

# THE ECOLOGY OF BLACKBIRD (*AGELAIUS*) SOCIAL SYSTEMS

GORDON H. ORIAN

*Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California\**

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## INTRODUCTION

The conspicuousness of adaptive radiation in morphology tends to conceal the fact that often the slight differences between closely related species give no clues to their widely differing ecologies, because many of the important differences between species are the result of behavioral and not morphological adaptations. This study analyses the role of social organization of the Red-winged Blackbird (*Agelaius phoeniceus*) and the Tricolored Blackbird (*A. tricolor*) in the different ways in which these two species exploit their environment.

Knowledge of avian social systems began with natural history studies, but certain phases, such as territoriality, early attracted special consideration. In the 1930s, social systems began to be studied from the viewpoint of the comparative ethologist, who is primarily interested in the motivational and evolutionary aspects of behavior patterns, but whose publications contain a wealth of information about many ecological features of avian social systems. The mathematical approach to population parameters has provided a basis for considering the consequences of changes in social system characteristics upon basic population parameters, but biologists have in general been suspicious of this approach, which seemed to rest upon assumptions of doubtful biological validity. The result is rather widespread failure to realize the significance of certain features of social systems in quantitative terms, and failure to record and publish relevant information. Finally, the study of social

systems from the modern ecological viewpoint has lagged behind other approaches because few observers have made use of the background of a century of Darwinian thinking in evaluating their observations.

In this study I have considered all features of social systems to be the products of natural selection just as are any physiological or morphological adaptations. To the question whether or not differences between social systems are adaptive, three types of answers are possible. Firstly, it may be assumed that the particular features of a social system are surely adaptive. Secondly, it may be assumed that the traits are purely fortuitous, without selective significance. Thirdly, it may be assumed that the particular traits are not adaptive but that they are associated with other, as yet unrecognized, differences which are adaptive (Maynard Smith 1958). In this paper I shall attempt to interpret as far as possible the characteristics of social systems in the light of the first of these three assumptions. The second is rejected because it is sterile as a basis for research and because the widespread and consistent differences to be discussed cannot be without selective significance. The third can never be easily accepted, for unless this statement of faith is followed by attempts to discover the traits of adaptive significance and their connection with the supposedly unadaptive trait, nothing is really explained. Furthermore, no such case involving polygenic traits has been shown to be true, and separation of desirable from undesirable traits will almost certainly occur with time.

Because the closely related and morphologically similar Red-winged and Tricolored blackbirds differ

\* Present address: Dept. of Zoology, Univ. of Washington, Seattle 5, Washington.

strikingly in their social organization, they are excellently suited to studies developed from the premises just given. Furthermore, these and other species of the family Icteridae are common, easily observed, and well-known. Moreover, their social systems range from routine territoriality to extreme coloniality and from monogamy to promiscuity and parasitism. My studies of these two blackbird species were carried out in north-central California from 1957 through the spring of 1960. The behavioral aspects of this investigation are being treated separately, and a report on autumnal breeding in the Tricolored Blackbird has already been published (Orians 1960).

This entire study was conducted under the supervision and guidance of F. A. Pitelka. The manuscript has also been read by P. Marler and G. L. Stebbins, both of whom have made valuable suggestions. Field work was made possible through the cooperation of F. Barnett of Lodoga, California, and C. Haskell of Marysville, who permitted access to their excellent marshes and also kindly provided lodging. A. S. Leopold generously made available his notes on blackbird activity at the Haskell Ranch since 1954. J. Parker of the East Bay Regional Park District permitted me to erect an observation tower on the small marsh at Jewel Lake during the spring of 1958. G. M. Christman aided in the preparation of the illustrations and provided data on Californian Indians. At many times during the course of this study I was aided in the field by fellow graduate students, including J. L. Brown, R. B. Root, E. O. Willis, M. Konishi, N. K. Johnson, D. R. Medina and J. Frost. Exchange of ideas with G. Collier, who is studying different aspects of the same species at Los Angeles, has been a helpful stimulus. For the two academic years 1958-1960 I was supported by a National Science Foundation Graduate Fellowship which permitted me to spend extensive periods in the field during the blackbird breeding season. Travel expenses were in part defrayed by a grant from the Museum of Vertebrate Zoology. Finally, my wife helped type the manuscript. To all I express my sincere appreciation.

#### STUDY AREAS

Field work was concentrated at four main areas, with supplementary observations at other localities (Fig. 1). Studies were first begun at Jewel Lake, Tilden Regional Park, Contra Costa County, in 1957. The lake, formed by a dam constructed across Wildcat Creek in the Berkeley Hills about 1900, has a maximum depth of 10 ft and is about 510 ft above sea level (Gullion 1953). About one-third of its 2.7 acres is filled with emergent vegetation, chiefly cattails (*Typha angustifolia* and *T. latifolia*), in which Redwings nest. No Tricolored Blackbirds breed there though occasional individuals roost in the autumn and winter. During the non-breeding season the marsh harbors a large roost of male Redwings, but females are normally present only during the nesting season. This marsh was studied intensively during 1958 and less frequently in 1959 and 1960.



FIG. 1. Study areas in central coastal California. Jewel Lake is marked by the large "X," the East Park Reservoir by the large circle, and the Haskell Ranch by the large square. Other study areas are indicated by small dots. Areas of large breeding concentrations of Tricolored Blackbirds are shown by diagonal lines.

Both species of blackbirds breed commonly at the East Park Reservoir in the Coast Ranges of Colusa County, a body of water formed in 1910 by a dam across Stony Creek. Because its waters are used to irrigate orchards in the Sacramento Valley near Orland, in the summer it may be reduced to a mere remnant of its winter size and, as happened in 1959, may completely dry up. Most of the shoreline of this large reservoir is devoid of emergent vegetation but there are two large marshes where two major streams enter it. In addition, there are small patches of cattails in some of the indentations along the shores (Fig. 2). The reservoir is surrounded chiefly by heavily grazed blue oak (*Quercus douglasii*) parkland, chaparral (chiefly chamise, *Adenostema fasciculatum*), and, at the south end, by cultivated fields. I first visited the area briefly in 1957 and 1958, but at the end of March, 1959, I established a camp on the shores of the reservoir which served as a base for field work through the breeding season. By early June the water had already dropped to such a low level that no blackbirds remained there. Before the reservoir completely refilled in March of 1960, the cattails in the marsh at the southeast end were completely burned. Blackbirds began to breed as soon as new growth permitted and regular observations were also made throughout the second spring.

The Haskell Ranch, eight miles southeast of Marysville, Yuba County, is located in the heart of a ranching district. The marsh is surrounded by irrigated pastures and owes its existence to the run-off



FIG. 2. Two of the isolated patches of cattails at the East Park Reservoir, Colusa County, California, April, 1959.

of excess water from them. It is burned every winter or early spring and cattails are cut to keep certain water areas open for duck hunting. None of these activities greatly influences the blackbirds, however, as the cattails sprout immediately following burning and there are always large areas which are not cut. Both Redwings and Tricolors breed there, and sometimes Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) as well, though they were absent in 1959 and 1960. My studies were limited to these two years, though Dr. Leopold's notes were available for earlier years.

Observations were made during May and June, 1959, and throughout the fall, winter, and spring of 1959-1960 in the rice-growing and duck-hunting areas of Colusa and Glenn counties where extensive areas of cattails are maintained as duck habitat. Also, the rice fields are favorite feeding grounds for Tricolored Blackbirds, so that this region supports large populations of this species, Redwings and smaller numbers of Yellow-heads.

In addition to these four major study areas, observations were made in the rice-fields in Sacramento County and in the course of road travel between the study areas. Prospecting trips were made to other areas in the valley and foothills during each spring, and in 1958, an exploratory visit was made to areas in the San Joaquin Valley and foothills of the Sierra Nevada. Upland breeding Redwings were also briefly observed on Brooks Island in San Francisco Bay.

## METHODS

The basic method in this study was simply to record in detail all features of social organization seen in the field, though advantage was taken of natural experiments offered by habitat differences, variations in weather, and human interference. In addition, I conducted elimination experiments in 1959 and 1960 to study repopulation. Each of the major displays and vocalizations of both species was assigned a symbol which enabled me to record more fully the activities of an individual bird as long as it remained in view. At Jewel Lake in 1958, I watched male Redwings several mornings each week throughout the breeding season. Less extensive observations were made in the afternoons. Extensive use has been made of these observations and the samples of activity sequences they include in the development of time and energy budgets. Particular attention was paid to the temporal and spatial aspects of social organization, as these are two features in which the two species differ most strikingly.

## GENERAL BIOLOGY OF THE SPECIES

The widespread Redwing breeds from the Atlantic to the Pacific and from Central America almost to the Arctic Circle in west-central Canada (Bent 1958). Most individuals migrate from the colder portions of the range in the winter but some of the southern races, including the Californian ones, are resident. The Tricolored Blackbird has a much more restricted distribution, breeding from southern Oregon and the Modoc Plateau of northeastern California, south through the lowlands of California west of the Sierra Nevada to northwestern Baja California (Grinnell & Miller 1944). The species is not migratory but is nomadic and highly colonial (Fig. 3), though the pattern of nomadism is poorly known. Large flocks appear suddenly in areas from which they have been absent for months, they breed, and then quickly withdraw. Size and location of colonies vary from year to year, though certain sites, such as the East Park Reservoir and the Haskell Ranch, are regularly used. In his extensive studies of Tricolor distribu-



FIG. 3. The Marysville Tricolor colony during the nest building period, Yuba County, California, May, 1959.



tion, Neff (1937) observed striking shifts in the location of colonies in the Sacramento Valley (Table 1), and to show that the variation is not simply due to variability in searching time, I have recalculated his data to express it as thousands of nests discovered per man-day spent searching (Table 2).

TABLE 1. Estimated nesting populations of *Agelaius tricolor* (figures represent thousands of nests; data from Neff 1937).

County	1931	1932	1933	1934	1935	1936
Butte.....	—	28	106	32	3	4
Colusa.....	—	32	16	37	3	5
Glenn.....	—	68	61	282	4	4.5
Merced.....	—	50	58	2	37	10
Sacramento.....	—	121	101	80	1	15
Sutter.....	—	10	13	6	1	3
Yolo.....	10	38	3	2	10	2
Yuba.....	113	2	7	50	5	5

TABLE 2. Thousands of nests discovered per man-day expended (calculated from data given in Neff 1937).

County	1931	1932	1933	1934	1935	1936
Butte.....	0	9.3	26.5	16.0	1.5	4.0
Colusa.....	0	10.7	5.3	18.5	1.5	5.0
Glenn.....	0	11.3	6.1	6.3	2.0	2.3
Merced.....	—	50.0	1.9	0.7	7.4	2.5
Sacramento.....	0	24.2	33.7	26.7	0.5	3.0
Sutter.....	0	5.2	6.5	6.0	1.0	3.0
Yolo.....	0.2	12.7	1.0	1.0	5.0	1.0
Yuba.....	1.9	0.03	0.1	0.8	0.1	2.5

The plumage of these two species is so similar that museum specimens are sometimes misidentified. The adult male Tricolor has a bluish luster to its black plumage, and the red of the epaulets is a dull crimson in contrast to the bright scarlet of the male Redwing. The most conspicuous feature of the male plumage, and the one which gives the species its common and scientific names, is the broad white border to the middle wing coverts. In most races of the Redwing these feathers are tipped with buffy, but in those races occupying the central Coast Ranges and Great Valley of California, the metropolis of the Tricolor, they are black so that the wing lacks the light stripe. This plumage difference between males is not only conspicuous to the human observer, it is the most important means of species identification used by the birds themselves. Occasional Redwings in a flock of Tricolors are singled out for special attack by a resident male Redwing in whose territory the flock lands.

Females are less easily distinguished because, although female Tricolors are darker than most races of the Redwing, in the area of distributional overlap female Redwings are the darkest of that species. Thus, the need of making accurate specific identification notwithstanding, there is a convergence of female plumage in the area of sympatry in contrast to the

TABLE 3. Comparative measurements of blackbirds.

Measurement	Species	Sex	Mean (mm)	Standard deviation (mm)	Range (mm)
Wing.....	Redwing	♂♂	124.5	2.4	118.8-131.6
		♀♀	102.9	2.6	97.5-108.5
	Tricolor	♂♂	120.8	2.1	115.5-125.2
		♀♀	105.2	2.1	102.2-111.2
Tail.....	Redwing	♂♂	84.7	3.6	75.9- 93.8
		♀♀	67.9	3.6	60.6- 76.0
	Tricolor	♂♂	81.1	3.1	75.4- 89.7
		♀♀	68.9	2.3	64.0- 78.6
Tarsus.....	Redwing	♂♂	28.2	1.1	25.0- 32.8
		♀♀	24.9	0.9	22.5- 26.6
	Tricolor	♂♂	28.1	1.0	26.6- 30.4
		♀♀	25.2	0.8	23.1- 26.8
Culmen.....	Redwing	♂♂	22.6	1.1	19.8- 24.9
		♀♀	19.4	0.9	17.5- 22.2
	Tricolor	♂♂	24.5	1.0	22.4- 27.3
		♀♀	21.8	1.0	19.8- 24.5
Bill depth.....	Redwing	♂♂	8.7	0.5	7.6- 10.1
		♀♀	7.5	0.5	6.1- 8.3
	Tricolor	♂♂	8.0	0.3	7.5- 8.5
		♀♀	6.9	0.8	6.3- 8.0

divergence in the males. In general, female Tricolors are more uniformly sooty than female Redwings, there being less contrast between throat and breast. In the autumn, female Redwings are strongly tinged with rusty on the back, a feature never shown by the female Tricolor.

Sexual dimorphism in size, though great in both species, is less in the Tricolored Blackbird. Measurements of winter and spring specimens of both species are given in Table 3. In these specimens the male Tricolors are smaller than male Redwings in wing, tail, tarsus, and bill depth, but are larger in culmen. On the other hand, female Tricolors are larger than female Redwings in wing, tail, tarsus, and culmen, but are smaller in bill depth. This longer, narrow bill of the Tricolor is one of the most reliable morphological differences between the species.

The comparative weights of the two species are less certain. Among the MVZ specimens the male Tricolors average heavier than male Redwings and females heavier than female Redwings. However, in a sample of 47 male Tricolors and 31 male Redwings collected in the Sacramento Valley in October and November, 1959, the male Tricolors averaged lighter than the male Redwings, the difference being due to a decrease in the mean weight of male Tricolors.

Specimens collected in the autumn of 1959 were also measured for wing spread, maximum wing width, and total wing area. Wing spread and wing width are the same in females but the male Redwing has a greater wing spread and broader wings than the male Tricolor (Table 4). As a result, the Tricolor carries more weight per unit of wing surface than the Redwing (Table 5). The slender, more pointed wing of the Tricolor is conspicuous enough in the field to enable an experienced observer to identify the species at great distances.

As will be discussed later, the roles of the sexes are more similar in the Tricolor than in the Redwing and the species is less polygamous. The lesser degree

TABLE 4. Wing measurement of blackbirds.

Measurement	Species	Sex	Mean (mm)	Standard deviation (mm)	Range (mm)
Wing spread....	Redwing	♂♂	15.4 in.	.30	15.0-16.1
		♀♀	13.2	.23	12.7-13.3
	Tricolor	♂♂	15.1	.19	14.8-15.6
		♀♀	13.2	.27	12.7-13.7
	Wing width....	♂♂	3.9 in.	.11	3.7- 4.1
		♀♀	3.2	.10	3.0- 3.3
Wing area.....	Redwing	♂♂	3.5	.10	3.4- 3.7
		♀♀	3.1	.12	2.9- 3.5
	Tricolor	♂♂	45.5 sq. in.	2.05	42.4-50.4
		♀♀	31.4	1.12	28.6-33.0
	Tricolor	♂♂	39.4	2.17	36.2-42.6
		♀♀	29.6	1.31	27.2-32.4

TABLE 5. Wing loading.

Species	Sex	Mean wing (sq. in.)	Mean weight (g)	Weight per square inch of wing surface (g)
Redwing....	Male	45.5	66.1	1.45
	Female	31.4	42.4	1.35
Tricolor.....	Male	39.4	63.3	1.60
	Female	29.6	46.5	1.57

of sexual dimorphism in size thus fits in with the general picture in the Icteridae, where there is a correlation between the degree of size dimorphism and the extent of promiscuity (Selander 1958). The Tricolored Blackbird not only travels extensively during its nomadic wanderings, but both sexes fly great distances when gathering food for the young, a time when speed is of great importance. The narrow, more pointed wing has probably evolved in response to this need as it has in other avian groups. The Redwing male does not feed the nestlings, but engages in frequent conspicuous display flights over the territory. The broad wing is therefore useful as a display organ. The Tricolor has no such aerial displays.

## THE SOCIAL SYSTEMS

### 1. THE RED-WINGED BLACKBIRD

*Non-breeding Period.* Outside the breeding season Redwings are highly gregarious, travelling and feeding in flocks of varying size, and roosting together in favored sites, usually over water, which attract birds from distances up to twenty miles or more. On evenings for which counts of roosting birds, mostly males, were made at Jewel Lake, the total number varied between 1,544 and 2,596; the number of flocks between 159 and 205; and the average flock size from 8.6 to 14.1 (Table 6). Flocks were smaller at the beginning and end of the roosting time, and the rate of flock arrival was greatest in the middle, so that the bulk of the birds arrived in a short period of time (Fig. 4). Arrival time, which closely fol-

TABLE 6. Evening roosting of Redwings, Jewel Lake, fall, 1958.

Date	10/16	10/23	11/6	11/13	11/20	11/27	12/4
Number of birds ...	1,544	1,368	2,134	2,296	1,701	1,686	2,596
Number of flocks...	173	159	205	191	152	173	184
Average flock size...	8.9	8.6	10.4	12.0	11.2	9.7	14.1

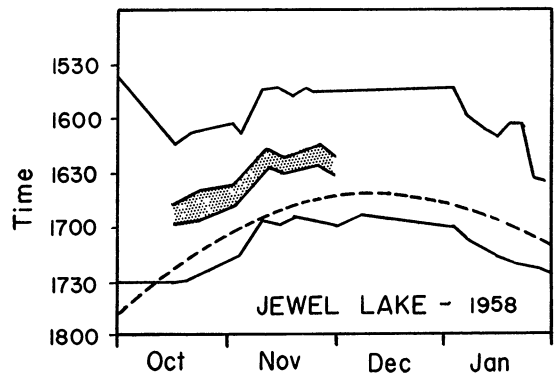


FIG. 4. Roosting of male Redwings at Jewel Lake. Solid lines indicate the arrival of the first and last roosting birds. The time of local sunset is shown by the dashed line. The period during which at least one-half of the birds arrived is indicated by the dotted area.

lowed the time of local sunset, was usually spread out over about one and one-half hours.

Enormous numbers of blackbirds roosted at the Colusa marsh in the autumn of 1959. Redwings and Tricolors were by far the most numerous but there were also many Brewer Blackbirds (*Euphagus cyanocephalus*), Cowbirds (*Molothrus ater*), Yellowheads and Starlings (*Sturnus vulgaris*). This roost attracted birds from an enormous area from the Sacramento River west to the foothills of the Coast Ranges and for at least ten miles north and south of the marsh. During the major part of the roosting flight on the evening of October 15, I estimated that 500-1000 birds per second were crossing a road south of the marsh, so that perhaps 750,000-1,500,000 birds entered the roost from that direction during the 25-minute period of maximum arrival. Since large flocks were also approaching the marsh from other directions as well, at least several million birds were roosting there at this time.

Whereas birds straggled in for over an hour in the evening, the morning exodus lasted only about 30 minutes. After the main morning feeding, the birds returned to the cattails where they rested, preened, sang, and bathed for much of the remainder of the day. Another major feeding flight in mid-afternoon preceded roosting for the night. Though the marsh was always full of birds at mid-day, there was a steady movement in and out and individual birds probably fed at least once each day in addition to the two main feeding periods.

A striking feature of Redwing social organization during the fall and winter is the segregation of

the sexes which, though by no means complete, is very pronounced. As already mentioned very few females roosted at Jewel Lake, and though both sexes roosted abundantly at Colusa, most flocks seen feeding during the day were wholly or largely composed of one sex.

The enormous numbers of Redwings in the Sacramento Valley in the autumn obtain most of their food from agricultural land. I did not examine any stomachs, but by observing feeding birds it is easy to determine what they are taking. In late summer the birds concentrate upon seeds of the water grass (*Echinochloa crusgalli*), which is abundant around the edges of all rice fields and ditches in irrigated country, and rice, which is then coming into the milk stage. The greatest damage to the rice occurs at this time though the birds continue to utilize it heavily until it is harvested. Mechanical methods of harvesting rice leave large amounts of grain scattered on the ground among the stubble which the blackbirds continue to use until the fields are plowed. At this time of year, newly sprouting alfalfa fields are also used as sources of insects. As the autumn progresses, more and more fields are harvested and plowed, and feeding conditions become progressively worse. This is partly offset by the flooding of many fields to attract ducks for hunting, because these fields are not plowed and also produce many insects. Nonetheless, by early January the populations of Redwings and Tricolors in the Sacramento Valley are greatly reduced from their mid-autumn level. One can drive great distances in late winter and see few blackbirds where earlier there had been millions. It is not certain where they go at this time, but they probably move to the San Joaquin Valley and other areas to the south where agricultural practices are different.

**Initiation of Breeding.** The onset of the breeding period in the Redwing is marked by the establishment of territories by the males early in January in north-central California. At first the territories are occupied for only brief periods in the early morning and late afternoon, but gradually the amount of time spent there increases until the birds are present on or near the territories all day. At Jewel Lake in the winter, territorial males roost in the marsh together with a large number of birds which leave to nest elsewhere. The resident males briefly remain on their territories after the roosting birds have left, and then also leave for the rest of the day to feed (Fig. 5). It is not until mid-March that the males begin to feed in the area and not until early April that they remain all day and find the bulk of their food either on the territory or close to it. Females begin to arrive in early March, and by the end of the month most of them roost in the marsh with the males.

At the East Park Reservoir the initiation of the breeding season follows the same general pattern as at Jewel Lake except that events occur about two weeks later. Nights are much colder and vegetational development slower in the foothills than in Berkeley, where the influence of the Pacific Ocean moderates

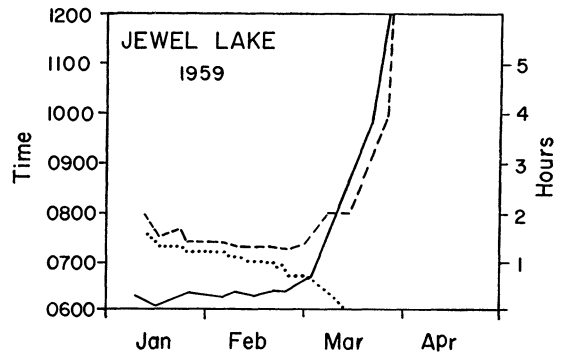


FIG. 5. Occupation of territories by male Redwings. The departure of the main roosting flock is shown by the dotted line; the departure of the territorial males by the dashed line; and the difference in departure time by the solid line.

late winter and early spring temperatures. However, the pattern at East Park Reservoir is also modified by other factors such as the rate at which the reservoir refills and the incidence of burning. In 1960 it was not until mid-March that the cattail marshes were completely reflooded, and no birds roosted there prior to that time. Burning results in the destruction of roosting and nesting cover, which delays the onset of breeding as the birds must wait until the new growth of cattails is high enough to support their nests. In normal years the first nests are constructed in dead cattails.

**Nesting Habitat.** Redwings nest in a wide variety of habitats (Allen 1914, Sherman 1932, Todd 1940, Nero 1956a), but most nests are located in emergent vegetation, particularly cattails. In California they commonly nest in vegetation bordering irrigation ditches, roadside and fencerow vegetation, riparian situations, weed and brush patches, cropland such as alfalfa and cereal grains, and even upland areas of mixed chaparral and grass. The chief requirement is apparently vegetation strong enough to support the nest surrounded by suitable feeding grounds. Burned cattail areas are used before the new growth sprouts if enough charred stumps remain. In fact, at the East Park Reservoir in 1959, burned areas were chosen instead of dense, unburned patches when both were available on one marsh area. On Brooks Island, the Redwing is a common breeding bird throughout the island, nests being located in bushes of poison oak (*Rhus diversiloba*) and coyote brush (*Baccharis pilularis*) even on the tops of the main ridges. I have not found this situation duplicated elsewhere, but I know of no mainland area with such varied, ungrazed vegetation as is found on the island.

**Time of Breeding.** The most complete studies of breeding chronologies were made at Jewel Lake in 1958 and East Park Reservoir in 1959. The major features of the breeding season for both areas are summarized in Figs. 6 and 7. Less complete observations at Jewel Lake in 1957 and 1959 show that, with minor modifications, the same pattern held for those

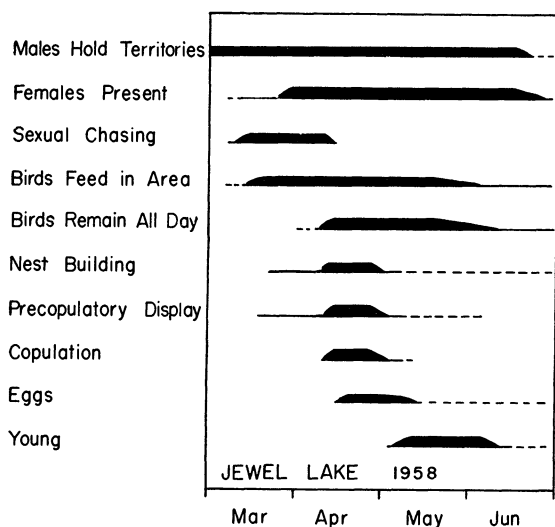


FIG. 6. Breeding chronology of Redwings, Jewel Lake, 1958.

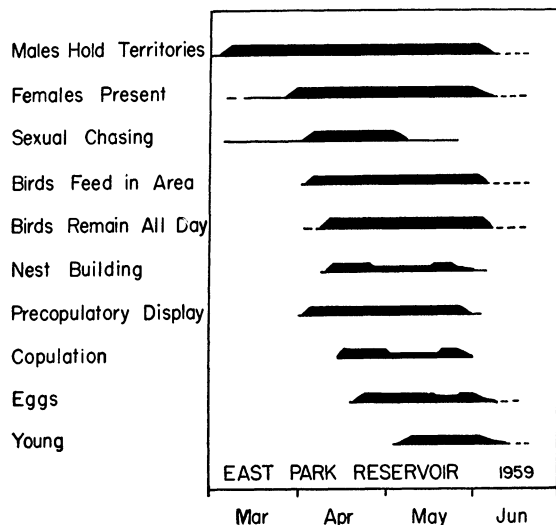


FIG. 7. Breeding chronology of Redwings, East Park Reservoir, 1959.

years as well. For example, the arrival of females, the beginning of chasing of the females by the males and the start of precopulatory displays were within one week of their 1958 time in 1959. Egg-laying in 1957 began two days earlier than in 1958. Because of burning, events were delayed in 1960 at the East Park Reservoir, but in the unburned areas, nesting began four days earlier than in 1959.

A general picture of timing of breeding in the Sacramento Valley was obtained by a census of territorial males along 60 miles of highway between Vacaville and Williams on the west side of the valley. The census area traversed irrigated and non-irrigated cropland and orchards not all of which were suitable blackbird habitat. Territorial males were counted

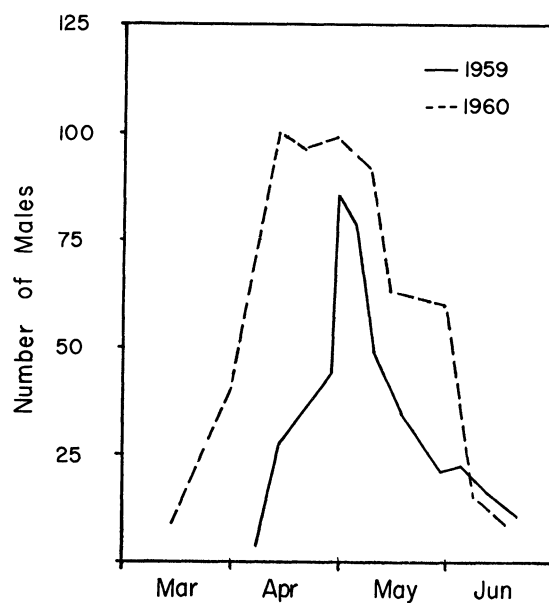


FIG. 8. Territorial male Redwings along 60 miles of highway on the west side of the Sacramento Valley. Birds were counted from an automobile travelling approximately 45 miles per hour.

from an automobile travelling approximately 45 miles per hour. Such a census can give only relative numbers but it does provide a rough picture of time of breeding in the area sampled (Fig. 8). Two points are of interest. Firstly, there is a sharp reduction in the number of birds in mid-May when many of the crops are cut, destroying nesting sites. Secondly, there is only a short period of time during which many birds are present. In 1960, the relatively longer plateau of high numbers was maintained only through continual occupation of new sites throughout the period, since cutting of crops and progressive destruction of nesting areas began in late April. Relatively few sites were suitable for a long enough period to permit the completion of the breeding cycle. Elsewhere in the valley, also, many nests were destroyed before the young had fledged, and though there are no quantitative data, it is quite certain that reproductive success in crop-nesting Redwings is generally poorer than in marsh-nesting birds.

At the East Park Reservoir in 1959, territories on the periphery of the marsh were occupied first and these areas were the most fiercely contested throughout the breeding season. As early as February 19, males displayed in the strip of marsh adjacent to the road for over three hours and more territories were set up than were maintained (Fig. 9). Once six males engaged in vigorous communal displays on the road, walking around each other in full song spread. The time of territory establishment by females and the start of nest building paralleled the pattern of territory establishment by the males.

Normally the females in a given marsh are out of phase with each other (Nero 1956b), but syn-



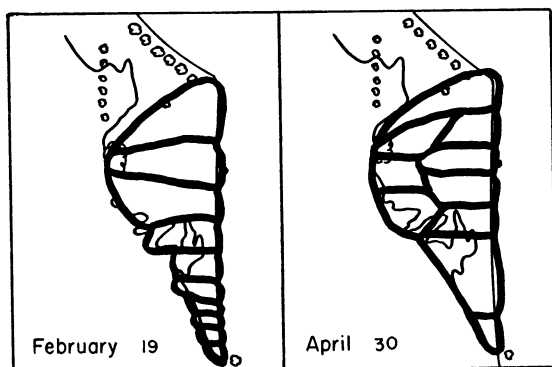


FIG. 9. Size of Redwing territories, East Park Reservoir, 1959.

chrony may be notable at the start of the breeding period. Most females began to nest at about the same time in 1959 in the isolated patches of cattails along the east shore of the East Park Reservoir. Even when all seven patches are lumped together, 51 of 72 nests were started within three days of each other (Fig. 10). It follows that most males in these areas were copulating with more than one female during the same period. Because of nest fail-

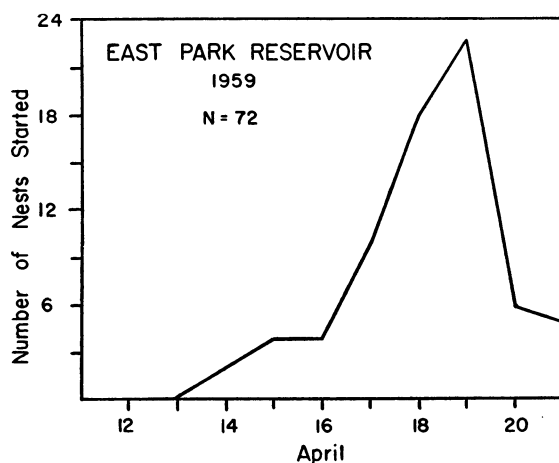


FIG. 10. Breeding synchrony among Redwings in the isolated cattail patches at the East Park Reservoir. The graph is a composite curve representing the pooled data from all seven cattail groups.

ure, second nestings, and the arrival of new females, nestings went out of phase so that by May 15 there were some nests in all stages of construction, others with eggs and young, and free-flying young in the same areas. A check of 30 nests at the Haskell Ranch on May 13 gave a similarly asynchronous picture.

**Territory.** The territories of the males are defended by means of song, displays and chasing, but little is known about the variations in territory size and the factors influencing them. Linford (1935) found that territories of polygamous males were

twice the size of those of monogamous males, but Nero (1956b) found no such relationship. I also failed to find any correlation between number of females and territory size.

The East Park Reservoir afforded the opportunity to study territory size in marsh areas of contrasting characteristics. Progressively more food is obtained on the territories in the small clumps of isolated cattails, the peripheral strips of cattails along the main marsh, and the main marsh itself, in that order. Territories were substantially the smallest in the isolated cattail clumps, larger in the peripheral strips, and largest in the main marsh (Table 7). Territory size was also determined for a portion of the Haskell Ranch marsh for both 1959 and 1960. In 1959, territories averaged larger than at the East Park Reservoir; but in 1960, they were comparable to territories at the periphery of the main marsh at the reservoir (Table 8). There are no other data from the valley floor with which to compare the results obtained at

TABLE 7. Size of Red-winged Blackbird territories, East Park Reservoir, 1959.

Situation	Number of territories	Average size (sq. ft.)
Isolated cattail clumps surrounded by grassland.....	21	2,512
Strip of marsh at the edge of the reservoir.....	17	8,477
Main marsh area, including both central and peripheral territories.....	22	10,653

TABLE 8. Size of Red-winged Blackbird territories, Haskell Ranch.

Year	Number of territories	Average size (sq. ft.)
1959.....	10	13,720
1960.....	16	8,575

the Haskell Ranch. Nero (1956b) reported the average size of 17 territories in Wisconsin to be 3,550 sq ft. Average size, however, increased from 1947 to 1953 as the breeding population declined. Linford (1935) found much larger territories in Utah (average: 31,603 sq ft) but his birds gathered most of their food on the territories whereas Nero's birds did not.

There is thus a general correlation between the size of Redwing territories and the proportion of food obtained within the confines of the territory. However, it is doubtful whether food *per se* is the *proximate* factor by which territory size is regulated. The available evidence suggests that many bird species use features of vegetative physiognomy as their major cues in evaluating environmental suitability (Lack 1940), though the mechanisms by which



this is accomplished are unknown. That this is also the case with the Redwing is suggested by change in territory size in response to stage of vegetative succession (Martin 1960) and by the response to burning of the marshes. The exceptionally complete burn at the East Park Reservoir marsh in 1960 left large areas devoid of emergent vegetation until the new growth appeared. In these areas the Redwing territories were initially several times larger than in 1959, but as the vegetation grew, additional birds inserted themselves, and territories became smaller (Table 9) though never as small as in the previous year.

TABLE 9. Size of Red-winged Blackbird territories on burned marshes, East Park Reservoir, 1960.

Roadside study area	Number of territories	Average size (sq. ft.)
April 29.....	3	26,500
May 15.....	4	19,875
North study area		
April 29.....	2	32,300
May 15.....	4	16,150

Food for the young may be gathered either on the territory or adjacent to it. The cattail areas at the south end of the main marsh at the East Park Reservoir were surrounded with sedge meadows from which much of the food was gathered, but often the birds flew across the road to an alfalfa field. Much food was gathered within the territory among centrally located territories. Where oak parkland adjoined the marsh, the birds frequently foraged among the grass and trees.

Several types of evidence suggest that territorial behavior is limiting breeding density on the study areas. Firstly, territorial challenges by newly arriving males are common much of the breeding season, and they may be vigorous and prolonged. For example, on April 19, 1959, I watched an intruding male, easily identified by his more orange epaulets, attempting to take over a territory for more than an hour. When first discovered at 0730, the intruder was submissive to the resident male, but by 0745 he began to give full song spreads on perches and in flight over the territory and began diving at the resident male, each time evoking a chase. By 0800 he was at times flying over the territory unchallenged by the resident, and his attacks were intensified so that he hit the resident while diving. By 0824 he was displaying to females flying over the territory, and had apparently succeeded in taking over, but at 0836 the resident male became more vigorous in his defense of the territory and the intruder left. He returned again at 0842 but was immediately chased by the resident and left again. By 0900 I had seen no further sign of him nor did he reappear later.

On April 30 at one of the isolated cattail patches I observed another unsuccessful territorial challenge which lasted intermittently from 1330 to 1445. The

challenger held a nearby territory without cattails or other emergent vegetation which could support a nest. These are extreme cases, but the frequency of occurrence of territorial challenging by both sexes suggests that more birds would settle if they could. Nero (1956b) has reported at length on this aspect of territoriality in Wisconsin Redwings.

A second line of evidence is provided by the behavior of birds which have been trapped and banded. Twice, males which I had trapped fought to regain their territories from new males even though the duration of their confinement could not have been longer than a few hours. Nero (1956b) reported this also.

To test the matter further, the males from an area at the East Park Reservoir, containing 7 territories, were shot on May 8, leaving only one color-banded male whose vocalizations were being studied. The following morning, this male and a bird from across the stream had expanded their territories to include most of the vacated area, and though this was late in the season, there were five replacements by May 17 (Fig. 11). Since this was later in the season than any new areas were occupied in this region, it is likely

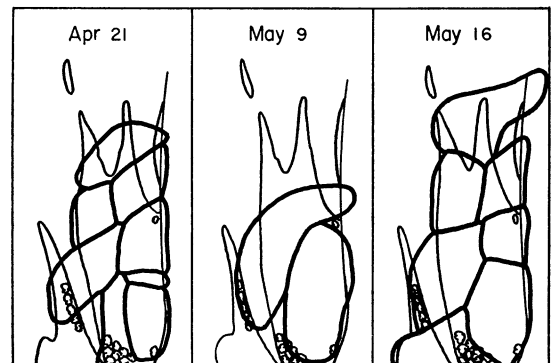


FIG. 11. Repopulation of a small marsh by male Redwings following shooting of the established territorial males. East Park Reservoir, 1959.

that the invading individuals were birds which had been prevented from breeding by the prior occupation of all territories by other males.

On the basis of these preliminary results, the experiments were continued in 1960. A section of the Haskell Ranch marsh and another area at the East Park Reservoir were selected as removal sites. Males were removed from the Haskell Ranch marsh eight times and from the East Park Reservoir five times (Table 10). At both sites first-year males, which do not normally hold territories, did so as removals continued. All such birds had functional testes. How long they would have been able to defend their territories successfully is not known. One of the replacement adult males, on the other hand, had non-functional testes.

Observations following shooting demonstrated that replacement was often quite rapid. Dr. Leopold observed the Haskell Ranch area on the morning of April 12, the day following the first shooting, and

TABLE 10. Red-winged Blackbird removal experiments, 1960.

HASKELL RANCH		EAST PARK RESERVOIR	
Date	Number of ♂♂ shot*	Date	Number of ♂♂ shot
April 11	5	April 11	2
April 20	5	April 28	3
April 23	3	May 7	3 (1)
April 28	2 (1)	May 15	3 (1)
May 8	3	June 8	2
May 15	3 (1)		
May 30	3 (1)		
June 16	2		

\* Figures in parentheses indicate first-year males.

found all territories reoccupied. Several times I observed a replacement to occur within an hour and once within fifteen minutes. Particularly during April, when activity is at its peak, it would probably be possible to get daily replacement, so that the removals actually made give no idea of the number of birds which could be taken from a marsh during a season, nor what the seasonal pattern of time required for replacement might be.

Ever since the publication of Howard's (1920) book, territoriality has attracted considerable attention, but progress has not been commensurate with the effort expended (Hinde 1956). Data from blackbirds suggest some new avenues of approach. The role of territorial behavior in limiting the density of breeding birds, strongly indicated for the Redwing, should be tested for more species. Howard believed that density was limited by territorial behavior, but his view has been challenged by Lack (1954). Stewart & Aldrich (1951) and Hensley & Cope (1951) observed repopulation following shooting in coniferous forest insectivorous birds, but their experiments were performed during a spruce budworm outbreak and the results may not be generalizable.

The role of different factors in influencing territory size may profitably be explored by studying variability in territory size in different habitats. Some species, such as the Redwing, change their spacing system with habitat, providing clues to its significance. The value of comparative studies of closely related species has been largely ignored, but often such species differ strikingly in their territorial behavior. This aspect of blackbird spacing will be discussed following the presentation of data on the Tricolored Blackbird.

**Mating System.** It is well known that the Redwing is polygynous, the females maintaining territories within the larger territories of the males. Females regularly breed when they are one year old though it is not known if they always do so. Males do not normally breed until two years of age, though they have been observed holding territories (Beer & Tibbits 1950) and, rarely, breeding (Wright & Wright 1944, Nero 1956b) when one year old. First-year males, some of them reproductively ma-

ture, were common around the marshes and attempted to occupy territories. Some held small areas for short periods of time, but I had no evidence that they ever succeeded in fertilizing any females, nor is it known whether any of the first-year males which held territories after removals copulated with females.

Determining the number of males on a given marsh is a relatively simple task, but females are much more difficult to count. Counting all the nests in the area only gives a rough estimate of the number of females because of the many repeat nests following failure. Consequently, I was able to determine the actual sex ratios in only a small portion of the Redwings I studied. Precise figures are also rare in the literature. On my study areas the number of females per male has ranged from one to six. My data and those from the literature are given in Table 11.

TABLE 11. Red-winged Blackbird sex ratios.

Source	Number of ♂♂	Number of ♀♀	Average number ♀♀:♂
Smith (1943).....	23	37	1.61
"	40	110	2.75
"	42-46	115-117	2.50-2.78
Nero (1956).....	25	49	1.96
This study:			
E. Pk. Res....	29	108	3.72
Haskell R.....	13	37	2.84

They suggest the possibility of geographical variation in sex ratio, but in the absence of data on temporal variation nothing definite can be said.

Male Redwings take no part in nest building or incubation. Most of them do not feed the nestlings either, but I observed one male at the Haskell Ranch and one at the East Park Reservoir regularly bringing food to the nestlings. Also, one male on Brooks Island was seen with food in his bill. Once the young fledge, however, the males regularly feed them.

**Clutch Size and Nesting Success.** Reliable information on clutch size is available only for 1960 (Table 12). No clutches of five or six were found at the East Park Reservoir in 1959, a drier year, suggesting that there might be some yearly variation in clutch size, but more data are needed to confirm this. Nesting success was also better in the wetter spring of 1960 (Table 13).

**Feeding Behavior of Adults.** During the breeding season, adult Redwings and Tricoloreds utilize a wide variety of animal and vegetable foods. The use of the bill in gaping in almost all feeding situations makes it possible for these birds to utilize effectively food resources unavailable to species which do not gape (Beecher 1951). Gaping appeared in my hand-reared Tricoloreds by the time they were two weeks old. The effectiveness of gaping is most striking when the birds are feeding in shallow streams. I have observed Redwings turning over stones weighing as much as

TABLE 12. Clutch-size in the Red-winged Blackbird.

Location	Year	No. OF EGGS PER CLUTCH					Mean clutch size
		2	3	4	5	6	
Haskell Ranch.....	1960	1	9	10	—	—	3.45
E. Park Reservoir....	1960	2	23	55	4	1	3.75

TABLE 13. Fledging success of Red-winged Blackbirds, East Park Reservoir.\*

Year	Number of nests	Average number of young per nest
1959.....	16	2.31
1960.....	12	3.00

\* Note: Estimates based upon nests fledging at least one nestling; nestling counted as fledged if it reached at least an age of one week.

45 grams either by inserting the bill underneath the stone and gaping it up and away from the body with the upper mandible, or by pushing it toward the body with the lower mandible. This exposes the plecopteran and dipteran larvae beneath the rocks. Excrement of grazing animals is similarly handled.

Floating debris among stones and aquatic vegetation is frequently moved by a sideways motion of the head with the bill fully gaped. This same movement is also used when feeding in grassland where it is used to move dead material from the ground surface. It has also been reported to be used to extract spittle bugs from their froth (Macklin 1958). Regular gaping movements are also used in cattails and in grassland, the bill being inserted into the vegetation and then gaped to expose any insects and seeds within. Gaping is also used when the adults are feeding among the foliage of trees, but much foliage gleaning is achieved by merely searching from leaf clump to leaf clump without any gaping movements, and the same holds true for grassland feeding. Redwings have been reported splitting open dead ragweed stalks in the winter, thereby exposing pupae of *Epiblema strenuata* (Fischer 1953). In all gapers the skull morphology is modified to permit them to see straight ahead between the widely spread mandibles (Lorenz 1949).

In calm weather, the adults, especially the males, successfully catch insects on the wing, though they are definitely less adept than flycatchers or waxwings. On warm April and May mornings at Jewel Lake, when emerging dragonflies ascended from the cattails in their first flights, male Redwings were able to catch a large percentage of them, but if the bird missed on its first try, the insect was subsequently able to outmaneuver it, although waxwings still readily caught them at this stage. Both Redwings and Yellow-headed blackbirds utilize emerging dragonflies heavily in other areas also (Kennedy 1950).

In Californian annual grassland, filarees (*Erodium botrys* and *E. cicutarium*) are among the most

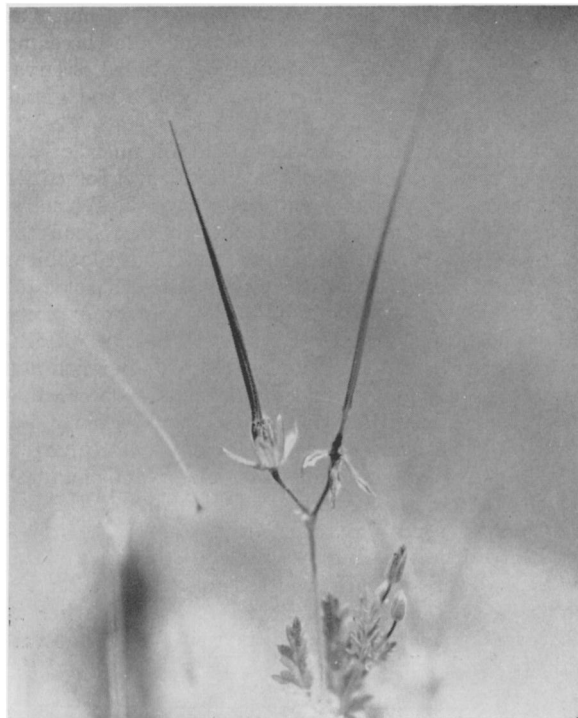


FIG. 12. Stripping of *Erodium* seeds by Redwings; seed on the right has been stripped.

abundant plants. When the seeds ripened in mid-April at the East Park Reservoir, the Redwings stripped the plants (Fig. 12), attacking the seeds from the base and peeling them off. In 1959, nearly all *Erodium* plants around the reservoir had been completely stripped by early May.

## 2. THE TRICOLORED BLACKBIRD

**Non-breeding Period.** Outside the breeding season, Tricolored Blackbirds feed in the same situations as Redwings and mixed flocks are common. Roosts are located in the same types of habitat and are often shared between the two species. Tricolors roost later in the evening than Redwings, and, in my experience, the sexes do not segregate at any time. As in the Redwing, there is a mass exodus from the Sacramento Valley in the late winter, birds being absent from large areas for several months. Since the Tricolor is not known to occur in large numbers outside the Great Valley of California, it is likely that the bulk of the population moves to the San Joaquin Valley where personnel of the U. S. Public Health Service, working on encephalitis control, observe them in enormous numbers.

**Initiation of Breeding.** The Tricolored Blackbird has long been known to be highly colonial when breeding (Heermann 1853, Mailliard 1900, 1914, Tyler 1907, Dawson 1923, Neff 1937, Lack & Emlen 1939), but little was known about the organization and operation of these colonies. In particular, no one had seen the events leading up to and culminating in the starting of a colony, nor had individuals been observed closely from blinds. It was one of the ma-

major objectives of this study to find out as much as possible about the organization of the breeding colonies of this species. I obtained detailed observations at the East Park Reservoir in 1959, and at the Haskell Ranch in 1960.

There is no other marsh within 30 miles of the East Park Reservoir, so that birds are forced to roost close to where they will nest. By mid-February, 1959, the reservoir had filled enough to reflood the marshes and several thousand Tricolored Blackbirds were roosting there. During mid-March some of the males began to display and preliminary exploration of cattails began. Birds flew to the cattails, sang, preened, and then suddenly shifted position and repeated the performance. From an observation tower erected April 5, however, I could clearly tell that while most males sang, few displayed. On April 15 only five or six males out of several hundred showed any signs of territorial behavior, and I had seen only one nest-invitation display.

The birds came to roost progressively later (Fig. 13) following the time of sunset, but after the first week of April they began to arrive earlier in the evening and spent more time singing in the cattails in the morning (Fig. 14). However, most of the

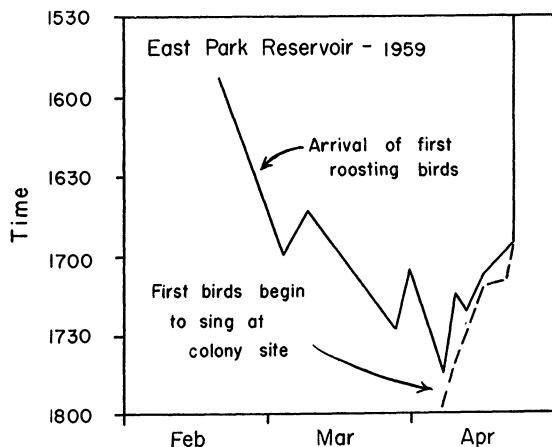


FIG. 13. Roosting of Tricolored Blackbirds, East Park Reservoir, 1959.

day was still spent, and most food was gathered, 10-15 miles from the roosting area.

Dense concentrations of flocks of birds at different loci in the marsh, first observed April 10, was quite conspicuous the subsequent week. Suddenly all the resting birds would fly up and gather in one spot, some of them landing, others fluttering above the vegetation. After a few minutes they dispersed again, only to repeat the performance at another spot a few minutes later. This continued through the first few days of colony establishment, and was noted at several other colonies during the nest-building period. At no time was I able to detect any change in the environment which might have triggered such behavior, and the latter may simply be a part of a colony-site investigation ritual.

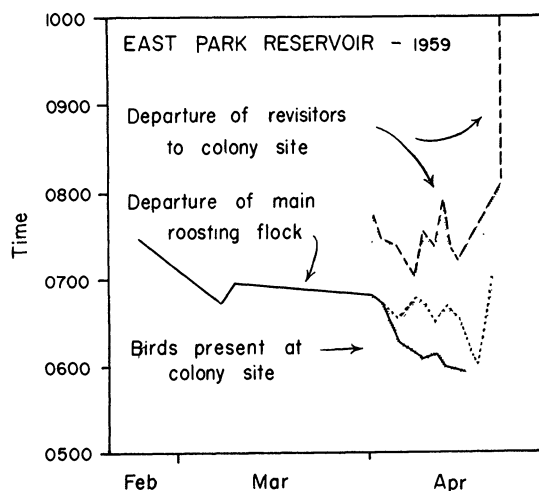


FIG. 14. Initiation of breeding among Tricolored Blackbirds at the East Park Reservoir, 1959.

Early in the morning of April 12, I first observed females carrying nesting material in their bills for a few minutes before dropping it. They were observed to do this again on April 14 and April 16, but it was not seen thereafter until true nest building started. In fact, evening activity of Tricolors around the marsh was generally reduced from April 16 to April 19, giving no sign of impending events.

On April 20 the birds remained all day. Hundreds constantly streamed back and forth from the cattails to the grassland feeding areas surrounding the reservoir. Displaying birds in the cattails shifted sites, formed dense concentrations, flew off to feed and returned. At times the whole marsh was deserted, all birds being scattered on the adjacent hill-sides, and then a few minutes later hundreds would stream back into the cattails. At 1300 I observed the first females carrying nesting material and early the next morning many were building vigorously. Though many birds immediately settled on territories others shifted from place to place in the cattails through most of April 22, but by April 21 most of the males were singing from platforms of bent cattails low in the vegetation. Often loud choruses came from a seemingly empty marsh.

By morning of April 22 nest building was intense in all areas which I could observe closely, and I saw the first copulation at 10:30. By afternoon copulations were occurring everywhere and many nests were already being lined. Both nest building and copulations continued all the next day and in the morning of April 24 I found the first eggs. By April 28 nest building was nearly over, but copulations continued everywhere. Many females were then incubating clutches of three eggs. By April 29 the males had nearly deserted the marsh and I saw only two females still carrying nesting material. I saw the last copulation April 30, after which there was no activity other than the feeding flights of incubating



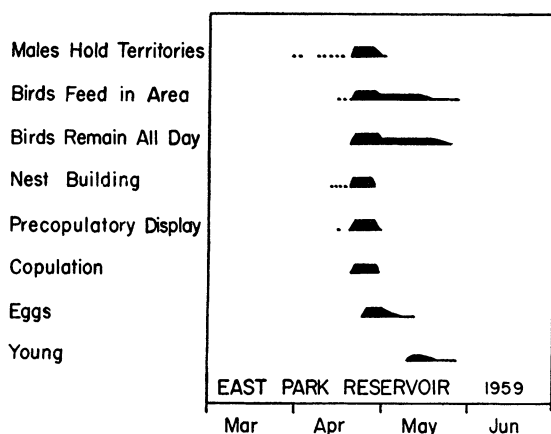


FIG. 15. Breeding chronology of Tricolored Blackbirds, East Park Reservoir, 1959.

females. The major features of timing of events in this colony are shown in Fig. 15.

In many areas in the valley Tricolors do not roost at the site prior to colony establishment. At the Haskell Ranch in 1960, small flocks occasionally flew over the marsh, but no birds were roosting in the breeding marsh as late as April 11. Nonetheless, thousands of birds were building nests April 19. Other observers have noticed active colonies in areas which were devoid of birds a few days earlier (Neff 1937), although in most cases early morning activity would not have been noticed.

**Nesting Habitat.** In addition to cattails and other emergent vegetation, Tricolor colonies are situated in a number of other vegetation types. Of the twenty-five colonies I have studied, 16 have been in cattails and other emergent vegetation, four in grain fields, one in alfalfa, one in a mustard patch, one in a safflower field, one in thistles along an irrigation ditch, and one in trees along a river. Of 236 colonies found by Neff (1937), mostly in the Sacramento and San Joaquin valleys, from 1932 through 1936, 224 were in cattails or other emergent vegetation. These differences may result, at least in part, from differences in searching habits of the different observers, but in most areas draining has been much more complete than it was when Neff made his studies. The favorable rice-growing areas are now virtually devoid of marshes, so that there is reason to regard at least some of the difference as real.

**Time of Breeding.** Extreme synchrony, as found at the East Park Reservoir, is characteristic of most colonies of Tricolored Blackbirds (Tables 14 and 15). Even in colonies as large as 50,000 to 100,000 nests, all eggs may be laid within one week. The number of nests started daily in a large colony (Haskell Ranch) and a small colony (Lake Isabella) are shown in Figs. 16 and 17. On the other hand, some colonies, such as the one at the Capitol Outing Club in 1959 and 1960, grow through the addition of new birds on their peripheries so that, while any given area is uniform, different parts of the colony vary. For example, at the Capitol Outing Club on June 5, 1959, young were being fed in nests in the northeast

TABLE 14. Time of events in Tricolored Blackbird colonies—Spring 1959.

Colony	Number of nests	Nest-building	Egg-laying	Incubation	Feeding young
E. Park Res. ....	1,500	Apr. 21-Apr. 28	Apr. 25-May 1	Apr. 28-May 11	May 10-May 20
Haskell Ranch. ....	15,000	Apr. 28-May 6	Apr. 30-May 9	May 2-May 22	May 14-June 5
Mustard Patch. ....	14,000	May 1-May 8	May 5-May 12	May 7-May 25	May 19-June 10
Marysville. ....	40,000	May 3-May 10	May 6-May 13	May 8-May 31	May 20-June 14
Cap. Outing C. ....	80,000	May 8-June 9	May 11-June 12	May 14-June 16	May 28-June 28
Alfalfa Field. ....	50,000	May 9-May 15	May 13-May 18	May 16-May 30	May 28-June 15
County Line. ....	75,000	May 15-May 21	May 18-May 24	May 20-June 6	June 3-June 20

TABLE 15. Time of events in Tricolored Blackbird colonies, 1960.

Colony	Number of nests	Nest-building	Egg-laying	Incubation	Feeding young
Haskell Ranch-A. ....	1,500	Apr. 18-Apr. 23	Apr. 22-Apr. 25	Apr. 25-?	destroyed
E. Park Res.-A. ....	50	Apr. 21-Apr. 25	Apr. 25-Apr. 29	Apr. 28-May 9	May 7-May 29
Marysville. ....	800	Apr. 29-May 4	May 2-May 6	May 5-?	destroyed
Madison. ....	70,000	May 4-June 13	May 8-June 17	May 11-June 29	May 22-July 13
Buttes. ....	6,000	May 10-May 15	May 14-May 19	May 17-?	destroyed
Gridley. ....	35,000	May 11-June 14	May 15-June 17	May 18-June 28	May 30-July 15
County Line. ....	4,000	May 17-May 25	May 20-May 29	May 23-June 9	June 2-June 30
E. Park Res.-B. ....	600	May 17-May 22	May 21-May 25	May 24-June 6	destroyed
Riego Road-A. ....	500	May 17-June 3	May 21-June 7	May 24-June 18	June 4-July 5
Cap. Outing C. ....	100,000	May 17-June 16	May 21-June 19	May 24-June 25	June 5-July 10
Haskell Ranch-B. ....	15,000	May 23-June 25	May 27-June 29	May 30-July 11	June 10-July 28
Safflower. ....	20,000	May 28-June 1	June 1-June 5	June 4-June 16	June 15-July 3
Riego Road-B. ....	30,000	May 28-June 1	June 1-June 6	June 4-June 17	June 15-July 4

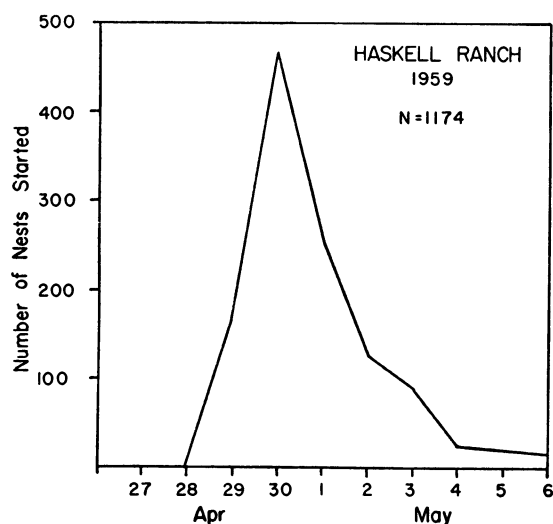


FIG. 16. Breeding synchrony in a large colony of Tricolored Blackbirds.

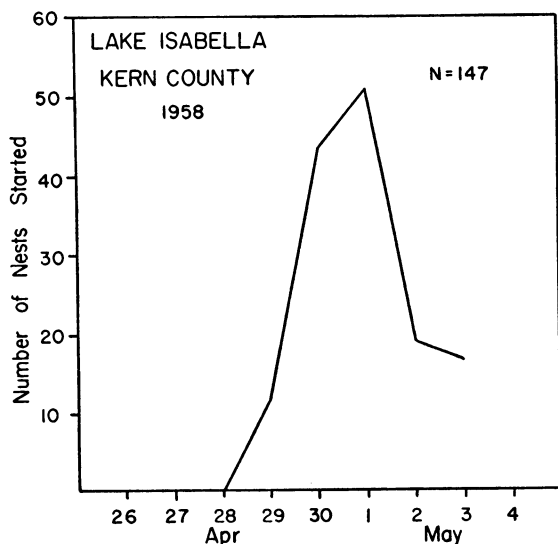


FIG. 17. Breeding synchrony in a small colony of Tricolored Blackbirds.

part of the colony, farther southwest all females were incubating, and at the extreme corner of the colony nests were still being constructed. This type of colony organization has been noted before (Tyler 1907, Dawson 1923, Lack & Emlen 1939), and Dr. Leopold has observed it in previous years at the Haskell Ranch.

Occasionally shortage of nest sites forces still a third form of synchrony not heretofore reported. In a colony found May 4, 1958, in Kern County, nests with eggs, others with nestlings, and still others with fledged young were mixed throughout the colony situated in a small patch of cattails growing in a stock-watering pond, which was the only marsh for miles. Apparently successive waves of birds moved

into the cattails to establish territories as soon as the preceding males vacated theirs. Two waves of birds established themselves in the Madison colony in 1960, and nests in all stages of construction and occupation characterized the two autumnal colonies studied in 1959 (Orians 1960).

Time of breeding varies considerably within small areas. Starting dates in colonies I have observed have ranged from April 1 to May 28, and eggs have been reported in the literature from April 1 to June 17 (Bent 1958). Basically, three major types of areas are utilized for breeding; the grazing lands and dry farming areas of the foothills, irrigated agricultural areas in the valley with little or no rice, and the rice-growing areas. In both 1959 and 1960, breeding began earliest in the foothills and latest in the rice country (Table 16) even when one includes the nesting at the East Park Reservoir in 1960, which was greatly delayed by burning. Early breeding in the foothills, also reported by Dickey & van Rossem (1922), occurs in spite of the fact that spring temperatures are cooler in the foothills than in the valley. It is adaptive because in non-irrigated country the vegetation dries up in May with the termination of the rains. However, before planting time in late April, the rice fields are dry and barren. After being reworked and fertilized, they are flooded with about eight inches of water and seeded from the air. To discourage other grasses from invading, the water is maintained at this depth until the rice has sprouted some 18 days later. When this occurs, the water level

TABLE 16. Time of breeding in the Tricolored Blackbird.

Year	Habitat	Number of colonies	Range of starting dates	Mean starting date
1958.....	Foothills	5	Apr. 1-Apr. 30	Apr. 20
1959.....	Foothills	1	April 21	Apr. 21
1960.....	Foothills	2	Apr. 21-May 17	May 4
1959.....	Valley cropland (no rice)	2	Apr. 28-May 3	May 1
1960.....	Valley cropland	4	Apr. 18-May 23	May 6
1959.....	Rice country	4	May 1-May 15	May 8
1960.....	Rice country	7	May 10-May 28	May 17

is lowered until only 1-2 inches remain. At this time adult blackbirds are able to wade through the shallow water or hop from clod to clod, gathering the insects which by then are becoming more common. Before this time the rice fields could not support Tricolor colonies.

*Territory.* Territory sizes in dense Tricolor colonies are difficult to measure accurately, but by estimating distances between neighboring males I have determined that territories are usually 35 sq ft or less in dense vegetation although they may be larger in less suitable cover. The area is defended without aerial displays from a low platform of bent cattails. The tops of the vegetation form neutral ground over which prospecting males and females move without being attacked. It is only when an intruding male actually moves lower down into

the vegetation that he is chased. The male defends his territory only for that week when the females are nest building and actively soliciting copulation. Once the clutches are complete he leaves and may not visit the territory again until the young hatch.

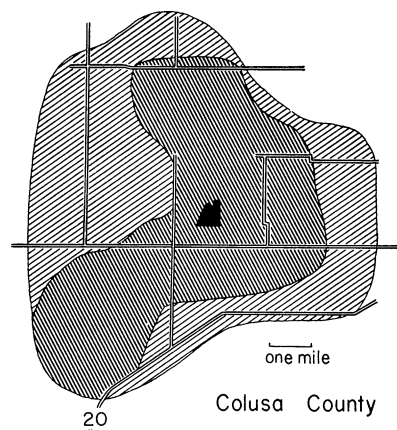
To support the food needs of thousands of young birds, a large area must be exploited by the adults and this area forms the ecologically significant territory. Figs. 18 and 19 show the pattern of utilization around the East Park Reservoir and the Marysville and Colusa colonies in 1959. At these colonies, birds travelled up to 4 miles from the colony site and more than 30 sq mi of land were exploited for food. At the Marysville colony, conditions were excellent for observing changes in feeding pattern during the nesting period.

Details of the temporal pattern of environmental utilization are given in the thesis manuscript deposited in the library of the University of California. The general picture which emerges from these observations is that Tricolors react quickly to any changes in the surrounding environment which make food supplies more readily available. As soon as pastures were flooded or a crop cut or raked, thousands of birds descended upon the newly exposed insect supply. The source of food is apparently communicated to others by the direction from which incoming birds approach the colony. I observed no spe-

● Colony site    ▨ Heavy Use    ▩ Light Use



FIG. 18. Feeding grounds of Tricolored Blackbirds during nest building and incubation periods at the East Park Reservoir, 1959.



● Colony Site    ▨ Heavy Use    ▩ Light Use

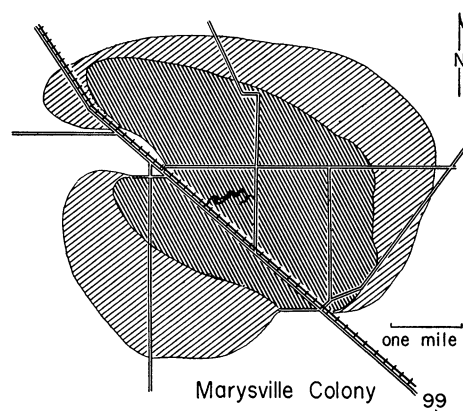


FIG. 19. Feeding grounds of Tricolored Blackbirds at the Colusa and Marysville colonies, 1959.

cial behavior which might have assisted with this, but communication was nonetheless efficient.

**Mating System.** As in the Redwing, the males do not breed until their second year, but at least some females do so when they are one year old. Two females banded as nestlings at the East Park Reservoir in 1958 were among the breeders in 1959. Yearling males regularly establish territories in the breeding colonies, but they are crowded into the less desirable sites. At the Haskell Ranch in 1960, three yearling males defended territories for several days around my observation blind. They gave the full complement of reproductive displays and vocalizations, and successfully evicted prospecting adult males. One of the yearlings attracted a female that started building a nest, but she stopped when it was half completed. I saw no first-year males copulating with females, but cannot assert that they never do. In contrast, Lack & Emlen (1939) reported that first-year males did not hold territories but rather dashed in for attempted copulations. Since I did not observe first-year males

holding territories until I watched closely from blinds erected within the colonies, perhaps their failure to see this is a byproduct of their observing from a distance.

Sex ratios are difficult to determine accurately in dense colonies, but my observations and those of Gerald Collier suggest that normally there are only two females per male, rarely more. In many cases there is only one nest constructed in an area defended by one male. To determine the breeding sex ratio requires hundreds of marked birds, something which no one has yet achieved. Lack & Emlen (1939) closely observed three males, one of which had two females, the other two had three, but little can be said from such a small sample. They also estimated a ratio of 47 ♂♂ : 100 ♀♀ in birds coming in to feed the young. Even assuming this estimate was accurate, it cannot be interpreted definitely until the relative feeding rates of males and females are known. Estimates are also complicated by the presence, for short periods of time, of more females within the territory of one male than actually complete nests. The mechanisms by which the sex ratio in a colony is determined are unknown. Females are not aggressive toward each other as female Redwings are, but the possibility of subtle behavioral interactions between females cannot be excluded because they do have a special call which is given when approaching and leaving the nest.

Nests are built by the females only. Although males often manipulate nest material in nest-site demonstration displays, I have only once seen a male carry nest material any distance. The nest normally is completed in four days or less. Materials used are similar to those utilized by the Redwing but Tricoloreds usually line the nest with green grass while Redwings use dry grass. Most of the material for the nest is gathered on the marsh, but at the lining stage the females may travel for some distance to a good grassy area to gather the fine green lining material.

Incubation is performed by the females alone. The males leave the marsh during the day at this time, returning at night to roost, but not necessarily roosting on their territories or even within the confines of the colony. Incubation takes 11-12 days (Emlen 1941. Confirmed by my studies). During the incubation period, the females take long feeding flights several times each day, there always being a mass exodus the first thing in the morning and then again late in the afternoon. At the East Park Reservoir on May 1, 1959, there was a mass exodus of females at 0515, the first birds returning at 0607. During the rest of the day small groups regularly flew back and forth from the marsh to the feeding areas. In the afternoon I watched a flock of 200-300 feeding in chamise about one mile northeast of the colony. The flock remained approximately the same size for over an hour but during that time its membership changed several times as new birds joined the flock and others left it and returned to their nests. The unity of the

feeding group was maintained because outgoing birds followed the paths of returning birds.

**Clutch Size.** Estimates of clutch size may easily be made by walking through the colony during the incubation period. Because of inevitable losses prior to the time of counting, such estimates represent the minimum clutch size. For example, Paynter (1941) found an average clutch size of 2.38 in the Herring Gull (*Larus argentatus*) whereas histologic examination of the ovaries shows that invariably three eggs are ovulated (Davis 1942). During this study I made clutch size determinations at six colonies. Omitting rare clutches of 1, which are almost certainly incomplete, estimates ranged from 3.01 to 3.44 (Table 17). It is of interest that all three 1960 determinations are larger than the 1959 ones. Emlen (1941) found a mean clutch size of 3.6 eggs in 141 nests, a

TABLE 17. Clutch-size in the Tricolored Blackbird.\*

Locality	Date	NO. OF EGGS PER CLUTCH					Mean clutch size
		2	3	4	5	6	
North Colony, E. Park Res.....	4/29/59	5	34	23	—	—	3.29
Main Colony, E. Park Res.....	5/ 2/59	32	99	34	—	—	3.01
Main Colony, E. Park Res.....	5/29/60	12	93	97	2	—	3.44
Haskell Ranch.....	5/13/59	164	715	259	2	1	3.09
Haskell Ranch.....	4/27/60	13	77	56	—	—	3.33
Marysville.....	5/20/59	56	147	89	—	—	3.11
Marysville.....	5/ 8/60	7	78	74	—	—	3.42

\* .Note: rare clutches of 1 are omitted.

value larger than any I found, but the data are not sufficient to establish annual variations in clutch size. Autumnal clutch size was similar to that of spring (Oranis 1960). Clutches of 5 or more may represent contributions from more than one female, but they are so infrequent that they do not appreciably influence mean values.

**Nesting Success.** During my studies I have observed nest failures of three main types. At the Marysville colony on May 30, 1959, when the oldest young were about 10 days old, I visited hundreds of nests. In only three nests were there three young older than one week, and in each of these nests one of the nestlings was considerably smaller than the other two. Even in nests with only two young one week old or older, one was normally a runt. There were hundreds of dead young beneath the nests. Neff (1937) also reported the death of many of the smallest of the nestlings, finding that this percentage was greater later in the season than earlier. He attributed this to the great heat of the marshes in June which caused incubation to be therefore less synchronous. Since feeding conditions are probably poorer later in the season, the youngest nestlings might have died of starvation whether or not hatching was asynchronous. Starvation of nestlings was also widespread in the autumnal colonies (Oranis 1960).



A second form of nest failure is desertion. At the East Park Reservoir in 1959, mass desertion began on May 2. At that time I found only 188 nests with warm eggs out of 491 nests checked. Two Scrub Jays (*Aphelocoma coerulescens*) were seen flying from the colony with eggs in their bills, but they could not have accounted for more than a fraction of the eggs destroyed and were most likely taking already deserted eggs. By May 7, there were no more than 15 active nests where there had been over 1,000 one week earlier. On May 15, only eight females were feeding young. Neff (1937) also noted a number of colonies which deserted full clutches of eggs with no obvious cause. He also noted desertions resulting from wind damage to the cattails. At the East Park Reservoir there was no such disturbance, and nests and eggs were intact when deserted. Mass desertion also occurs in other colonial species (Brown 1958).

The spring of 1959 was unusually dry. Less than one inch of rain fell in April and only a trace in May. Consequently, the growth of annual grasses around the reservoir was exceedingly poor, and by mid-April the hills were already turning brown. No measurements of insect populations were made but they were surely far below normal. Possibly the birds made an assessment of the food available in the surrounding feeding areas by means of the feeding flights to be described, and nesting was abandoned because of the inadequacy of the food resources. Mass desertion of full clutches also occurred in the autumnal colonies in 1959, where it again could be correlated with inadequate food supplies in the surrounding areas. The reasons for believing that an abundant and readily available food supply is especially critical for colonial species will be dealt with later.

A third form of nest failure is loss to predators. I have not witnessed nest destruction in this species, but several colonies have been destroyed within a few days. In 1959, a small colony at the East Park Reservoir north of the main marsh was destroyed at the same time the main colony deserted. On May 7 all the nests were intact but empty. In 1960 both the Haskell Ranch colony and the Marysville colony were destroyed. Bits of eggshell or yolk stains were found in some of the nests, but in most of them there was no sign of disturbance. Mass destruction of nests has also been reported by Mailliard (1900), Neff (1937) and Lack & Emlen (1939). Various predators have been accused, among them snakes, hawks, owls, crows, mink and raccoons. I have seen both Scrub Jays and Yellow-billed Magpies (*Pica nuttalli*) taking eggs from colonies, but the number of birds present could have taken but a small fraction of the eggs and young lost. It is more likely to have been snakes (*Thamnophis* and *Pituophis*), which are able to climb cattails to the nests, are common in the marshes at this time of year, and have been seen robbing Redwing nests.

*Feeding Behavior of Adults.* Food and feeding of adult Tricolors appears, without examination of

stomach contents, to be similar to that of the Redwing, but their social organization results in their feeding in different areas even when the two species are nesting in the same marsh. A flock of Tricolors feeding in a grassland or other uniform place progresses by the flight of the rear birds over the rest of the flock to the front. A given individual usually spends 25-40 seconds in one spot before flying to the front of the flock. Thus, the flock smoothly progresses across the ground even though its individual members move only twice per minute. In rice fields and flooded pastures no such uniform pattern of flock movement is possible and individuals move more at random with respect to each other.

*Colony-size Limitation.* Evidence has been presented for the Redwing indicating that territorial behavior limits the density of the breeding population. In the Tricolored Blackbird, territory size varies little from colony to colony unless the vegetation prevents the nests from being as close together as they normally are in undisturbed cattails. Furthermore, except in rare instances, the total nesting space is only partly utilized by the colony, so that territorial behavior would be ineffective in preventing additional birds from settling to breed. Nevertheless, when enormous numbers of individuals must be fed from a fixed spot, the relationship between colony size and food supply is critical because a colony too large for the surrounding environmental resources might be a complete failure. Certain evidence strongly indicates that there is some mechanism of colony-size adjustment, although its details are yet to be determined.

Firstly, colony size is correlated with the suitability of the surrounding environment. In the grazing lands of the foothills I have never found colonies larger than a few thousand nests. The agricultural country of the valley supports larger colonies, the largest being in the rice-growing areas where rich insect supplies are produced in the shallow water (Table 18).

TABLE 18. Tricolored Blackbird colony sizes.

Habitat type	NUMBER OF COLONIES WITH		
	<1,000 nests	1,000-10,000 nests	>10,000 nests
Foothills . . . . .	7	2	1
Valley cropland (no rice)	3	2	3
Rice country . . . . .	0	3	7

Secondly, territorial challenges are frequent during the colony-establishment period. Territories are often taken over by a new male while the resident is absent for a few minutes feeding, but such intruders are quickly expelled by the owners when they return. At any time during the colony-establishment period there are many unsettled birds which continually move back and forth over the colony looking for unoccupied territories. In fact, from a distance it appears that most birds are wandering aimlessly

through the colony area. Actually, the established males are all singing and displaying low in the vegetation, and the movements are almost entirely composed of unestablished birds. This is not correlated with availability of territory sites because it is equally true whether there is a shortage of nest sites or whether only a small portion of the marsh is occupied. Apparently intruders attempt only to substitute themselves for already established birds rather than to increase the colony size.

Thirdly, in all colonies observed at the time of territory establishment, the number of birds present was always greatly in excess of the number which actually remained to breed. At the East Park Reservoir in 1959, about twice as many birds were present the first few days as bred. At the Haskell Ranch in 1959, about three or four times as many birds as nested were present the first few days. Some of this overflow may have moved to the Marysville Colony about eight miles to the northeast, but even here the colony at its maximum extended nearly one-fourth mile farther along the drainage channel than the limit of actual nests. In none of these cases was there a shortage of nesting sites.

The evidence suggests that during the first few days of colony establishment an assessment is made of the food supply available in the surrounding environment by means of mass feeding flights. During this period the birds make what appears to be an excessive number of feeding trips to the surrounding country, and by watching from a blind it can be determined that unestablished birds make far more trips than established ones. These mass feeding flights form the most conspicuous activity around colonies at this time. At the East Park Reservoir in 1959, I observed 17 mass feeding flights, involving most of the birds in the colony, in 6.5 hrs on April 20, the day the colony started. On April 21 I observed 14 such flights in 4.75 hrs and on April 22, 5 in 2.25 hrs. This yields an average of 2.7 flights per hour. It seems unlikely that such a rate of feeding is necessary for the adults merely to gather the amount of food they need.

This is simply a special case of the general phenomenon of environmental evaluation among birds. Many species are known to adjust their clutch sizes and/or territory sizes to food supply of the environment, and it is well known that colony size in many colonial species is in some way adjusted to the capacities of the environment to support breeding (see references in Lack 1954). Such an adjustment could be made in the Tricolored Blackbird through the mass feeding flights.

Data for the Redwing and Tricolored Blackbird relative to spacing can be summarized as follows. In the Redwing, territorial behavior strongly limits density, forcing part of the population into less suitable areas and probably totally preventing some individuals from breeding. Fighting over territories begins early and is most severe in areas where territory size is ultimately the smallest. Variability is related to habitat in two ways: (1) The nature of

the nesting vegetation may influence territory size, as was shown following burning. Under undisturbed conditions, however, this is likely to be of minor importance. (2) More important is the nature of the surrounding feeding grounds. Territories are largest where most of the food is obtained on them and smallest where the least food is obtained on them. Territory size is unrelated to the number of females building nests within it, nor is it related to the action of known predators, though this point is less certain.

In the Tricolored Blackbird, territories are uniformly small unless the vegetation is not dense enough to permit such a high concentration of nests. Territorial behavior does not limit density. Instead, the important variable, colony size, changes with environmental conditions, being smallest in the grazing and dry farming areas and largest in the rice growing areas. There is suggestive evidence of a mechanism of colony size limitation.

Therefore, whereas in neither species is there a "food territory" in the classical sense, the spacing within the systems is intimately related to the exploitation of the environment, and the known patterns of variability in territory size can be attributed primarily to it. More data will be needed to clarify the roles of other factors.

#### TIME AND ENERGY BUDGETS

The amount of time and energy which a bird devotes to different activities must inevitably influence its survival and reproductive rates. It follows that there exists for a species in a given environment an optimal time and energy budget. It is of particular theoretical interest to investigate the conditions influential in determining the relative significance of different patterns of time and energy budgeting (Hutchinson 1957, Fisher 1958:47). The general evolutionary trend has been to reduce both the number of gametes produced and the amount of energy devoted to their production. At the same time there have been increases in the energy content per female gamete, and the time and energy devoted to the care of those few offspring produced. It is not surprising that these trends are correlated since giving extended care to offspring is incompatible with producing enormous numbers of them, and production of large gametes is incompatible with production of large numbers of them. Beyond these obvious trends, however, there are many unstudied variations in the time and energy budgets of species producing similar numbers of gametes of approximately equal energy contents.

There are three major ways in which a species can modify its expenditure of time and energy. Firstly, the total energy expenditure may remain approximately the same but its distribution among different activities varied. Secondly, the total energy budget may be increased, and thirdly, it may be decreased. The amount of time spent on reproductive activities may vary in like manner. It is the purpose of this section to present quantitative estimates of

time and energy expenditures in the Redwing and Tricolored Blackbird.

These estimates are of necessity rather crude. Firstly, the lack of adequate physiological data forces me to make assumptions about the energy demands of certain activities which may not be highly accurate. Secondly, the field data are based upon only a few individuals, whereas observations in other areas have shown that the pattern varies geographically. No previous attempt has been made to establish the budgeting of time and energy in natural populations, but Pearson (1954) made an estimate of the daily energy requirement of an Anna Hummingbird (*Calypte anna*). Hence, in spite of the various difficulties involved, crude attempts will nevertheless be ventured because the differences between the two species of blackbirds are so striking and because of their theoretical importance.

Ideally, one should present estimates of the entire annual time and energy budgets but the data do not justify such extended treatment and non-breeding differences appear to be minor. Instead, I have limited the comparison to those features in which the two species differ most strikingly, namely territorial defense and feeding of the young. The slight differences in the time and energy devoted to nest building and egg laying are ignored. These restrictions serve to concentrate attention upon the major differences, in terms of energetics, between the two social systems, preparing the way for a discussion of the evolution of these differences. Since no attempt is made to quantify the entire time and energy budget, it is impossible to express any time and energy expenditures as fractions of the whole. I have therefore expressed them as percentages of energy increase above the resting metabolic level, or as additional hours of time expenditure, as the case may be.

My most complete information on the Redwing is based upon several males studied intensively at Jewel Lake in 1958. During February the males spent about fifteen minutes on the marsh in the morning, defending their territories, after the departure of the main roosting flock. They then left for the day, returning in the evening shortly before the main roosting flock at which time they also engaged in territorial behavior. In March, the time spent on the marsh gradually increased to about 3.5 hrs in the morning, but the evening arrival time did not appreciably change. On the average, about two extra hours were spent on the territories during this month. By the end of the first week of April the birds remained all day and nesting was soon underway. This pattern continued for about two months until nesting was completed, after which the birds again left the area.

Once the males remained all day, about  $\frac{3}{4}$  of their time was spent on the territory; the rest on nearby feeding grounds. From my notes I have determined that about  $\frac{1}{4}$  of the time spent on the territory was occupied with actual defense of the territory, either by means of vocalizations and dis-

plays or through actual chasing and combat (see later).

As females are much more difficult to watch, I do not have comparable quantitative data, but they spend much less time in territory defense than males, and the period of time during which they do so is shorter. Territory defense at Jewel Lake lasted from mid-March until the hatching of the eggs, but during the incubation period the frequency of contacts between females was low as incubating birds stirred from their eggs only when new females arrived on the area. During the period of active territorial defense, I estimated that about  $\frac{1}{8}$  of the female's time is so spent.

Once the young hatch, the pattern of activity suddenly changes for the females, but not for the males, which continue much as before. On the average, a female visits the nest at least once every fifteen minutes with food. Most of her time is spent among

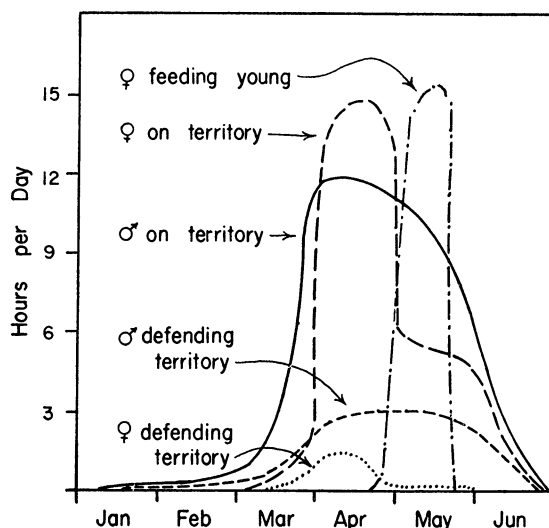


FIG. 20. Time and expenditure during the breeding season by a typical pair of Redwings.

the grass searching for food, only about 1.5% of it being required for flying to and from the nest. The remainder of time is devoted to feeding herself, preening, and resting. An estimate of the time expenditure of a typical male and female Redwing is summarized in Fig. 20.

In the Tricolored Blackbird, the pattern is strikingly different. Prior to the start of nesting almost no time is devoted to activities concerned with breeding, but activity is intense as soon as the colony forms. Since continued observations of individuals in these colonies is so difficult, estimates are based upon group behavior, supplemented by observations of individuals from a blind. Males devote about  $\frac{1}{2}$  of their time to territory establishment and defense during that one week period when nests are built and eggs laid. Thereafter, such activity ceases for the remainder of the breeding period. Since nests are started the first day, females spend almost no

time in aggressive behavior. Once the eggs are laid, all territorial behavior on the part of all birds stops.

During the colony-establishment period considerable energy is devoted to the conspicuous mass feeding flights. About 26 minutes of every hour were devoted to feeding flights, a portion of which apparently forms a part of the environmental assessment of the breeding birds.

During the nestling period, both sexes actively bring food to the young, but in contrast to the Redwing, the major expenditure is in flying from the nest to the feeding area and back again. Since areas up to four miles from the nest are utilized when feeding the young, virtually half of the adults' time must be spent in flight, leaving much less time for gathering food than is available to the Redwing. If as much time were spent on foot by Tricolors, the rate at which food could be delivered would be greatly reduced, and the reproductive rate lower, although this is partially offset by male participation in feeding of the young. Since the clutch size of the Tricolor is only slightly less than that of the Redwing, it is apparent that searching time has been reduced substantially. An estimate of the time expenditure of a typical male and female Tricolor is given in Fig. 21.

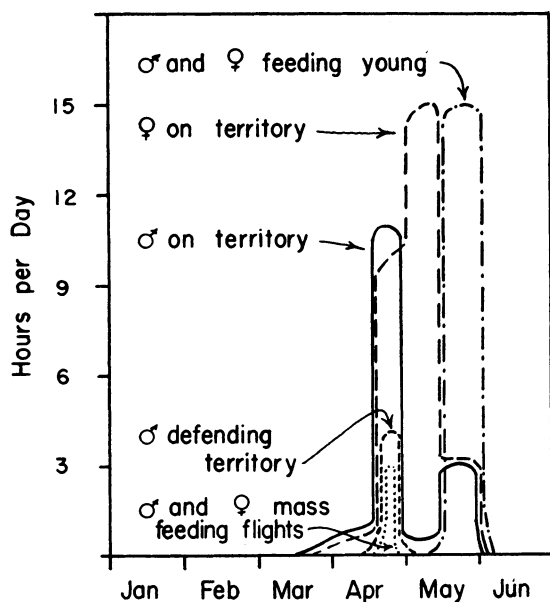


FIG. 21. Time expenditure during the breeding season by a typical pair of Tricolored Blackbirds.

Knowing the frequency of occurrence of different behavioral patterns during the nesting cycle, it is possible to calculate the energetic drain incurred by individuals of the two species. I am assuming that the physiology of avian protoplasm is similar to mammalian, an assumption supported by recent work of James R. King (pers. comm.). Estimates are based upon data given in Brody's book (1945) and Pearson's (1950) work on hummingbirds. Behavior

concerned with territorial defense may be divided into three categories: vocalizations, displays, and chasing and combat. The first two are energetically much more efficient means of accomplishing the objective and are consequently prominent in avian territorial behavior. For the purposes of calculation I assume that the energy required to produce song and other vocalizations raises the metabolic level of the bird 10 per cent above its resting level. This is equivalent to the additional energy required for standing as opposed to lying in man and several domestic animals (Brody 1945). Displays are assumed to double the metabolic rate much as walking does for man. Flight is assumed to require five times as much energy as resting, as found by Pearson for hummingbirds. Even if the flight of other birds is found to require an increase in energy less than that incurred by hummingbirds, the general picture obtained here will not be seriously altered.

Approximately six vocalizations per minute were given by male Redwings on their territories at Jewel Lake. Of these, five, mostly songs, were directly concerned with territory. Since the average duration of a song is slightly less than 1.5 seconds, about seven seconds per minute were devoted to this activity. Three displays concerned with territory were given per minute, averaging two seconds each, for a total of six seconds per minute. Flights and fights occupied about 1.5 seconds per minute. Thus, as mentioned earlier,  $\frac{1}{4}$  of the bird's time is devoted to activities of territorial maintenance. Calorie-wise, the vocalizations require an increase of 0.7% in energy expenditure, the displays an increase of 5% and the flights and fights another increase of 5%, for a total increase of 10.7%. Furthermore, this 10.7% additional energy must be obtained in  $\frac{3}{4}$  the time otherwise available for this purpose, and time available for other activities is correspondingly reduced. Since the male takes no part in feeding the young, his reproductive energy expense is restricted to this category until the young leave the nest.

In females the duration of territorial defense is only about one-half that of the males, and all forms of territorial behavior are indulged in less frequently, especially chasing and fighting. I have used an energy increase of 5% as an approximation of female territorial energy expenditure. However, once the young hatch, female time and energy expenditure changes radically. Assuming that walking on foot searching for food doubles the metabolic rate of the bird, the energy increase of females is about 157.5% above the resting level, about 150% of this coming via the search on foot and the remainder in flight between the nest and the nearby feeding grounds (Fig. 22).

In the Tricolor, the energy devoted to territorial defense and maintenance is greatly reduced in both sexes. All such activity takes place within the period of one week, and no energy is devoted to it during the incubation and nestling periods by either sex. Using mass behavior observations I have estimated that for one week, male Tricolors are at least twice as active



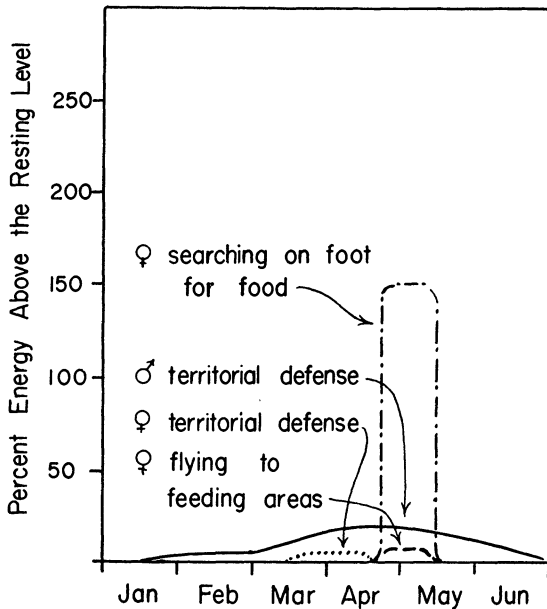


FIG. 22. Energy expenditure during the breeding season by a typical pair of Redwings.

in territorial defense as male Redwings, but that females are much less so than female Redwings. To this estimate must be added the energy expense of mass feeding flights, one half of which will be assumed to be in excess of that merely needed to sustain the adults.

The major energy expenditure accompanies feeding the young because of the great distances flown. Using the calculations of time spent flying and walking given in Fig. 21, it can be concluded that the energy increase totals about 317%, 250% of which is expended in flying and 67% in walking, just the reverse of that found in the Redwing. The other contrast is that both sexes are involved. Energy expenditure is estimated in Fig. 23 for a typical male and female.

In determining the total energy requirements of a social system it is important to consider not only the energy demands of the activity, but also the duration of that demand. In comparing the two systems I have therefore expressed the energy expenditure, firstly, in terms of the period during which it occurs and, secondly, in terms of the total energy increase for the year (Table 19).

Clearly the colonial system of the Tricolor is more demanding of energy but less demanding of time than the territorial system of the Redwing. This is due to the fact that most time-consuming events are energetically less demanding than events compacted into short periods of time. Since the colonial system of the Tricolor is energetically more expensive, the species would stabilize at a lower population level, other things being equal (Slobodkin 1953). However, it is probable that the system evolved because it made other things unequal, and that the population level

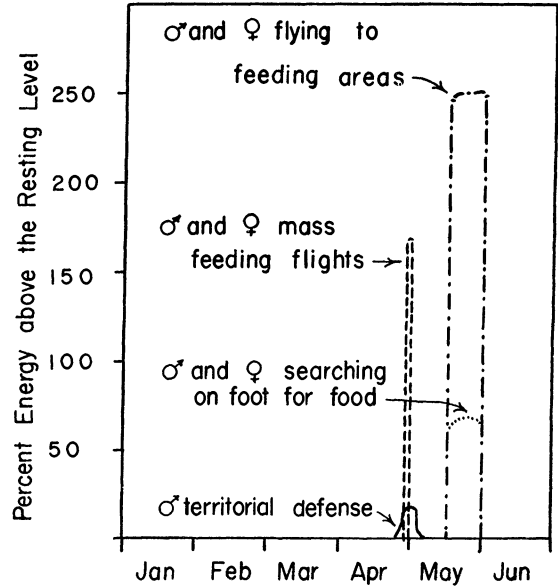


FIG. 23. Energy expenditure during the breeding season by a typical pair of Tricolored Blackbirds.

was increased by the adoption of the nomadic colonial system under the particular conditions to which it has been exposed during its history (see later).

Because of the high rate of food gathering, the Tricolor colonial system demands more favorable environmental conditions in which to operate than the Redwing territorial system. These more exacting requirements may help to explain the peculiarly spotty distribution of the species during the breeding season. A detailed study of food supplies available in different feeding areas, in relationship to their distance from the nests and the frequency of their utilization, would be most rewarding.

One of the major differences between the species is the early occupation of territories by male Redwings. Since testis maintenance is probably energetically cheap, only a very slight advantage for the males to be in reproductive condition early is needed to offset the energy loss incurred through the long-term maintenance of functional gonads. The advantages of early testis maturation are (a) early occupation of territories with the attendant advantages of prior residency, (b) the advantage gained by being able to mate with the first females to come into breeding condition (Fisher 1958), and (c) the ability to inseminate females whenever the opportunity arises. The relative importance of these factors varies with the particular mating system employed by the species and the ecology of the area. In many regions early occupancy of territories by the males is prevented by ecological unsuitability of the nesting area prior to the time of nesting.

In contrast, since the maturation of ovaries and the production of eggs is energetically very expensive, selection can be assumed to favor such metabolic exertion when and only when the chances for success-

TABLE 19. Comparative social system energy expenditure (expressed as % increase above the resting metabolic level).

Activity	REDWING						TRICOLORED BLACKBIRD					
	Duration		Energy increase %		Total energy increase %/yr.		Duration		Energy increase %		Total energy increase %/yr.	
	M	F	M	F	M	F	M	F	M	F	M	F
Territory defense.....	10 wks	5 wks	10.7	5.0	2.2	0.5	1 wk	1 wk	13.0	1.0	.25	.02
Mass feeding flights....	—	—	—	—	—	—	4 days	4 days	165	165	1.8	1.8
Feeding young.....	2 wks	2 wks	T	157.5	T	7.8	2 wks	2 wks	317	317	12.6	12.6
(flight to feeding area).	—	—	—	(7.5)	—	(0.3)	—	—	(250)	(250)	(10)	(10)
(search on foot).....	—	—	—	(150)	—	(7.5)	—	—	(67)	(67)	(2.6)	(2.6)
Total.....			10.7	162.5	2.2	8.3			330	318	14.65	14.42

Note: Duration of territory defense in the male Redwing may last up to 20 weeks but for part of this time the territory is occupied morning and evening only. The figure of 10 weeks represents an amount of time roughly equivalent to the total hours of full-time occupation.

ful breeding follow with a high probability. Furthermore, early breeding does not carry selective advantage for the female as it does for the male because the modal breeding time is necessarily the most advantageous if the breeding period is to stabilize, as it does. Hence, females are at a selective advantage if they come into breeding condition only upon arrival at a suitable breeding area where environmental conditions are favorable and a male is present. Thus, we should expect the female gonadal cycle to lag behind that of the male and the stimulatory effects of the male upon ovarian maturation to be strong, and this is the case.

Viewed in this light, the early occupation of territories by male Redwings in California, where winters are mild and the species is non-migratory, is reasonable, but male Tricolors fail to occupy territories prior to the time of breeding under the same environmental conditions. One of the requirements for adaptation to nomadism, the need for rapid response to suitable environmental conditions whenever and wherever they are encountered, leads to close group synchrony. Since the time and place of suitable breeding sites are unpredictable for nomads, no advantage can be gained through attempted occupation of sites in advance of the main group of birds. Instead, close flock organization at all times is most advantageous and the male's chances of leaving offspring are greatest if he remains with the group.

#### THE EVOLUTION OF MATING SYSTEMS

In most species of birds for which there is information, the sex ratio among nestlings is equal (Mayr 1939, Lack 1954:10), and there are important theoretical reasons for believing that the primary sex ratio should be close to 50:50. Fisher (1958) has argued that natural selection will tend to equalize parental expenditure devoted to the production of offspring of the two sexes, and Kolman (1960) has expanded the theory to show how this fixes the sex ratio but not the variance. As yet there has been no experimental confirmation of this hypothesis, but experiments with house mice are currently underway at the University of Pennsylvania. If, however, we

assume that Fisher is correct, there will be equal numbers of male and female blackbirds at the time they become independent of their parents, as found by Williams (1940). McIlhenny (1940), however, reported a sex ratio of 77% ♂♂ : 23% ♀♀ in Redwings from Louisiana, sexed at the age of five days in nests from which all young were known to have survived to the day of sexing. He did not state how he sexed the individuals, however, and Selander (1960) has since found that the sex ratio in Boat-tailed Grackles does not differ significantly from 50:50, though McIlhenny claimed to have found 30% males and 70% females. Selander concluded that McIlhenny sexed the nestlings on the basis of size only, and that his determinations are not trustworthy. Williams (1940) sexed 119 young Redwings, representing the full egg complements of 35 nests, finding 57 ♂♂ and 62 ♀♀. Among 94 young which successfully fledged the sex ratio was even. Hence, there are no reliable data which would suggest that the primary sex ratio in Redwings deviates significantly from equality, nor is there any reason to expect significant differences in the mortality rates of the two sexes during the nestling period. Once the adult plumage is attained, males might be expected to have higher mortality rates, but this does not influence the evolution of the primary sex ratio (Fisher 1958).

Unfortunately, there exist no satisfactory data on the sex ratio of adult Redwings or Tricolors. For much of the year sexes segregate in the Redwing, so that random field counts are worthless. Only at the time of breeding can the sex ratio be accurately determined, and this tells nothing about the sex ratio in the non-breeding segment of the population. Normally, the sex ratio among breeders has been assumed to be the same as in the population as a whole of breeding age but this is not likely to be true. The interesting data of Williams (1952) on the Brewer Blackbird demonstrate that this simple answer is insufficient.

It is well known that in many monogamous species occasional polygamous matings occur. Let us assume, then, that in many species there is a certain proportion of males having a genotype which makes it pos-

sible for them to have two mates. If, by having more than one mate, the male can produce more young than if he had just one mate, selection will always occur in favor of polygamy. Justin Frost has pointed out to me that the system is self-accelerating once it has started, so that once some polygamy has been established, fewer and fewer offspring are required per female mate from polygamous males to keep the selection going. This is true no matter how the mechanism is inherited and no matter what the sex ratio in the population as a whole. Thus, one can equally well ask why monogamy is so prevalent as why some species are polygamous. In view of this, and the theoretical likelihood of equal numbers of both sexes at the time of achieving independence, it is unnecessary to consider polygamy as the by-product of unbalanced sex ratios in the population as a whole, or as the by-product of a slower maturation rate of one sex.

In addition to the advantage conferred upon males having more than one mate, polygamy may be fostered by the advantage of having fewer males present on the breeding grounds to consume valuable resources (Pitelka 1959). In many species, particularly herbivorous mammals and precocial birds, the value of the male may be limited, if not non-existent, once fertilization has taken place. It is noteworthy that monogamy is rare among herbivorous mammals where the male is physiologically incapable of contributing to the nutrition of the young.

Counteracting this tendency toward promiscuity are other factors which must be operating in most species to maintain monogamy in the face of strong selective pressure against it. In species, such as carnivorous mammals and most birds, in which the male is able to make a significant contribution to the care of the offspring, a given male may not be able to leave more offspring by mating with more than one female if he is thereby unable to contribute as much to the care and feeding of these offspring. Moreover, it would be of advantage to the female to retain a male for herself since his contribution must increase her reproductive success. Behavioral patterns on the part of the female which have as their function the expulsion of other females from the territory of the male will thus be expected to evolve. Such behavior is well developed in female Redwings. Furthermore, if polygamy has, as a by-product, failure of many mature males to contribute any genes to future generations, there will be strong pressure from these excluded individuals to be admitted to the breeding group. Thus, those males attempting to defend more than one mate will find themselves under increased pressure from other males, a pressure which will be increased the more out of phase his females are, and, hence, the longer period of time they are available for fertilization by another male. Having more than one female will be of no selective advantage to a male if other males successfully inseminate them. Presumably, the stabilized sex ratio observed is the outcome of the interaction between these and perhaps other, as yet unknown, factors.

How they will act to stabilize the system must depend upon the basic ecology of the species and the features of its social system but this has not been investigated in any species.

In species where the male is incapable of contributing much to the welfare of the young, as in many male mammals, the evolution of his role is more easily understood than in such species as blackbirds where this is not the case. In many closely related species, such as meadowlarks and orioles, the males actively feed the nestlings and the Redwing and Tricolor differ markedly in this respect. Since, as will be developed later, the Tricolor is probably an offshoot from the Redwing, the main problem is to determine why the male Redwing lost his role in feeding the young, and why the Tricolor has subsequently regained it. At present there seems to be no satisfactory answer, but certain lines of approach can be suggested.

Polygamy in passerines is characteristic of species occupying habitats in which feeding areas are widespread but nesting sites are restricted. For example, it occurs widely in the ecologically similar savannah-inhabiting ploceids, sturnids and icterids. This is correlated with the evolution of slower maturation rates on the part of the males so that males of some of these species do not breed until they are two years old though females do so when one year old (Friedmann 1949). This type of ecological situation may be very important in shifting the balance in favor of polygamy in species in which the males probably fed the young at the time polygamy was initiated, and may continue to do so. Once polygamy is established, the loss of feeding of the young by the males probably follows in many cases because of the time needed to insure fertilization of all the females, and the importance of extended territory defense when several asynchronous females are present.

The development of sexual dimorphism follows polygamy and promiscuity among icterids (Selander 1959). There must have been an initial advantage enjoyed by the males having a slight development of secondary sexual characteristics so that there was something upon which female selection could have operated (Fisher 1958). As in the development of polygamy, the speed of development of sexual characters is a self-accelerating system which will progress geometrically until it encounters counterselection in the form of an increased mortality rate of the more excessively ornamented males, or their reduced efficiency in caring for their offspring.

The evolution of slow maturation rates in the males poses an even more difficult problem, since such individuals have a much reduced intrinsic rate of natural increase (Cole 1954). In fact, if a male Redwing produces ten offspring per year and no mortality is assumed, the potential production of offspring in four years is reduced from 14,540 for a male beginning to reproduce at the age of one year, to 130 for a male beginning to reproduce at the age of two years. Nonetheless, such a male must leave

more surviving offspring during the period when he is replacing a more rapidly maturing genotype if his genotype is to have selective advantage over one with a faster maturation rate (MacArthur 1960). Slow maturation rates in birds are not correlated with the size of the bird but are characteristic of species in which breeding sites are limited. Probably these are all species which are very ineffectively controlled between breeding seasons so that surpluses of breeding birds are regularly present. Shortage of resources must inevitably be necessary to cause the replacement of rapidly maturing genotypes by more slowly maturing ones, but the exact mechanisms are yet to be worked out.

In the Redwing, the sex ratio of 2-3 ♀♀ per ♂ in the breeding populations studied probably does not reflect the sex ratio in the population as a whole, though the number of males of breeding age is certainly less than the number of females since the males do not breed until they are two years old. The present balance is probably maintained because the advantages to the males of more extreme polygamy are counteracted by the problem of defending successfully a larger territory and preventing stolen copulations as the number of females increases. The females, by defending territories within the territory of the male, exert an active role in determining the number of females able to breed there.

In the Tricolored Blackbird, the situation is quite different because neither sex defends much of an area nor devotes much time to it. The sex ratio here probably mirrors the actual population sex ratio more closely than in the Redwing. With the development of extreme coloniality and the utilization of distant feeding grounds, strong selective pressure in favor of male participation in feeding the young has apparently caused an evolution back toward a more monogamous situation and more equal division of labor between the sexes. However, the tentative nature of these conclusions serves to stress our ignorance about the factors responsible for the evolution of mating systems and maturation rates.

#### THE EVOLUTION OF BLACKBIRD SOCIAL SYSTEMS

Since no fossil evidence can reveal the nature of social systems in the past, their evolution will probably never be worked out. Nonetheless, certain clues from present-day operation of the systems can be used to suggest conditions likely to have influenced their evolution. Furthermore, in the case of the Redwing and Tricolor, their great morphological similarity leaves little doubt that they are closely related and hence monophyletic. Therefore, the pancontinental Redwing population was probably divided into two isolated groups, one of which evolved into the present day Tricolored Blackbird. In view of the uniformity of the social system of the Redwing throughout its wide range today and the fact that this system is closer to the normal form of organization among passerines, it is probable that the social system at the time of separation was similar to that of the

Redwing today. Therefore, it is the evolution of a nomadic, colonial form of social organization from a more stable, territorial one which calls for explanation.

Today the Tricolored Blackbird is most abundant as a breeding species within the confines of the Great Valley of California where its nomadism is also most pronounced. Breeding is unpredictable, both as to location and size of colonies. To support the food needs of colonies as large as 50,000-200,000 nests, large areas are exploited. Food is gathered chiefly in the shallow water of rice fields, irrigated pastures, ripening and cut grain, and annual grass pastures. The presence of abundant and easily available food is a prime requisite for a successful colony.

At the time of the arrival of European man, conditions in the Great Valley were radically different from today. Dense riparian growth followed all the major watercourses, and on either side of the major rivers were extensive marshes and alkali flats. Prairies and oak parklands covered large areas between the rivers. None of these vegetation types remain today over significant areas and European annual grasses have almost completely replaced the native perennials. Gone, also, are the great numbers of locusts which characterized the grasslands of the valley. Since locusts formed an important item of food for most of the Indians of the Great Valley and surrounding foothills (G. M. Christmas, MS), plagues must have been a regular feature of these areas. It is probable that the locusts also formed the staple food for breeding colonies of Tricolored Blackbirds, as they do today for nomadic, colonial starlings in Asia and Africa (Schenk 1929, 1934, Serebrennikov 1931, Roberts 1940). In the steppes of Asia, locusts are also a staple food for gulls, many species of shorebirds and ducks during the breeding season (Formosov 1937).

Nomadic, colonial social organization in birds evolves most frequently in semi-arid regions of great climatic fluctuations. It is rare in North American birds, but in Australia, for example, 26% of breeding species are nomadic (Keast 1959). For the marsh-nesting Tricolor to evolve such a system, it is necessary that, in addition to unpredictability of breeding areas from year to year, there must be expanses of open feeding grounds surrounding the nesting areas and that these feeding grounds be characterized by an insect population which is very abundant for a short period of time. Without such conditions it is doubtful that the system could operate successfully.

Conditions of instability and broad expanses of open ground surrounding the marshes have probably been characteristic of the Great Valley of California since the early Pleistocene, if not earlier. Instability was produced by the annual winter flooding of large expanses of the valley (Fig. 24). The pattern of flooding and its severity, by changing from year to year, would produce different conditions each breeding season. What were suitable breeding marshes one year might be unsuitable the next and the time



at which areas became suitable would be expected to vary greatly, depending upon the time that winter flood waters receded. Rainfall may have been much greater during the Pleistocene, but since the same trees which now grow in the San Francisco Bay region grew there throughout the glacial period (Chaney 1951), it may be assumed that the climate was still Mediterranean. Thus, the entire present-day

of sufficient ecological differences to permit co-existence. With the Redwing and Tricolor, on the other hand, the contrasting social systems, evolved in response to different environments, result in radically different patterns of environmental exploitation, and thus sympatry might have been achieved in spite of more recent separation.

Certain other evidence favors a more recent separation of the two species. In addition to their morphological similarity and the present day restriction of the Tricolor to California, there is reason to believe that conditions for isolation in California were excellent during the Pleistocene. Several other species pairs are thought to date from this period, e.g., California and Gambel quail (*Lophortyx californica* and *L. gambelii*) and Ladder-backed and Nuttall woodpeckers (*Dendrocopos scalaris* and *D. nuttallii*), and there are many more segregations at the subspecific level. Moreover, there is reason to believe that the grasslands of California have not been as effectively exploited by birds as other grassland areas in North America. There are fewer passerine species which are independent of trees during the breeding season than in any other grassland area (Table 20) so that a marsh-nesting bird might find it more profitable to range further afield in search of food than in areas with more highly developed avifaunas. Thus, though there is no conclusive evidence for choosing between a Pleistocene separation in California or an earlier one, there or elsewhere in western North America, it seems more likely, in the light of evidence now available, that the Tricolor evolved in California, whether early or late.

Today in the Great Valley dams and levees have virtually eliminated extensive winter flooding, most of the vast marshes have been drained, and the alkali flats and prairies are now under cultivation, so that it might be expected that the Tricolored Blackbird, its system no longer adapted to present-day conditions, would be in danger of extinction. Indeed, for a while this was feared to be the case (Neff 1937). However, the attributes of the social system which adapted it to former conditions have actually pre-adapted it to agriculture. For example, the major problem faced by birds utilizing cultivated land is that it is difficult or impossible to nest in many areas which contain rich food supplies. Grain is cut before nesting can be completed, crops are plowed, irrigated pastures are regularly flooded with enough water to drown ground nests, and rice fields are similarly excluded. But Tricolored Blackbirds, being able to concentrate enormous numbers of nests into small areas and to exploit distant feeding areas, are well adapted to utilizing these croplands. Not only this, but their method of communication of food supplies permits them to take advantage of the frequent changes in croplands which make food more readily available. Thus, the Tricolored Blackbird is not only in no danger of immediate extermination, but it is, in fact, one of the passerines best adapted to utilize the abundant supply of insects in agricultural

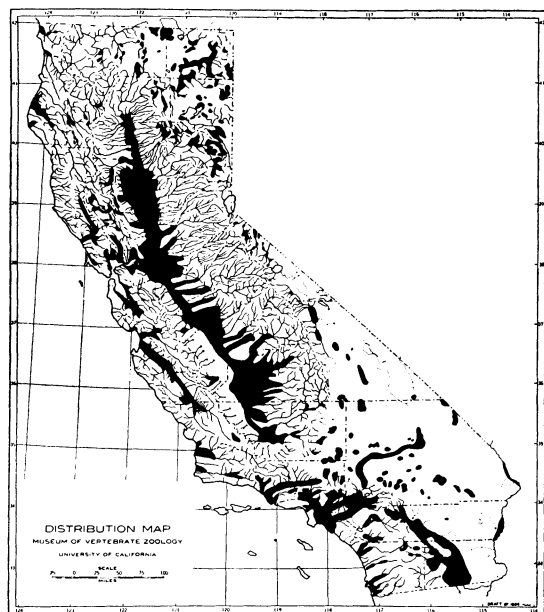


FIG. 24. Areas of California normally subjected to winter flooding.

range of the Tricolor has probably been subject to regular flooding and drying out for long periods of time.

To what extent conditions suitable for Tricolors were present in the Great Basin during the glacial period and earlier is not known. The presence of fossil floras containing species now restricted to California indicates that such conditions might have been more widespread well back into the Tertiary (Axelrod 1958) but the presence of certain plant species does not necessarily imply suitable conditions for year-round exploitation by a complex avian social system. In any case, if the Tricolor formerly had a more widespread distribution than it does today, its range had contracted to California before the arrival of European man in western North America.

A pre-Pleistocene origin for the Tricolored Blackbird is suggested by the distribution of past floras and by the good reproductive isolation of the species. Many species pairs in North America are thought to date from the Pleistocene, but in none of these cases is there extensive sympatry. Often there is considerable hybridization along the narrow zones of contact (Rand 1948). However, it might be argued that, in these cases, conditions during isolation were not different enough to have caused the development

TABLE 20. Breeding passerine birds of North American Grasslands (only those species independent of trees).

Californian Grassland	Southwest Desert Grassland	Great Basin Grassland	Great Plains Grassland
Horned Lark	Horned Lark	Horned Lark	Horned Lark
—	—	—	Sprague's Pipit
—	—	Bobolink	Bobolink
Western Meadowlark	Eastern Meadowlark	Western Meadowlark	Western Meadowlark
—	—	—	Dickcissel
—	—	—	Lark Bunting
Grasshopper Sparrow	Grasshopper Sparrow	Savannah Sparrow	Savannah Sparrow
—	—	Grasshopper Sparrow	Grasshopper Sparrow
—	—	—	Baird's Sparrow
—	—	Vesper Sparrow	Vesper Sparrow
—	Botteri's Sparrow	—	Clay-colored Sparrow
—	Cassin's Sparrow	—	—
—	—	—	McCown's Longspur
—	—	—	Chestnut-collared Longspur

lands of the valleys of California during the breeding season.

### SUMMARY

The selective significance of various features of the social organization of the morphologically similar Red-winged and Tricolored blackbirds was studied in north-central California. Data were obtained primarily from simple observation but some field experiments were performed. Particular attention was paid to spatial and temporal aspects of social organization.

Whereas the Redwing breeds throughout most of temperate North America, the Tricolor is virtually restricted to the lowlands of California, but it is nomadic within its narrow range. Outside the breeding season both species are highly gregarious.

Male Redwings begin to establish territories in north-central California in early January, but until late March or early April the territories are occupied only in the early morning and late evening. Nest-building begins in early or mid-April at most sites; but females become out of phase with each other and nesting in any given marsh extends over long periods of time. Nesting habitats include emergent vegetation (particularly cattails), ditch banks, roadsides, fencerows, riparian vegetation, weed and brush patches, cropland, and occasionally upland stands of chaparral and grass. In cropland, however, most nests are destroyed by harvesting before fledging can be completed and reproductive success is poorer than in the marshes.

There is a general correlation between the size of Redwing territories and the proportion of food obtained within their confines, but food is probably not the proximate factor by which territory size is regulated. That territorial behavior strongly limits breeding density is suggested by (a) the frequency and severity of territorial challenges, (b) the regular occupation by newcomers of the territories of birds held for a few hours in a trap, and (c) the rapid and regular reoccupation throughout the breeding season of territories from which the occupants have been removed. Normally, first-year males do

not maintain territories and breed but some may occupy areas from which the adults have been shot. Sex ratios among breeding birds are difficult to determine but on certain study areas there were 2.8-3.7 ♀♀ per ♂, with a range of 1 to 6. Usually the role of the male is confined to territorial defense and insemination of the females, but a few males occasionally or regularly feed the nestlings.

In contrast, territories are not established by male Tricolored blackbirds until the morning of the day breeding begins, and territories are only about 35 sq ft in area. Moreover, nesting is usually highly synchronous, all nests being constructed within the period of one week even in colonies as large as 50,000-100,000 nests. Some colonies, however, grow peripherally. As in the Redwing, most nests are placed in emergent vegetation but the birds also use grain, alfalfa, and safflower fields, mustard patches, ditchside vegetation, and occasionally trees. Breeding begins in April and May, being earliest in the foothills and latest in the rice growing country, in both cases being timed to optimal feeding conditions. To feed the enormous numbers of young involved, adults fly as far as four miles and more than 30 sq mi of land may be exploited by a single colony. The males actively feed the young but in other respects the mating system resembles that of the Redwing.

Sometimes colonies are completely destroyed by predators and at other times mass desertions, which may be related to poor food supplies, occur. Territorial behavior cannot limit the sizes of breeding colonies but several lines of evidence suggest that colony size is nonetheless adjusted to the capacities of the environment. Apparently an assessment of the environment is made during the period of colony establishment by means of mass feeding flights but the exact mechanism remains obscure. Thus, whereas in neither species is there a 'food territory' in the classical sense, the spacing within the systems as a whole is intimately related to environmental exploitation.

Combining assumptions regarding the energy demands of various activities and the tabulation of field data on activity sequences, tentative time and energy

budgets for the two breeding systems are constructed. The colonial system of the Tricolor is more demanding of energy, because of the great energy expended in flight to distant feeding grounds but less demanding of time. Moreover, the colonial system is more exacting of high concentrations of food supplies which may help to explain the peculiarly spotty distribution of breeding colonies. The value of early occupation of territories by male Redwings is discussed.

Theoretical arguments and field data support the idea that the primary sex ratio in the polygamous Redwing is equality and it is shown that selection can easily favor polygamy despite equal sex ratios. Thus the evolution of polygamy cannot be viewed as the product of unbalanced sex ratios but must be considered on its own merits. Ecological factors favoring monogamy and polygamy are discussed and evaluated and it is concluded that the evolution of slow maturation rates in male blackbirds and other species must inevitably be related to the presence of surplus breeding populations.

The colonial system of the Tricolor probably evolved in California in response to the instability produced by regular winter flooding of its breeding range and the concentration of food provided by locust plagues. The time of separation from the pancontinental Redwing population is uncertain but it may be as recent as the Pleistocene. The features of the colonial social system of the Tricolored Blackbird which adapted it to former conditions have preadapted it for utilizing agricultural lands as well.

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