controlling for DATE     | 0.471**<br>(45 df)          | —                  | —                            |
| Controlling for DISTANCE | —                           | 0.453**<br>(45 df) | —                            |

\*\* =  $P < 0.01$ .

of days the focal female laid her first egg earlier (+) or later (–) than the second female in the dyad. We used first-egg dates to indicate date of settlement in 1985 as well as 1986 because, although our observations of settlement in 1985 were precise enough to determine relative order of settlement, they were not precise enough to give the absolute dates required in the present analysis.

For the two females in any one dyad, the data on winning percentage, distance, and date were not independent. For example, if female A won 80% of her encounters with B at a particular location, then B must have won 20%; if A's nest was 8 m closer to the platform, B's nest must have been 8 m farther, etc. Therefore, it would artificially inflate the degrees of freedom to use the data on both females in one dyad. Instead, we randomly chose one member of each dyad for inclusion in the analysis.

Simple correlations of WON with DISTANCE and DATE were significantly positive and of similar magnitude, while the correlation of DISTANCE with DATE was lower and not significant (Table 2). Partial correlations showed that DISTANCE and DATE were correlated with WON independently of each other (Table 2).

We also performed a stepwise multiple regression with WON as the dependent variable. DISTANCE entered the regression first, producing the equation  $WON = 45.68 + 1.80(DISTANCE)$ . The regression coefficient was significantly greater than 0 ( $T = 4.08$ ,  $P < 0.01$ ). DATE entered the regression second, producing the equation  $WON = 43.40 + 1.58(DATE) + 1.46(DISTANCE)$ . Both regression coefficients were significant in this equation ( $T = 3.41$ ,  $P <$

0.01 for DATE;  $T = 3.58$ ,  $P < 0.01$  for DISTANCE). The addition of DATE significantly increased the amount of variation in the independent variable explained ( $F = 11.63$ ,  $df = 1,45$ ,  $P < 0.01$ ). The  $R^2$  for the multiple regression was 0.416.

## DISCUSSION

The firmest conclusion of the study was that proximity to nest was related to dominance in female Red-winged Blackbirds. This relationship was established both by correlations between dominance and proximity and by platform-moving experiments, in which manipulating the distance of encounters from nests changed dominance in the predicted fashion. The results on order of settlement were less conclusive because we were unable to manipulate settlement order. Another problem was that we relied on nesting order to estimate settlement order, and, while these two parameters are positively correlated, the correlation is by no means perfect (Searcy in press, unpubl. data). Nevertheless, the importance of settlement order to dominance was supported by results showing that early settlers are more likely than chance to be dominant within dyads and by correlations between percentage of encounters won within dyads and relative nesting date holding proximity constant.

The relationship of settlement and dominance can be explained in several ways. One possibility is that settlement order has no direct, causal effect on dominance, but is instead correlated with some other female trait that affects resource holding power (Parker 1974). The obvious possibility for such a correlated trait is age. Age is known to affect dominance in birds in some cases, for example in male Red-wings (Wiley and Harnett 1976, Searcy 1979b). Also, older female Red-wings settle earlier than younger ones (Allen 1914, Crawford 1977). We found that age was positively (though not significantly) correlated with order of settlement, but age did not show a strong relationship with dominance. Thus, age seems unlikely to explain the relationship between settlement order and dominance, although there may be some other correlated trait of which we are unaware.

It is also possible that order of settlement affects the benefits that females receive from winning encounters. Game-theory models have shown that this type of "payoff asymmetry" is

expected to influence outcomes of aggressive contests (Maynard Smith and Parker 1976). One way for a payoff asymmetry to arise is if knowledge of a resource increases its value. In our study the resource directly fought over was the seed placed on the platforms, and we do not believe knowledge of this resource could increase its value. There may be other, longer-term benefits of establishing dominance, but we cannot judge whether prior knowledge would increase such benefits because we cannot identify these benefits.

A final possibility is that order of settlement is an "arbitrary asymmetry," i.e. a factor used to settle aggressive encounters even though it is unrelated to either resource holding power or payoffs. Again, game-theory models have shown that abiding by an arbitrary asymmetry can be an evolutionarily stable strategy for both the winner and loser of a contest (Maynard Smith and Parker 1976, Maynard Smith 1979). There is experimental evidence that arbitrary asymmetries are used to settle contests in some cases (Davies 1978, Yasukawa and Bick 1983).

The influence of proximity to the nest on dominance may be due to a payoff asymmetry, since a food resource close to the nest is worth more because of low travel costs. An additional factor may be defense of the nest site to prevent interference with the nest and its contents. Although it is not known whether female Red-wings actually pose a threat to each others' nests, aspects of their behavior are consistent with their defending against such a threat. Aggressiveness of female Red-wings toward other females increases with increased proximity to the nest (Searcy 1986), and female Red-wings repulse attempts of other females to visit their nest sites (Nero and Emlen 1951). The effect of proximity to nest on dominance in our study was clearest in the platform-moving experiments. In each of these experiments the nearest nests were within 5 m of the platform, which certainly may be close enough to be considered part of the nest site. Finally, proximity to nest sites may represent an arbitrary asymmetry.

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