

INFLUENCE OF POPULATION SIZE ON HABITAT USE BY TERRITORIAL MALE RED-WINGED BLACKBIRDS IN AGRICULTURAL LANDSCAPES

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ABSTRACT.—Fretwell and Lucas's (1970) model relating settling patterns and habitat suitability was tested by examining the distribution among habitats of male Red-winged Blackbirds (*Agelaius phoeniceus*) at relatively low (26 males/km² in 1978) and high (45 males/km² in 1979) overall population densities. Wetlands and hayfields were identified as the most suitable breeding habitats on the basis of habitat selection patterns of territorial males and other evidence, whereas forest, cropland, and human-occupied areas generally were avoided. Some "packing" of males into hayfields occurred when population level increased, but the greatest changes were recorded from less suitable habitats. Occupancy of wetlands and hayfields remained relatively stable. These results were in general accordance with predictions from Fretwell and Lucas's model, but their model did not account for some aspects of spacing behavior. This is because habitat imprinting, site fidelity, and chance events, in addition to territorial behavior, likely contributed also to the spacing patterns of male Red-winged Blackbirds observed. Received 20 March 1986, accepted 24 September 1986.

A THEORETICAL framework for testing ideas concerning the effects of territoriality on the distribution of birds among habitats has been developed (e.g. Fretwell and Lucas 1970, Fretwell 1972). Because acquisition of a territory in highly suitable habitat is usually associated with higher reproductive success, highly suitable habitats should be occupied at relatively high densities regardless of overall population size because individuals should attempt to move to the best breeding areas. As a result, when population level increases, less suitable habitats should support proportionately more birds (provided that they had been relatively empty) because highly suitable habitats should already be occupied, likely by the most dominant individuals.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a good species with which to examine habitat selection models (Fretwell and Lucas 1970, Fretwell 1972) because male competition for territories is intense, and some subordinate males are unable to establish territories (e.g. Orians 1961, 1980). Estimates of Red-winged Blackbird population size obtained from the

annual North American breeding bird survey and independent assessments showed that the populations increased from 1978 to 1979 in southwestern Quebec (Clark et al. 1983). We identified habitats where the density of male Red-winged Blackbirds increased the most from 1978 (low population) to 1979 (high population). If males are distributed across habitats as predicted by the Fretwell-Lucas model, then in a year of increased male density (1979) we would expect most of that increase to occur in habitats of lower suitability. This follows because highly suitable breeding habitats should already be occupied near carrying capacity, leaving the additional males to occupy the next best available habitats. Assumed here is that less suitable habitats were relatively empty when the population level was low (1978); if they had been relatively full, then the relationship between habitat use and population size would be more complicated (Fretwell 1972: 107). Furthermore, habitats of very low suitability (e.g. forests and croplands) should have relatively low occupancy rates regardless of population level. We tested the predictions that the greatest increase in density would occur in less suitable habitats and, in contrast, that the density in the most suitable habitats would remain relatively stable.

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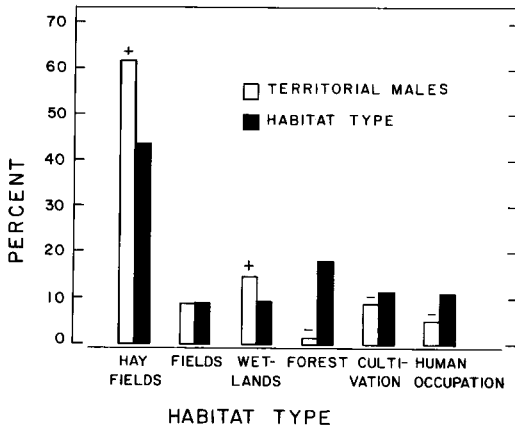


Fig. 1. Percentages of habitats and male Red-winged Blackbirds recorded along 55 roadside routes censused in 1978 and 1979, based on pooled data. Significant preference (+) and avoidance (-), based on *t*-tests, is shown for each habitat except fields, where use was proportionate to habitat occurrence.

METHODS

We censused the male Red-winged Blackbirds in various habitats, and estimated habitat composition, along 55 5-km roadside routes surveyed in both 1978 and 1979 in the agricultural region of the St. Lawrence River valley (details in Weatherhead et al. 1980, Clark et al. 1983). The number of males behaving territorially (Nero 1956) within 75 m of each side of the road were counted; the area censused was 75 ha. Routes were traveled twice per census, allowing a visual capture-mark-recapture estimate of the density of males within the census area (Hewitt 1967). Because each census involved traveling the same route twice, males that were either recaptured or sighted for the first time (i.e. on the second run) were assigned to a habitat type. Routes were censused twice each season, usually late in May and again about 2 weeks later. The values obtained from the two censuses were averaged to derive an estimate of the number of males in each habitat type for that route. When the estimates of males were completed, the proportions of each habitat type along the transect were estimated visually. The habitat designations followed Albers (1978): *hayfield*—tame and native hay, and pasture; *field*—old (weedy) and fallow fields; *wetland*—river edge, marshes and ditches, areas permanently or seasonally flooded and supporting lush plant growth; *forest*—wooded areas; *cropland*—primarily cereal grains (corn, oats, barley); *human-occupied areas*—urban and farmyard areas, orchards.

A set of five routes was censused in 1979 by two independent groups of observers. The routes overlapped by 80%, but we nevertheless wanted to assess

the extent to which observer bias may account for differences in the estimation of density of males.

We were interested in how the density of males in each habitat changed between years. Density of males was determined by dividing the number of males seen in each habitat by the area of the 75-ha census plot occupied by that habitat. Between-year change in the abundance of habitats and in the density of males was determined by paired *t*-tests (Zar 1984). We computed the percentage changes in the average density of males in each habitat from 1978 to 1979. Habitat selection was measured from the results of *t*-tests (Albers 1978): if the proportion of males recorded in a habitat was significantly greater than the proportion of that habitat, then that habitat was considered to be preferred, whereas habitats that occurred frequently but were not used by Red-winged Blackbirds were considered to be avoided. Preferred habitats were assumed to be of higher suitability than those used in proportion to their occurrence, which, in turn, were of higher suitability than habitats that were avoided.

RESULTS

The density of males in 1978 ($\bar{x} = 26$, $CV = 45$) was significantly lower than in 1979 ($\bar{x} = 45$, $CV = 59$), averaging about 40% fewer males ($P < 0.001$). This change was not due to observer bias alone because no difference was evident in the average density of males along the five routes censused by two independent groups of observers (Wilcoxon test, $P > 0.05$; Siegel 1956), indicating that neither group had consistently low or high estimates. The rank correlation between the two sets of data was nonsignificant but positive ($r_s = 0.50$, $P > 0.05$; Siegel 1956).

Decreases in the estimated area of cropland and wetlands were found, along with an increase in the estimate of human-occupied area (Table 1). Territorial male Red-winged Blackbirds showed consistent preferences for wetlands and avoided forested areas (Table 2); preference for hayfield habitat was evident in 1978. There was no preference or avoidance of fields or cropland in either year, or of human-occupied areas in 1979. However, *t*-tests of pooled data from both years showed that, overall, wetlands and hayfields were preferred, fields were used in proportion to their availability, and areas of human occupation, cropland, and forest were avoided (Fig. 1). These results showed the general patterns of habitat use by males, but the patterns of habitat use

TABLE 1. Distribution of habitats along 55 roadside routes censused in 1978 and 1979. Percentages shown are means \pm 1 SD.

Habitat	Year ^a	
	1978	1979
Hayfields	43.8 \pm 17.2	42.4 \pm 19.0
Fields	8.5 \pm 9.2	8.8 \pm 9.5
Wetlands	9.9 \pm 12.2 *	7.7 \pm 16.6
Forest	17.0 \pm 21.0	17.5 \pm 19.8
Cropland	12.4 \pm 11.8 *	9.4 \pm 9.2
Human-occupied area	8.4 \pm 10.3 **	13.5 \pm 16.5

** = $P < 0.05$, * = $P < 0.01$, paired *t*-tests.

between years varied substantially for certain types of habitat.

The density of males increased in human-occupied areas (400%), fields (74%), and, to a lesser extent, hayfields (16%) (Table 3). Wetlands supported more males in 1979 than in 1978, but the change in average density was small (22%) and not significant. In contrast, human-occupied areas and fields showed substantial increases. Male "packing" into hayfields occurred from 1978 to 1979, but the change was minor compared with fields and human-occupied areas.

DISCUSSION

There is debate regarding the relative suitability of wetland and hayfield habitats as breeding areas (Dolbeer 1976). In our study the strongest and most consistent habitat preference was found for wetlands, and this preference should reflect selection pressures acting on males to establish territories in the best possible breeding situations. Furthermore, we reported elsewhere (Weatherhead et al. 1980) that harem sizes of males in wetlands averaged about one female (50%) higher than harems of males in hayfield habitats in Quebec. Thus, in our study area females apparently preferred these habitats, the characteristics of the resident males, or both (Weatherhead and Robertson 1981). At higher population densities the available habitats become more restricted, possibly masking patterns of habitat preference (Wiens et al. 1985). This was evident to a limited extent in our data, but occurred mainly when comparing use of habitats of lower suitability from years of low and high population density.

TABLE 2. Comparisons of the proportions of habitats recorded and the proportions of territorial male Red-winged Blackbirds seen in each habitat along 55 roadside routes censused in 1978 and 1979. Values shown are *t*-test statistics; the percentages of habitats and males based on pooled data are shown in Fig. 1.

Habitat	Year ^a	
	1978	1979
Hayfields	1.72*	1.56 ^b
Fields	-0.25	0.36
Wetlands	1.77*	2.04*
Forest	-3.91**	-4.47**
Cropland	-1.19	-1.18
Human-occupied area	-2.93*	-1.52 ^c

** = $P < 0.05$, * = $P < 0.01$. Significant positive and negative *t*-statistics signify preference and avoidance of habitats, respectively.

^b $P < 0.07$.

^c $P < 0.08$.

The greatest changes in the density of territorial males were recorded in less suitable breeding habitats in fields and particularly in human-occupied areas, whereas the density of males in wetlands and hayfields varied less. In general, these findings were consistent with the Fretwell-Lucas model because the increased population level resulted in proportionately more male Red-winged Blackbirds attempting to establish territories in less suitable habitats when densities of males in the most suitable breeding habitats stayed relatively stable. This pattern likely resulted from the despotic be-

TABLE 3. Density (birds/ha) of territorial male Red-winged Blackbirds in habitats along 55 routes censused in 1978 and 1979. Shown are the mean, 1 SD, and number of routes (*n*) where the habitat was recorded each year.

Habitat	Year ^a					
	1978			1979		
	\bar{x}	SD	<i>n</i> ^b	\bar{x}	SD	<i>n</i> ^b
Hayfields	0.31	0.25	55	0.36	0.19	54
Fields	0.23	0.25	39	0.40	0.37	48
Wetlands	0.55	0.97	47	0.67	0.59	52
Forest	0.03	0.05	38	0.07	0.21	46
Cropland	0.19	0.23	42	0.23	0.25	44
Human-occupied area	0.08	0.12	37	0.40	0.45	54

** = $P < 0.05$, * = $P < 0.01$, *** = $P < 0.001$, paired *t*-tests.

^b Varies because not all habitats occurred on each transect both years. Therefore, the number of routes compared was determined by the smallest *n* of each habitat.

havior of territorial males, which prevented other males from establishing territories in preferred wetland habitats. The pattern of habitat use we found seems to be consistent with the idea that, in 1979, the maximum "compressibility" of some territories in hayfields and wetlands was reached (Huxley 1934) because some "packing" into hayfields was recorded when use of less suitable habitat increased.

Although our results provide support for the Fretwell-Lucas model, it seems that some birds were not attempting to move from less to more suitable breeding habitats. Because the preferred habitat apparently was not saturated in 1978, based on increases in the density of males observed in those habitats the following year, it appears that the males in marginal habitat may have had some opportunity to move to better habitat but did not; many males held territories in human-occupied areas and fields when the population level was low. We cannot state conclusively that males never moved to better habitats because we did not intensively observe marked birds. However, the patterns we recorded are consistent with results from a recent study by Eckert and Weatherhead (1987). In their study area, territorial males in marshes attracted more females than did males in upland habitats. In terms of a male's mating success, this implies that marshes were of higher quality than uplands. When both morphological and behavioral indices of male dominance were considered, they found that males from high-quality marshes were not consistently dominant to those from low-quality upland fields. Thus, competition among males over the available breeding habitat explains only part of the resulting male distribution. Other factors that may be of importance include site fidelity [males returning to the first territory they were able to establish, as suggested by Weatherhead and Robertson (1981)], chance events dictating who "wins" a vacated territory (e.g. which male arrives first may influence which one wins), or habitat imprinting (males prefer natal habitats regardless of competitive ability).

The distribution of males across habitats of varying quality has important implications for considerations such as the criteria females use to choose mates (Weatherhead and Robertson 1981). Therefore, it would be useful to learn the extent to which the factors mentioned above contribute to male distributions. One experi-

mental approach would be to study the movements of marked males following selective removals in an area where habitats of varying quality occur in a well-defined, small-scale mosaic.

ACKNOWLEDGMENTS

We thank R. D. Titman, W. A. Searcy, and an anonymous reviewer for their criticism of the manuscript. Thanks also to S. D. Fretwell for comments on an early draft of the paper, to the students who helped collect the data, especially M. Silverstone, H. Juul, R. Alisauskas, and M. McNeil, and to R. Hynes and R. McLandress for technical assistance. This study was funded by the Natural Sciences and Engineering Research Council of Canada, Agriculture Canada, and the Department of Supply and Services Canada. Personal support to RGC by the Quebec Department of Education and Canadian Wildlife Service is gratefully acknowledged.

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