

DOMINANCE STRUCTURING OF A RED-WINGED BLACKBIRD ROOST

PATRICK J. WEATHERHEAD AND DREW J. HOYSAK

Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6 Canada

ABSTRACT.—Observations of the behavior of roosting male Red-winged Blackbirds (*Agelaius phoeniceus*) indicated that after hatching year (AHY) males were dominant over hatching year (HY) males. This dominance resulted in AHY males occupying central roost positions in dense vegetation and HY males occupying edge positions in sparse vegetation. Overall, the birds preferred positions over deep water, although the edge positions of HY males were over deeper water than were the positions of AHY males. These results are consistent with the two-strategies roosting hypothesis (Weatherhead 1983), in that the dominance of older males allows them access to roost positions with relatively low vulnerability to predation. In this study, these positions also appeared to be microclimatically superior. These results also suggest that the bright plumage of adult males of sexually dimorphic species may be advantageous in some nonbreeding situations in addition to their more commonly recognized role in reproduction. Received 28 June 1983, accepted 21 February 1984.

THE traditional view of avian communal roosts has been that, of the various advantages that may be derived by participating individuals, there exists one principal advantage that is responsible for the behavior. Predator avoidance (Lack 1968) and the exchange of information regarding food location (Ward and Zahavi 1973) are the two most frequently invoked principal advantages. Recently, Weatherhead (1983) suggested that theoretical expectations and the available evidence were more consistent with there being more than one principal benefit to roosting communally, i.e. all participants are not in the roost for the same reason. According to Weatherhead's hypothesis, the correlation between foraging ability and dominance means that superior foragers roost communally because their status allows them access to central roosting positions that are buffered from predation by the surrounding subordinate individuals. The subordinate individuals pay the price of higher predation risk because of the foraging advantage they realize by following the dominant individuals to superior feeding locations.

In support of the two-strategies hypothesis, Weatherhead (1983) used the results of a study that found that Red-winged Blackbirds (*Agelaius phoeniceus*) caught in a decoy trap tended to be both younger and in poorer condition than those sampled randomly from a nearby roost (Weatherhead and Greenwood 1981). Because birds enter a decoy trap in response to the decoy birds simulating a foraging flock,

these results suggested that there is a cohort of the population (i.e. younger individuals in poorer condition) that predictably relies on other members of the population to locate food.

If younger birds rely on older birds to locate food, the following predictions from the two-strategies hypothesis can be made regarding the structuring of Red-winged Blackbird roosts. (1) Younger birds should be subordinate to older birds [Searcy (1979) found this relationship among captive birds]. Subordinate birds should be chased more frequently and should use aggressive displays differently. Because subordinate individuals can sometimes exhibit greater aggression than dominant individuals (Ewald and Carpenter 1978) the direction of the difference in displays cannot be predicted. (2) The dominance relationship should result in the older birds preferentially occupying roosting positions that are less vulnerable to predation. Because these two predictions address only one aspect of Weatherhead's (1983) hypothesis, their support would constitute only partial testing of the hypothesis, although their failure would bring into doubt the validity of the entire hypothesis.

In this paper we present the results of a study in which the above predictions were tested using a small population of male Red-winged Blackbirds roosting in a cattail (*Typha* sp.) marsh. Because the only age classes that can be distinguished are hatching year (HY) and after hatching year (AHY), our study was limited to comparing the status and roosting positions of

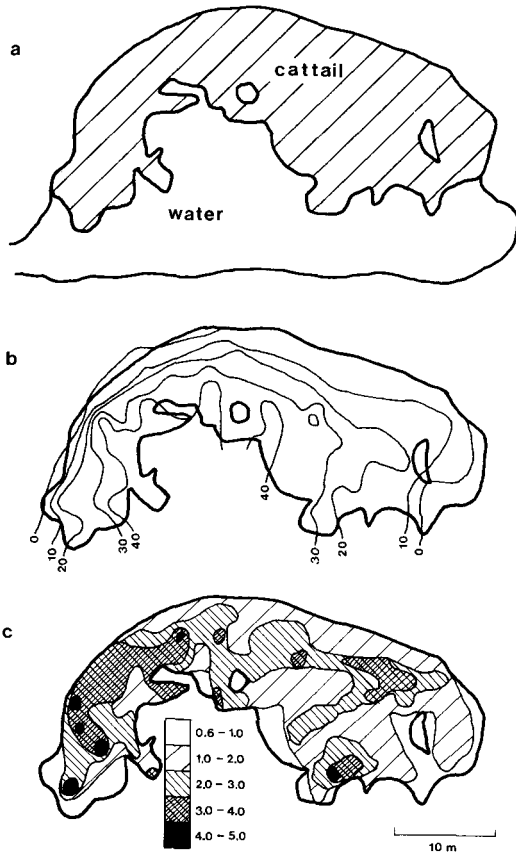


Fig. 1. Map of the study area illustrating (a) the distribution of cattail in the pond; (b) the patterns of water depth, measured in centimeters; and (c) vegetation density, measured as the number of stems per 0.625-m^2 quadrat.

these two cohorts. Specifically, we predicted that AHY males should be dominant over HY males such that individuals in the latter group would roost more often in positions that were peripheral, over shallower water, and in sparser vegetation. We assumed that birds in these positions would be more vulnerable to predation, because the roost was located in a city park near a river where the most likely potential predators would be domestic cats (*Felis catus*) and raccoons (*Procyon lotor*).

METHODS

The roost we studied was located in a pond in Mooney's Bay Park in Ottawa, Ontario. The pond was approximately 950 m^2 , of which 450 m^2 was cov-

ered by cattail. The remainder was open water (Fig. 1). The area surrounding the pond was mowed grass. The roost was used exclusively by approximately 200 male Red-winged Blackbirds.

Observations were made on 16 evenings between 2 October and 7 November 1982, beginning each evening when the birds began to arrive at the roost (1-2 h before sunset) and lasting until poor light conditions precluded distinguishing birds by age class (approximately sunset). We observed the birds with 7×35 binoculars from the branch of a tree that overlooked the pond and was 5 m from the edge.

Beginning at one end of the roost and scanning to the other end, we selected individual birds for observation as they were encountered in the field of vision. This scanning technique resulted in observations being made in each area of the roost approximately in proportion to the number of birds occupying that area. A single scan of the marsh produced 10-20 observations. Several scans were made each evening.

At the instant a bird was chosen for observation its behavior was noted. Behavioral categories included songspread (singing with epaulettes exposed), perching with epaulettes either exposed or concealed, and chasing and being chased (all classed as involving aggression) and preening, pecking at vegetation, and flying into or out of the vegetation (all classed as nonaggressive acts). Although the aggressive behaviors listed above are more commonly associated with reproduction and territoriality during the breeding season (Nero 1956), other observations of roosting Red-winged Blackbirds (Weatherhead, pers. obs.) indicated that these behaviors also occurred in nonbreeding situations.

Once the behavior of the bird was noted, its age was identified as either HY or AHY based on plumage characteristics. Because the plumage of some HY males is very similar to that of AHY males, it is likely that some HY males were incorrectly classified as AHY, but their number should not exceed 15% (Greenwood and Weatherhead 1982, in prep.). If the bird's age could not be determined confidently within approximately 15 s, the observation was discarded and a new individual chosen for observation.

After several observation periods in which only a bird's age and behavior were recorded, information on the bird's location in the roost was also collected. Following each observation, a bird's position in the roost was recorded on a scale map of the pond on which a $2 \times 2\text{-m}$ grid was superimposed. Finally, two features of the vegetation in which the bird was perched were recorded. Vegetation density was scored as "low" (the bird was in full view), "medium" (the bird was partially concealed), and "high" (only enough of the bird could be seen to score its age and behavior). The position of the bird relative to the nearest edge of the patch of vegetation in which it was located was recorded as "edge" ($<0.2\text{ m}$ from

TABLE 1. The proportionate representation of behaviors in observations of AHY and HY males.

Behavior	Proportion of total observations (<i>n</i>)		χ^2	<i>P</i>
	AHY (330)	HY (180)		
Involving aggression:				
Chasing	0.02	0.00	—	0.001 ^a
Being chased	0.00	0.03		
Songspread	0.13	0.01	18.8	<0.001
Perched with epaulettes				
Exposed	0.05	0.00	11.71	<0.001
Concealed	0.41	0.63		
Not involving aggression:				
Preening	0.20	0.18	0.31	>0.05
Pecking vegetation	0.10	0.07	1.00	>0.05
Flying in or out of vegetation	0.06	0.04	1.02	>0.05
Other	0.03	0.03	0.00	>0.05

^a Fisher exact probability test.

the edge), "intermediate" (0.2-0.5 m from the edge), and "central" (>0.5 m from the edge).

After the birds vacated the roost in early November the vegetation density and water depth under the roosting substrate were measured. Vegetation density in each 2- × 2-m quadrat of the roost was recorded as the mean density of cattail stalks in five 0.25- × 0.25-m-quadrat samples. Water depth was measured at the center of each 2- × 2-m quadrat. These data were used to draw vegetation density and water depth profiles of the roost (Fig. 1).

RESULTS

Consistent with our predictions, HY males were chased more often than AHY males and chased other males less often. These combined differences are significant (Table 1) and indicate that HY males were subordinate to AHY males. Because only the age of the focal bird was recorded, we do not know the age of the other birds involved in observations of chasing. Differences between the age classes were also found in the frequencies of the other behaviors involving aggression, AHY males being the more aggressive (Table 1). Combined with the chasing data, these results suggest that exposing the epaulettes and the songspread display are used by males to establish or maintain dominance. No significant differences were found between the age classes for any of the behaviors not involving aggression (Table 1).

The distribution of the two age classes of males differed with regard to their proximity to the edge of the vegetation in a manner con-

sistent with our hypothesis. A greater proportion of AHY than HY males occupied central positions, whereas the reverse was true for edge positions, although, overall, the majority of both cohorts were observed in central positions (Table 2).

Overall, the population showed a preference for positions over deeper water (Table 3). Contrary to the pattern predicted, however, the mean water depth under positions occupied by HY males was significantly greater than that under AHY males (0.32 ± 0.12 m vs. 0.29 ± 0.12 m, $t = 2.59$, $P < 0.02$). This resulted because HY birds were observed to a greater extent along the edge of the vegetation adjacent to the open water. The water depths for HY males and AHY males occupying central positions were not significantly different (0.28 ± 0.11 m vs. 0.26 ± 0.11 m, $t = 1.31$, $P > 0.05$).

TABLE 2. The distribution of AHY and HY males with regard to their proximity to the edge of the vegetation.

Location	Proportion of observations (<i>n</i>) ^a	
	AHY	HY
Central	0.68 (224)	0.51 (92)
Intermediate	0.19 (63)	0.14 (25)
Edge	0.13 (43)	0.35 (63)

^a Cochran rank-ordered, $\chi^2 = 26.57$, $df = 2$, $P < 0.001$ (Cochran 1954).

TABLE 3. The distribution of roosting birds (both age groups combined) relative to water depth.^a

Water depth (m)	Observed proportion of birds (n)	Expected proportion of birds ^b (n)
0.00-0.09	0.06 (29)	0.17 (81)
0.10-0.19	0.13 (62)	0.21 (100)
0.20-0.29	0.21 (100)	0.25 (119)
0.30-0.39	0.35 (167)	0.22 (105)
0.40-0.49	0.23 (109)	0.14 (67)
0.50-0.59	0.02 (10)	0.01 (5)

^a $\chi^2 = 117.0$, $df = 5$, $P < 0.01$.

^b Determined from the proportion of cattail over the different water depths.

We used the subjective estimate of vegetation density made at the time the birds were observed to compare roosting positions of the two age classes. This estimate shows that AHY males were observed significantly more often than HY males in medium- and high-density vegetation (Table 4). An analysis of the density of cattail stems per quadrat (0.625 m²) from the sampling conducted at the end of the study confirms that AHY males roosted in denser vegetation than HY males (2.31 ± 0.69 vs. 2.13 ± 0.90 , $t = 2.39$, $P < 0.02$).

We were unable to confirm for individual birds that they remained for the night in the positions they occupied when we observed them. The amount of movement in the roost during and following our observations was quite limited, however, relative to the size of the roosting population, suggesting that no wholesale changes of position were taking place.

DISCUSSION

Overall, the results of this study are consistent with the predictions from Weatherhead's (1983) two-strategies hypothesis regarding how a Red-winged Blackbird roost should be structured. Older males were dominant over younger males, a relationship apparently established through more frequent displays of aggression. Dominance allowed older males access to roosting positions that would reasonably seem to be safer from terrestrial predators. The one exception to this was the greater proportionate representation of younger birds over deeper water. This result appears to be due to

TABLE 4. Distribution of HY and AHY males relative to the subjective estimate of vegetation density.^a

Density	Proportion of observations (n)	
	AHY	HY
Low	0.04 (11)	0.24 (35)
Medium	0.70 (191)	0.62 (90)
High	0.26 (71)	0.14 (20)

^a Cochran rank-ordered, $\chi^2 = 31.30$, $df = 2$, $P < 0.001$ (Cochran 1954).

the relative distributions of vegetation edge, vegetation density, and water depth. Specifically, the outer edge of the cattails was associated with deep water and sparse vegetation (Fig. 1). Thus, a bird seeking a safe roosting position could get dense vegetation in a central location but sacrifice water depth or get a deep-water location but sacrifice both vegetation density and an interior position.

Another factor of potential importance to the roosting birds is microclimate, given that nighttime temperatures regularly approached 0°C during the study period. Although temperature would not be expected to vary substantially within the roost, heat loss due to wind could probably be reduced substantially by roosting in an interior position in dense vegetation. This makes the structuring of this roost an interesting contrast to the Rook (*Corvus frugilegus*) roost described by Swingland (1977). That roost was also structured on the basis of dominance, but in the vertical rather than the horizontal plane. Dominant Rooks usually chose the highest roosting positions, which would be best protected against terrestrial predators, even though in those positions they were more exposed to wind. Only on extremely cold nights did the dominant birds select lower positions in the roost trees. In a horizontally structured roost, such as that used by Red-winged Blackbirds in this study, the dominant individuals are able to obtain positions that are both protected from predators and microclimatically superior.

Finally, the role of the epaulettes and associated behaviors of male Red-winged Blackbirds in dominance interactions in the roost have interesting implications. Because of the considerable attention paid by researchers to

the polygynous mating system of this species, most investigations of the functional significance of plumage dimorphism and delayed maturation of male plumage have focussed only on their reproductive implications (e.g. Peek 1972; Smith 1972, 1976; Searcy 1979; Rohwer et al. 1980). The results of the present study suggest that plumage variation may have important fitness implications due to nonbreeding effects. For example, the acquisition of superior roosting sites by adult males means that, at least under these circumstances, bright coloration may be advantageous during the nonbreeding season. This contrasts with the traditional view that the evolution of bright coloration in males through sexual selection is balanced by natural selection against that coloration (Selander 1972), but is consistent with more recent evidence regarding coloration and dominance in nonbreeding birds (Ewald and Rohwer 1980). It would appear that a full understanding of the evolution of plumage variation within and between sexes in the Red-winged Blackbird will be possible only if the year-round effects of that variation are taken into account.

ACKNOWLEDGMENTS

Financial support was provided by Carleton University and the Natural Sciences and Engineering Research Council of Canada. Paul Ewald, Bill Searcy, and an anonymous reviewer provided helpful comments on an earlier version of the manuscript.

LITERATURE CITED

- COCHRAN, W. G. 1954. Some methods for strengthening the common χ^2 tests. *Biometrics* 10: 417-451.
- EWALD, P. W., & F. L. CARPENTER. 1978. Territorial responses to energy manipulations in the Anna Hummingbird. *Oecologia* 31: 277-292.
- , & S. ROHWER. 1980. Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. *Behav. Ecol. Sociobiol.* 7: 273-279.
- GREENWOOD, H., & P. J. WEATHERHEAD. 1982. Spring roosting dynamics of Red-winged Blackbirds: biological and management implications. *Can. J. Zool.* 60: 750-753.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. London, Methuen.
- NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. II. Territoriality. *Wilson Bull.* 68: 129-150.
- PEEK, F. W. 1972. An experimental study of the territorial function of vocal and visual display in the male Red-winged Blackbird (*Agelaius phoeniceus*). *Anim. Behav.* 20: 112-118.
- ROHWER, S., S. D. FRETWELL, & D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Amer. Natur.* 115: 400-437.
- SEARCY, W. A. 1979. Morphological correlates of dominance in captive male Red-winged Blackbirds. *Condor* 81: 417-420.
- SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180-230 in *Sexual selection and the descent of man 1871-1971* (B. Campbell, Ed.). Chicago, Aldine.
- SMITH, D. G. 1972. The role of the epaulettes in the Red-winged Blackbird (*Agelaius phoeniceus*) social system. *Behaviour* 41: 251-268.
- . 1976. An experimental analysis of the function of Red-winged Blackbird song. *Behaviour* 56: 136-156.
- SWINGLAND, I. R. 1977. The social and spatial organization of winter communal roosting in rooks (*Corvus frugilegus*). *J. Zool. London* 182: 509-528.
- WARD, P., & A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis*. 115: 517-534.
- WEATHERHEAD, P. J. 1983. Two principal strategies in avian communal roosts. *Amer. Natur.* 121: 237-243.
- , & H. GREENWOOD. 1981. Age and condition bias of decoy-trapped birds. *J. Field Ornithol.* 52: 10-15.