Condor, 81:417–420

MORPHOLOGICAL CORRELATES OF DOMINANCE IN CAPTIVE MALE RED-WINGED BLACKBIRDS

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Male birds of polygynous species are thought to be larger than females because large size is advantageous in competition for mates (Selander 1958, 1972); however, the mechanism by which large size confers such an advantage is not always clear. In Red-winged Blackbirds (*Agelaius phoeniceus*), females are strongly influenced by territory quality in making their choice of mates (Searcy 1979a). If large size gives a male an advantage in aggressive encounters with other males, and winning such encounters is important in securing and defending a territory, then a simple mechanism exists by which large size could lead to higher mating success for males. Thus, the relationship between body size and dominance in conflicts in male Red-winged Blackbirds is of evolutionary importance. I report here on the results of an aviary study designed to examine this relationship.

A second objective of this study was to examine the relationship between dominance and epaulet size and color. Plumage characteristics may be used to signal social status in birds (Rohwer 1975, 1977); for example, correlations between dominance and plumage coloration exist in Harris' Sparrows (*Zonotrichia querula*; Rohwer 1975) and White-throated Sparrows (*Z. albicollis*; Harrington 1973). Blackening the epaulets of territory-owning male Red-winged Blackbirds causes many to lose their territories (Peek 1972, Smith 1972). Epaulets of first-year males are smaller and more orange than those of adults, and first-year males are generally subordinate (Wiley and Harnett 1976). These observations suggest that features of the epaulet signal dominance status, although other interpretations are possible. My study was designed to determine whether dominance and epaulet characteristics are correlated in male Red-winged Blackbirds.

METHODS

The blackbirds used in this study were captured with mist-nets placed in and around roosts in Dutchess County, New York between 27 September and 10 October 1978. I formed groups of 4, 5, 5, and 6 males. A maximum of 13 days separated the dates when the first and last birds were placed in a group. The groups were housed in separate compartments, each approximately 3 × 3 × 2.5 m, in a domed aviary.

I will refer to birds younger than one year as "first-year males" and to birds older than one year as "adults." Each of the four groups contained one or two first-year males and three or four adults (Fig. 1). Dwight (1900) described the first-year winter plumage of male Red-winged Blackbirds as having "dull orpiment-orange" epaulets, "each feather with subterminal bars or spots of black." The epaulets of winter adults are "bright scarlet-vermillion." In both age classes, the feathers of the head and back are mottled with "buff and ferruginous brown," but first-year males have more mottling on the belly and breast than do adults. Selander and Giller (1960) reported overlap in both epaulet color and degree of mottling between fall first-year males and adults.

I compared the orange-red portions of the epaulets of captive males to Royal Horticultural Society color sheets (Wilson 1938) and found epaulets ranging from 12 (orange) to 17 (mandarin red) with no discontinuity. There was also no discontinuity in the range of variation in either the degree of brown mottling on the body feathers or the amount of black spotting on the epaulets. I classified as adults those males that both lacked appreciable black in their epaulets and had epaulet colors of 15, 16, or 17. No males with epaulet color 14 were used. Males with epaulet colors 12 and 13 were classified as first-year males.

I used length of the flattened wing as a measure of body size. Body weight was also recorded, although weight is a less reliable index of size because of its daily and seasonal fluctuation. I used two measures of epaulet size: distance from the bend of the wing to the farthest extent of red plumage (length of red) and to the farthest extent of yellow plumage (length of yellow). The Royal Horticultural Society color sheet scores were used as a measure of the color of the red-orange portion of the epaulet. A final characteristic recorded for each male was "residence," the number of days a male was present in a group before observation started. In forming the groups, I minimized the amount of variation in residence within each group as much as possible.

All birds were color-banded for individual recognition. Each group was observed from behind one-way glass for 16–22 half-hour periods between 13 October and 9 November 1978. I recorded the identities of the winner and loser in all displacements and fights. I used the ratio of the number of encounters won to the number lost (won/lost ratio) as a measure of dominance.

RESULTS

Aggressive encounters occurred most often over access to food, perches, or water. Infrequently, encounters occurred for unknown reasons when the two participants were both on the aviary floor.

Figure 1 presents matrices showing the number of encounters won and lost by each individual in each dyad for each group. The individuals in each matrix are ranked from top to bottom in order of declining won/lost

Group 1

WINNER \ LOSER	OB	BB	Y	O'	P	R'
OB	–	16	8	3	4	7
BB	0	–	26	6	7	29
Y	4	9	–	16	23	22
O'	0	8	3	–	11	12
P	0	1	2	2	–	8
R'	1	1	5	11	0	–

Group 2

WINNER \ LOSER	Y	O	W	G'	R'
Y	–	32	23	23	36
O	9	–	15	19	30
W	0	4	–	9	12
G'	0	2	4	–	8
R'	0	0	0	2	–

Group 3

WINNER \ LOSER	G	B	W	R'	Y
G	–	20	20	25	40
B	2	–	22	43	32
W	0	0	–	6	21
R'	10	0	4	–	12
Y	0	0	1	0	–

Group 4

WINNER \ LOSER	W	Y	R'	B
W	–	26	49	25
Y	1	–	4	55
R'	5	14	–	18
B	3	2	14	–

FIGURE 1. The number of encounters won and lost by each individual in each dyad. Birds are ranked from top to bottom in each group in order of declining won/lost ratio. 'indicates bird is a first-year male.

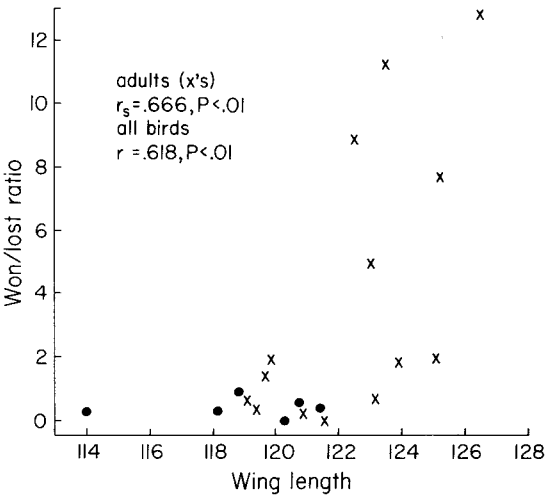

FIGURE 2. Relationship between won/lost ratio in aggressive encounters and wing length in captive male Red-winged Blackbirds. x indicates an adult; • indicates a first-year male.

ratios. The hierarchies are characterized by a high proportion of reversals, in which normally subordinate individuals defeat higher ranking ones. Thus these are peck dominance hierarchies (Masure and Allee 1934) rather than peck right hierarchies (Schjelderup-Ebbe 1922).

Table 1 presents Spearman rank correlation coefficients for the relationships between won/lost ratio and the morphological characteristics. Coefficients are given for the sample of 14 adult males and for the combined sample of adults plus the six first-year males. Wing length is significantly correlated with won/lost ratio for both samples ($P < .01$, Fig. 2). The correlation between weight and won/lost ratio is lower for both samples and is not significant in either case ($P > .05$).

For the combined sample, the three epaulet measures (color, length of red, and length of yellow) are all significantly, positively correlated with won/lost ratio. For the adult sample, on the other hand, none of the epaulet measures correlates significantly with won/lost ratio ($P > .05$).

Table 1 also gives the correlations between won/lost ratio and residence. Even though I attempted to minimize variation in length of residence within each group, there is a positive correlation between residence and won/lost ratio for both samples, although the correlation is significant only for the combined sample ($P < .05$). These positive correlations suggest that the correlations between dominance and morphological characteristics may not reflect biologically significant relationships between these variables but instead reflect accidental relationships between the morphological characteristics and residence. This alternative hypothesis cannot be accepted for the size-dominance correlations because there is no appreciable correlation between size and residence for either sample (Table 2). However, the correlations between residence and the epaulet measurements for the combined sample are larger and two are

TABLE 1. Spearman rank correlations between won/lost ratio and male characteristics. Sample sizes are 14 for adults and 20 for combined adults and first-year males. * Indicates one-tailed probability of $P < .05$; ** indicates $P < .01$.

	Wing length	Epaulet color	Body weight	Length of red	Length of yellow	Residence
Adults	.666**	.289	.273	.444	−.101	.341
Adults and first-year males	.618**	.552**	.269	.574**	.418*	.520*

TABLE 2. Spearman rank correlations between residence and morphological characteristics. Sample sizes are 14 for adults and 20 for combined adults and first-year males. * Indicates two-tailed probability of $P < .05$; ** indicates $P < .01$.

	Wing length	Epaulet color	Body weight	Length of red	Length of yellow
Adults	.097	.203	−.413	.224	.216
Adults and first-year males	.317	.574**	−.150	.440	.521*

significant (Table 2). Thus it is possible that the correlations between the epaulet measurements and dominance do not reflect biologically important relationships.

The six first-year males average significantly lower in won/lost ratio than the adults (Mann Whitney U = 16, $P < .05$). The average wing length of the first-year males (118.9 mm) is also significantly lower than the average wing length of adults (122.4 mm, t = 3.07, $P < .01$). The average weight of the first-year males (71.5 g) is not significantly different from that of the adults (71.2 g, t = .221, $P > .05$).

DISCUSSION

Dominance is strongly correlated with size in male Red-winged Blackbirds. The relationship between size and dominance is nearly the same in the combined adult and first-year male sample as in the adult sample (Fig. 2), suggesting that adults are dominant over first-year males mainly because of size. There is evidence from other studies, however, that previous breeding experience contributes to pairing success within the adult age class (Yasukawa 1979, Searcy 1979b). Therefore, experience as well as size may contribute to the adults' greater dominance.

Searcy (1979c) found that among free-living, adult Red-winged Blackbirds, large males had higher pairing success than small males in only one of three years. Thus, in many years, large males do not have a pairing advantage despite the strong positive relationship between size and dominance demonstrated in this study of captive males. A possible explanation for these conflicting results is that large males are at an energetic disadvantage to small males, and this disadvantage tends to offset the large males' advantage in aggressive encounters during competition for territories and mates (Searcy 1979c). The energetic disadvantage would be most important when environmental conditions are poor so that a positive relationship between size and pairing success would occur only in good years. In support of this hypothesis, I have shown (Searcy 1979c) that energy availability influences the amount of territorial and epigamic behavior performed by male Red-winged Blackbirds and that large males are more stressed for energy than small males during the spring.

Epaulet size and color correlate positively with dominance for the combined sample of adults and first-year males in this study but not for the adult sample alone. Unfortunately, the results for the combined sample are ambiguous because of the positive correlations between residence and dominance and between epaulet measures and residence. These correlations allow at least two possible explanations: (1) epaulet features either increase dominance or serve as a signal of some other characteristic that increases dominance, or (2) experience of residence in the aviary increases dominance, and the correlations between epaulet measures and dominance are just incidental to the correlations between residence and the epaulet measures. The former explanation seems more likely since the combined sample includes first-year birds that have smaller, more orange epaulets and have been shown to be subordinate to adults (Wiley and Harnett 1976). The duller plumage of first-year males may be adaptive because it evokes less aggression from adults (Rohwer 1978).

When only the adults are considered, there are no significant correlations between epaulet measurements and dominance. The correlation between length of red and dominance is positive and approaches significance ($.15 > P > .10$), and it may be that with a larger sample of adults a significant correlation would be found. However, even if the correlation between size of the red portion of the epaulet and dominance is real, the correlation is so low that this epaulet feature cannot be a very useful signal of dominance status. Relative body size would convey more information.

CONCLUSIONS

A strong, positive relationship between size and dominance exists in male Red-winged

Blackbirds. Large size could thus contribute to success in obtaining and defending good quality territories, which in turn should lead to high pairing success. This advantage of large size may be responsible for the evolution of larger male than female size, with size ultimately limited by the energetic disadvantage of being large.

If adults and first-year males are considered together, positive correlations exist between three measures of epaulet size and color and dominance. These correlations disappear when adults alone are considered. Thus epaulet size and color do not seem to function as signals of dominance in adult Red-winged Blackbirds.

ACKNOWLEDGMENTS

I thank Donald Kroodsma, Ken Yasukawa, Margaret Hairston Searcy, Susan Peters, Dorothy Cheney, and Robert Seyfarth for help in capturing birds. Ken Yasukawa, Dorothy Cheney, Robert Seyfarth, and Donald Kroodsma kindly read and criticized a draft of the manuscript. I thank Margaret Hairston Searcy for drawing the figures. Financial support was provided by N.S.F. grant BNS77 16894 to Dr. Peter Marler and NIMH grant PHS MH1525 to Rockefeller University.

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