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M. I. Dyer
Bureau of Sport Fisheries and Wildlife, Sandusky, Ohio

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INTRODUCTION

Red-winged blackbirds *(Agelaius phoneiceus)* have been studied intensively in the United States and Canada by research biologists of the Bureau of Sport Fisheries and Wildlife for more than a decade. The detailed information on population dynamics of the species that has been acquired is now being assembled and assessed. Definite patterns in the distribution of some of the eastern and mid-western populations have become apparent (Dyer et al., 1072; Power, 1069, 1970). A very complex distribution of territorial densities occurs in the western Lake Erie Basin of the U.S. and Canada (Dyer et al., 1972), where there are significant differences in density, both among widely dispersed areas and within isolated sections of single areas. These differences are caused by differences in availability of preferred habitat types and by differences in spacing distances selected by the territorial birds when preferred habitat is available. The pattern was made even more complex by changes in density within single study areas during a 3-year period while comparable areas in the region showed no such change. In some areas in the Lake Erie Basin, numbers of males dropped and then recovered; in one area, they increased steadily; and in another area they declined slightly but steadily.

Some progress has been made in the development of unifying theories to explain the apparent vagaries of population density and change noted for the redwing. For example, a relationship between distributional trends, latitude, and temperature led Power (1969, 1970) to postulate that distributions were related to thermoregulatory efficiencies in the populations he studied. If this postulate is correct, the speculation can be carried further to suggest that phenotypic variants with differing thermoregulatory efficiencies occupy isolated but adjacent breeding sites without the more obvious barriers often considered necessary for isolation (Mayr, 1963:ch. 16). Dyer (1964:143) presented data that suggest that such isolated redwing populations exist. The theory is supported further by the finding of Orians (1969) that the quality of the energy base in the breeding habitat is a principal factor in determining polygynous ratios and the ultimate productivity of the redwing population. In areas where the energy base is high, the ratio is low.

Therefore, it is becoming more apparent how interactions of genotype, phenotypic adaptation to the environment of the breeding area, and total energy available on the breeding grounds determine the success of any given redwing population. The present paper adds to this picture by describing population densities of territorial males in a well developed and stable agricultural community, and relates the results to population theory.

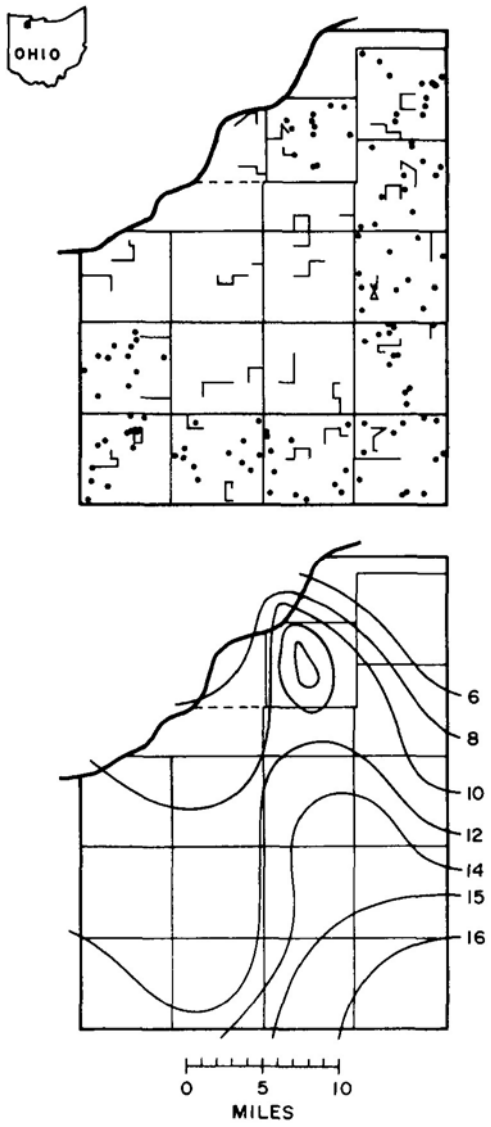

Figure 1. Distribution of sampling areas and densities of territorial male red-winged blackbirds in Wood County, Ohio (1964-1968). Upper county maps show distribution of sample sites for the two census types: lines within each sampling block (township) show location of 3-mile roadside routes censused; solid circles show approximately location of 10-acre field plots censused. Lower county map shows approximately distribution of territorial male redwing densities obtained from the roadside index method; males per 100 acres ranged from 5.9 in the northeast to 16.2 in the southeast.

MATERIALS AND METHODS

The study was conducted in Wood County, Ohio, from 1964 through the spring of 1968. This area was chosen because it was known to have a long and stable agricultural history, and to contain a relatively large nesting population of redwings in the upland habitats. The 17 townships in the county were used as sampling units (strata) (Fig. 1). In each (stratum, unit, township), two, 3-mile-long and 150-yard-wide roadside sampling areas were chosen for a Petersen-Lincoln index census (Hewitt, 1967). In addition, 10 (strata, units, townships) were selected at random, and 12 10-acre field plots, were randomly located within each (Fig.l). In each 10-acre plot, a total count was made of the number of territorial males per habitat type, and the proportion of the area represented by each of nine habitat types was estimated.

Three biologists conducted the census in 1964, 1965, and 1966; two in 1967; and one in 1968. The field data were collected during May of each year. In 1970, all field data were placed on machine punch cards in the same format used by Dyer et al. (1972), and were processed at the University of Minnesota. In the computer program, the population estimates derived from the Petersen-Lincoln index were converted to numbers of territorial males per 100 acres, and a two-way analysis of variance was used to test for differences among years and among areas. The population counts from the 10-acre plots also were converted to males per 100 acres; a Chi-square analysis was used to test differences in distribution among habitats. The Chi-square analysis tested whether birds selected for *(S)*, against (*A*), or neither for nor against (*N*) each of the nine habitat types (Table 3). Finally, a correlation analysis was used to compare the roadside census indices with the plot counts in strata where both kinds of counts were made.

RESULTS

The roadside census results for Wood County show a mean density of 11.59 territorial males per 100 acres during the 5-year study (Table 1.) The mean yearly densities were not significantly different ($p>0.1$), but the distribution of males

Table 1. Densities of territorial male redwings in Wood County, Ohio, 1964-1968. The data were collected from roadside census plots by Hewitt's modification of the Petersen-Lincoln index method.

Year	Mean number of male redwings per 100 acres of all habitat in Wood County
1964	11.62
1965	11.35
1966	11.67
1967	11.71
1968	11.59
5-year average	11.59

Table 2. Analysis of variance for the Petersen-Lincoln index data collected from the Wood County, Ohio censuses, 1969-1968.

Source of Variation	df	MS	F
Among years	4	2.6659	0.068
Among strata	33	3183.6655	9.824**
Error	132	1296.3493	
Total	169	4482.6807	

** Significantly different at 0.01 level

throughout the 17 strata in the county was not uniform ($p<0.01$) (Table 2). This non-uniform distribution is illustrated in the lower map of Figure 1 by approximate isopleths showing density gradients. In general, male densities were lowest in the northeastern part of the county, where there were 5.9 territorial males per 100 acres. Densities increased to 16.2 at the southeastern corner of the county. Densities reached 14.6 males per 100 acres in a small area in the north-central section of the county.

The plot data shows that densities in wetland habitat were very high (75.57 territorial males per 100 acres for both components of the wetland category, Table 3). The Chi-square analysis showed that males selected these habitat types throughout the 5-year period. The average density in upland habitat was 26.18 males per 100 acres (Table 3.) But, unlike in wetland habitat, males did not consistently seek out all components of the available habitat; the Chi-square analysis showed only hay to contribute consistently to the overall population. The numbers of males inhabiting pasture and fallow fields were insignificantly small in all years except 1965, when the numbers in pasture contributed significantly. Territorial males avoided tilled areas (made up of either the obvious years' stubble or newly plowed ground), while grain-fields were neither avoided nor sought out. Woods and miscellaneous habitat also were not selected for or against (Table 3).

The amount of each habitat available to breeding birds each year is shown in Table 4 (roadsides are excluded). Approximately 21.4 percent of Wood County was composed of upland habitat. Of this amount, well over half was in hayfields. Wetlands constituted about 3.47 percent of the area, most of which was ditch-type habitat. Cultivated land made up two-thirds of the area; much of the land surface (48.36 per-cent-) was tilled ground destined for spring-planted crops (primarily corn, soy beans, and cereals). The area devoted to grain mostly winter wheat) averaged 18.18 percent. Woods made up 6.5 percent of the area; and 2.11 percent of the area was in miscell-aneous habitat such as farmyards, open water, and road surfaces.

By combining the data from Tables 3 and 4, an estimate of the total population can be made. Data from tilled land, grain, woods, and miscellaneous categories were excluded since males in these habitats did not contribute significantly to the overall population. Slightly over 21 percent of the area of Wood County contained birds at a density of 26.18 territorial males per 100 acres (Table 3), and 3.47 percent of the county contained birds at a density of 75.57 males per 100 acres. The total area of available habitat (excluding urban development and road surfaces) was

543 square miles (347, 520 acres) (Rapparlie and Urban, 1966:50, 94; Ohio Dept. of Highways, 1970). In this area, there were approximately 19,470 territories in the uplands habitat and 9,113 territories in the wetland habitat; this is a ratio of 2.14 territories in upland to 1 territory in wetlands.

There was not significant correlation between the roadside index and the plot counts ($p>0.1$). The regression slope was $Y=7.6923 + 0.0808X$ (where Y= densities

Table 3. Distribution of territorial male red-winged blackbirds in nine habitats in Wood County, Ohio, 1964-1968. Figures show numbers of redwing males per 100 acres of habitat.

	Upland habitat			Wetland habitat		Cultivated land		Other	
Year	hay	past	fallow	marsh	ditch	tilled	grain	woods	misc.
1964	38.3^S	2.3^N	11.8^N	94.1^S	70.8^S	0^A	0.8^N	0^N	0^N
1965	34.6^S	30.1^S	12.6^N	75.0^S	50.2^S	0^A	2.3^N	0^N	4.4^N
1966	34.0^S	7.0^N	12.2^N	83.3^S	91.4^S	0.5^A	1.7^N	0^N	4.4^N
1967	30.2^S	11.3^N	18.6^N	90.0^S	78.1^S	0^A	2.5^N	1.3^N	0^N
1968	41.8^S	14.5^N	15.3^N	88.9^S	74.3^S	0^A	0.5^N	1.4^N	0^N
Averages:	35.78	13.04	13.9	86.26	72.9	0.1	1.56	0.54	1.76
		20.91			79.61		0.83		1.15
Weighted Averages[1]		26.18			75.57		0.50		0.84

S = Selected for habitat
A = Selected against habitat
N = Selected neither for nor against habitat
1 = Average number of birds per habitat type (upland, wetland, cultivated, and other) has been weighted by total habitat area from Table 4.

For example, wetland habitat averages =

$$\frac{(86.26)\ (0.68) + (72.96)\ (2.79)}{3.47} = 75.57$$

from the 10-acre plot results and X= densities from the Petersen-Lincoln roadside index results); the regression coefficient was 0.072, and s_{yx} was 4.169.

Table 4. Distribution of habitats in Wood County, Ohio, 1964-1968. Figures show percentages of total area occupied by each habitat

	Upland habitat			Wetland habitat		Cultivated Land		Other	
Year	hay	pasture	fallow	marsh	ditch	tilled	grain	woods	misc.
1964	12.63	3.63	4.96	0.71	2.71	46.24	19.96	6.75	2.42
1965	13.02	3.88	4.63	0.67	2.33	52.28	14.69	6.62	1.91
1066	12.85	2.39	6.18	0.42	2.85	46.94	19.80	6.60	1.89
1967	12.69	2.96	8.16	0.83	2.67	44.00	20.13	6.33	2.33
1968	9.45	2.31	7.26	0.76	3.39	52.35	16.34	6.22	2.02
Averages:	12.13	3.03	6.24	0.68	2.79	48.36	18.18	6.50	2.11
	21.40			3.47		66.54		8.61	

DISCUSSION

Population densities estimated by the two census methods were not significantly correlated in the present study in comparisons made by a simple correlation analysis ($p>0.1$). The main problem in making such an analysis is that the samples cannot be paired sufficiently. Strictly speaking, only census data collected by the two methods from areas lying adjacent to one another should be used. In the study of Dyer et al. (1972) such comparisons were possible and the results from the two methods were compatible. Therefore, in the present study in the Petersen-Lincoln index data (Hewitt, 1967) have been used for total population estimation and distribution; and the plot data have been used for habitat analyses.

The densities estimated from the Petersen-Lincoln index here are very similar to the densities for the nearby Stratum II estimated by Dyer et al. (1972); since these two study areas were adjacent, this was expected. The 5-year average density of males in roadside habitat in Wood County was 11.59 per 100 acres (Table 1), whereas for Stratum II the 3-year average was 12.3 (Dyer et al., 1972). During the 3-year study period, the

average estimated in another Ohio study area farther east (Stratum I) was higher (13.13 males per 100 acres) while estimates from southeastern Michigan (9.0) and southwestern Ontario (6.2) were much lower. The 3-year average for all habitats in the Lake Erie Basin was 10.17 males per 100 acres (Dyer et al,. 1972).

The overall densities in Wood County were lower than those reported by Hewitt (1967) for New York and Arkansas. Since no bases exist for standardizing the quality of habitat for the two regions, a comparison of densities probably is not valid.

The plot data from Wood County show that the mean density of males in the upland habitat (26.18 males per 100 acres) was nearly identical to the mean density (26.48) in the nearby Stratum II. Densities in wetlands were similarly comparable (75.57 in Wood County, 78.81 in Stratum II).

The high densities of redwings in wetlands (marsh and ditch) indicate that the males prefer these areas when they are available; but it is difficult to determine at this time whether the reported values represent maximum densities. From Table 4 it is easy to see that little wetland habitat exists in Wood County. Marshes are limited by agricultural practices, and ditches are determined by a combination of agricultural practices, and the amount of space allocated to right-of-way for roads and drainage areas. In Wood County, wetland habitat creates a large edge effect by being distributed in small patches or in long-drawn-out areas, such as along roads. It is problematical whether present densities would vary if the amount of space available for either the marsh or ditch habitats were to increase significantly, especially if large blocks of marsh were created.

Densities of male redwings in the pasture and fallow field components of the upland habitat of Wood County were quite similar to those in nearby Stratum II of the l968-1970 study, but densities in hay habitat were 39 percent lower in Wood County. In the prime upland habitat of Wood County (hayfields, mainly alfalfa and clover), there was considerable variability in density of territorial males. The pattern of this variability is very similar to that shown in the lower map of Figure 1. The distribution showed a continuum throughout the county, with the most dense population toward the southern edge.

Since both the Chi-square analysis of the plot data and the comparisons with data from Dyer et al. (1972) indicate that the principal nesting habitat is in hayfields rather than in other upland components, it is obvious that this nesting habitat is most responsible for sustaining the present population. Variation in extent of this habitat affects the overall population more than any other factor. Furthermore, the population size is not strictly a function of the total amount of space available for territories and nesting activity. Innate tolerance to crowding maybe as important as availability of hayfields (Dyer et al., 1972) in determining a population level. However, a reduction in hay habitat would cause a restriction of space, and territories soon

would be compressed to a maximum density. Crowding beyond this density would very likely cause a noticeable drop in the total population size by denying redwings adequate nesting space. Many potential behavioral feedback mechanisms, such as increased strife due to territorial defense and lack of food, could become realities and affect the total natural breeding cycle.

Overall, the size of the male territorial population in Wood County upland habitats was more than double that in the wetland habitats. Hayfields alone contained more territories than all wetland areas. The degree of stability of the blackbird population over the 5-year census period is quite remarkable. Even though the distribution of males within the county was not homogeneous, no major change in the total number of males was detected.

I have presented the view in another paper (Dyer et al., 1972) that the stability of the population is primarily based on very stable agricultural practices in the region. Two factors play a major role: 1) the total amount of space available for the redwings does not change appreciably from year to another; 2) the energy base provided by an agricultural community, especially where certain crops such as alfalfa are grown (Odum, 1959:73), is relatively high and stable. Thus, because food and space are interrelated, we can assume that during optimum conditions the breeding habitat in Wood County would support a high but finite number of birds. If neither of these two factors changed appreciably in time, the productivity potential would remain quite constant. Furthermore, if the birds inhabiting the region had been in residence long enough to establish maximum numbers per unit area, we could further assume that homeostatic mechanisms associated with long-term successful habitation had developed. This maximum number then would become the optimum for the redwing and could be referred to as the "carrying capacity" of the area.

It is well known that once a population is established, homeostatic mechanisms provide great resistance to change (Holling, 1966). In view of the stable nature of numbers of territorial males in Wood County for the 5-year period, it would logically follow that these assumptions must be true. From the present data, however, all that I can conclude is that the population is quite stable and that the energy flow through the agricultural ecosystem as it now exists will support this number of birds as an optimum. Since the alleged homeostatic mechanisms and their feedback actions have not been isolated at this time, little more can be done in the near future than to observe whether the population stability continues.

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SUMMARY

A 50 year study (1964-1968) of densities of territorial male redwings was conducted in all habitats of Wood County, Ohio, Two census methods were used, a

modified Petersen-Lincoln index conducted from a moving auto, and a 10-acre field plot count. A correlation analysis between the results obtained by the two methods showed no significant relationship ($p>0.1$), but since the census areas sampled were not significantly paired for such a comparison, no biological conclusions can be derived.

The roadside index method showed average densities (11.59 territorial redwing males per 100 acre) over the 5 year to be quite stable. These densities also were very similar to those reported from nearby areas. Within Wood County, the territorial redwing population was not distributed evenly ($p<0.01$). Densities were lowest in the northern portion of the county (5.9 territorial males per 100 acres) and increased steadily to the southern portion (16.2 territorial males per 100 acres). The analyses of data from the 10-acre plots showed densities in wetland habitat to be 2.89 times those in upland habitat. But, because of the small amount of wetland habitat, the total estimated upland population of territorial males was 2.14 times the wetland population. Alfalfa and other legume crops (hay) were the principal habitat for breeding redwings in the county. They alone contained a population 1.66 times that of all wetland habitat. The principal reasons for the maintenance of the large upland population appear to be redwing adaptation to the upland areas, the relatively large area available for territorial nesting activities, and the implied large energy base provided by the agricultural ecosystem.

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