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IN THE REDWINGED AND TRICOLORED BLACKBIRDS
OF SOUTHERN CALIFORNIA.

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Annual Cycle and Behavioral Relationships in the Red-winged and Tricolored Blackbirds of Southern California

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Zoology

by

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ABSTRACT OF THE DISSERTATION

Annual Cycle and Behavioral Relationships in
the Redwinged and Tricolored Blackbirds of
Southern California

by

Gerald Collier

Doctor of Philosophy in Zoology
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Professor Thomas R. Howell, Chairman

This study investigated ecological and behavioral factors affecting survival and co-existence during annual cycles of two close avian relatives, the Red-winged Blackbird (Agelaius phoeniceus) and Tricolored

Blackbird (A. tricolor). This approach lead to determination of behavioral cues by which each species achieves individual, populational, and interspecific recognition.

Basic methods involved field observation and measurement of morphology, ecology and ethology during all phases of the annual cycle. Behavioral stimuli and responses were tested in field experiments employing stuffed dummies and tape-recorded playbacks. Laboratory investigation analyzed food, gonadal histology, mensural morphology and behavior, the latter using photographs and sound spectrograms.

When not breeding, both species exhibit life-history similarity. Often, identical palustrine habitats are frequented. Diurnal flocking and foraging are quite similar. Tendencies to form monospecific flocks in roosting, resting and feeding sites form the major differences. Such activities reinforce positive intraspecific associations, and tend to pre-empt breeding habitat.

Both species concentrated breeding populations in favorable, restricted habitat. The Redwing shows intense territoriality, male defense starting many weeks before nesting. This prolonged breeding system restricts space available, and numbers of breeding adult males. It promotes high levels of polygyny. Nesting, incubating, and nestling-care are performed almost solely by females, with males actively feeding fledglings. Typical were larger clutches and more broods than in Tricolors. Dispersed

spatial relations of nests and marsh flooding afforded avoidance of most predators, while parental foraging adequacy in and near territories appeared requisite for young survival. The nomadic Tricolor remains highly social in breeding. Two weeks before nesting, flocks roost earlier, investigate potential breeding habitat in prospecting rituals, and culminate with sudden, synchronous breeding initiation or total desertion of unfavorable sites. Territoriality through incubation blossom simultaneously in much larger populations than in Redwings. Dense colonies typically show lax defense, tiny territories, abbreviated pair interactions, and male abandonment of nest sites during incubation. Male territorial reassumption and regular feeding of nestlings follow hatching. Tricolors show reduced polygyny and lower mean clutch size with predominant single-broodedness. Nesting success depends on adequate long-distance foraging exploitation by parents. Marsh-flooding constancy and nesting synchrony usually provide predator avoidance, with simultaneity and unpredictability of Tricolor presence important in dry-land sites.

The species' behavioral repertoires are distinctive, correlating with ecology of the breeding systems. Redwing display and vocalization emphasize effective territoriality, stable nesting, and immediate distant and proximate individual recognition. Tricolor interindividual distances are closer. Distant communication favors popula-

tional location and recognition. Close-proximity sounds and postures are unique, clearly effecting immediate recognition and reduction of aggression via appeasement. Males being more irregular than Redwings in territorial and sexual responses, correlates with their lower aggression above vegetation and during incubation, and preoccupation with foraging during nestling care. Commitment to such behavior conditions both Redwing and Tricolor to negative interspecific responses during interspecific strife over space and other resources.

Geo-climatic conditions during the North American Pleistocene allow reasonable hypotheses of divergence of a Californian blackbird ancestor into the Tricolor system. Extensive divergence in Redwing and Tricolor has apparently precluded hybridization.

I. INTRODUCTION

The concept of speciation is basic to evolutionary thought. The evolutionary process produces many discontinuities in the continuum of nature, of which the species is one. Problems of closely related species have been particularly intriguing to biologists. Whatever criteria define a biological species, there is general agreement that divergence of one interbreeding population of organisms into two or more distinct populations, by isolation and by accumulation and maintenance of small genetic changes, is involved and is prerequisite to all subsequent biological diversification. This is essentially the concept of species formation advanced by Mayr (1942) and quoted and rephrased endlessly since its pronouncement. Its simplicity of statement here is by no means intended to deny the possibilities of such variation upon the theme as species formation involving hybridization and genetic disjunction without prior geographic isolation. Each instance merits consideration of mechanisms producing that particular divergence. The assumption made in this investigation is that a divergence has occurred, and the object then is to determine its precise nature.

To consider most speciation as merely the production of trivial discontinuities in the evolutionary process, as has Huxley (1942: 389ff.), seems beside the point. Adap-

tive radiation, however subtly expressed, in every case represents another way in which a group or groups of organisms have taken advantage of an environmental situation available and not previously fully exploited. Whether such adaptations represent a major step in evolution --- as for example being on the main line of evolution to a higher taxonomic category, has little significance for my purposes here. This attitude of the triviality of speciation is extremely narrow, unproven, and indeed may well obscure a true appreciation of the multiple, often inconspicuous pathways of radiation.

This potential lack of appreciation of such subtle pathways strongly emphasizes a value of the study here undertaken. Seldom is the opportunity afforded for detailed examination of two species, which are completely sympatric and which show frequent and striking behavioral interactions, whose similarities strongly suggest recent descent from a common ancestor. The Redwinged Blackbird (Agelaius phoeniceus) and Tricolored Blackbird (A. tricolor) offer an unusual example of this situation.

These two species are members of the Icteridae, the New World passerine family of Troupials and Blackbirds. The Redwing is pancontinental in its distribution, while the Tricolor is restricted to California and southern Oregon west of the Sierra-Cascade Ranges (A.O.U. Checklist, 1957: 526).

Avian speciation is not merely a matter of adult external morphology, but includes many aspects of ecology and behavior in the life history of the organisms. It is the intent here to assume such a reasonably broad scope in approaching the problem, to analyze the ecology and behavior of the Redwing and Tricolor, and to integrate these with the distinctive morphological features found in the species. Completion of such a basic foundation will allow reasonable conclusions concerning origins of the two species, the effects of behavioral interactions at present and the selective forces they have exerted in the past, both within the social structure of the species and in interspecific encounters. As will be further documented, hybridization is not known to occur between these two species; the explanation of this condition involves the kinds of reproductive isolating mechanisms, their function, their origin and evolution.

Prior to 1960, literature on the Tricolored Blackbirds dealt largely with distribution and general natural history. There has been great need for a thorough study of this species and its relation to its congener, the Redwing. Orians (1960), in discussing the unusual phenomenon of fall breeding in the Tricolor, first provided a modern consideration of the ecological position of the species. As yet, little has been published on the behavioral interactions between Redwing and Tricolor (Orians and Collier,

1963). The sole prior mention in the literature of their interaction had been that of Lack and Emlen (1939: 229), in which the authors noted hostility between Redwings and Tricolor at the margins of a small breeding colony of the latter, in Yuba County, California.

Appreciation of the ethological aspects of avian natural history has progressed steadily in the last half-century, since the early work of Oskar Heinroth and his successor, Konrad Lorenz, (see esp. 1937) in Germany. Species-specific recognition signals have been demonstrated repeatedly in birds, and their stereotyped releasing functions in behavioral response are known to be critical in species and sex recognition (Tinbergen, 1948). In addition to elucidation of the ecology and social structure of the two blackbird species, this study attempts to ascertain, with the preceding assumptions in mind, the selective forces which have produced the behavior patterns exhibited by each species, and to determine which factors may have intensified or altered these patterns through interspecific contacts.

II. STUDY AREAS

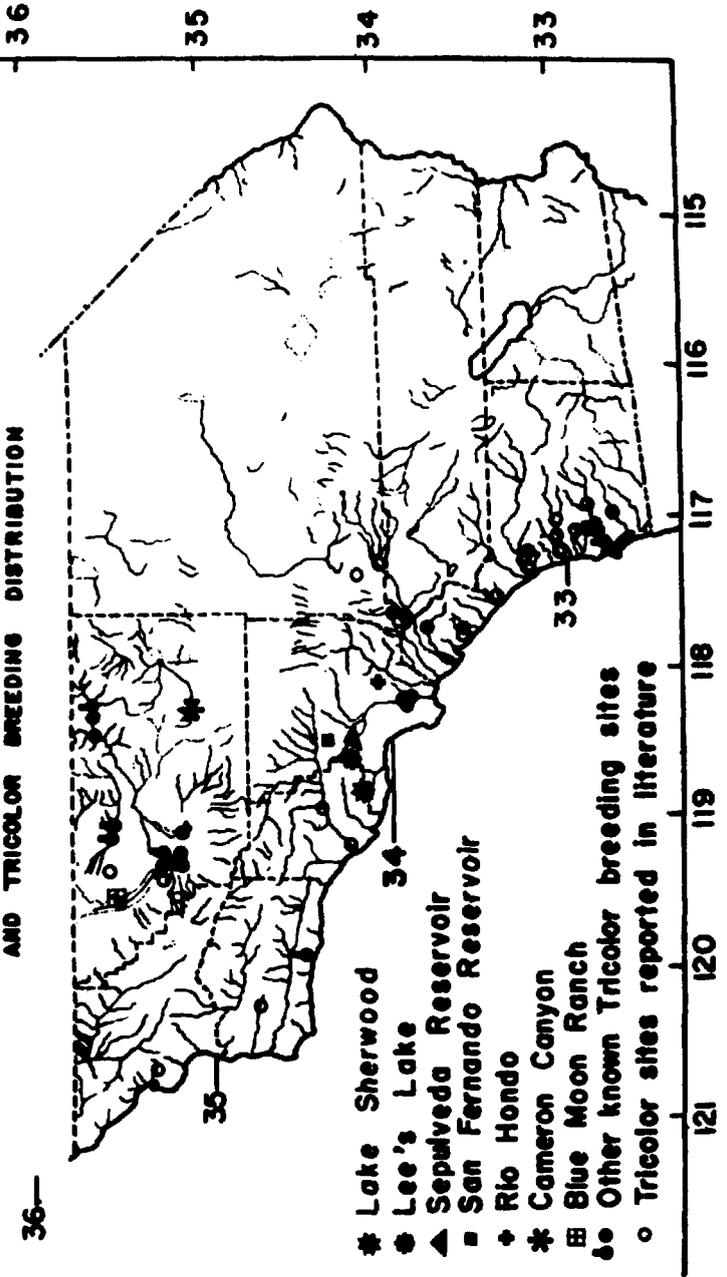
Blackbird habitats from a number of southern and central California localities have been studied. Geographic and ecologic diversity was very broad among these locations. The same type of habitat supported both species of blackbird at one site, but only one, or neither, of them at another. Such a variety of breeding and non-breeding localities doubtless furnished a representative spectrum of the ecologic preferences and requirements of Redwings and Tricolors. Figure 1 is a distribution map of southern California showing geographic positions of the study areas. The ensuing descriptions of the areas are intended to characterize them concisely, so that subsequently they may be designated by abbreviations.

In 1953, an investigation of the Redwing was begun along a quarter-mile section of the Rio Hondo in south San Gabriel, 12 miles east of metropolitan Los Angeles (Fig. 1). Flow in the river is ordinarily small, but may reach large proportions during winter rains --- even flood levels (Livingston, 1949: 119). Dense riparian growth, primarily willows (Salix sp.), occurred along this broad, sandy river course until late 1954. Farther east and west on the flood plain, stretched narrow, discontinuous bands of river-bottom woodland, characterized by scattered cottonwood (Populus fremontii), alders (Alnus

Figure 1 shows the nine counties included in southern California, and the drainages in that area. The numbers on the vertical and horizontal axes indicate, respectively, degrees of north latitude and degrees of west longitude. The various symbols listed in the figure indicate Tricolored Blackbird breeding areas from published accounts and those observed in this study (as designated). The plain closed circles represent known but unobserved sites in this study; and closed circles with attached bars indicate observed sites which were not actually studied. The plain open circles represent sites recorded from the literature, and not observed in this study.

DISTRIBUTION MAP OF SOUTHERN CALIFORNIA

SHOWING
BLACKBIRD STUDY AREAS
AND TRICOLOR BREEDING DISTRIBUTION



- * Lake Sherwood
- Lee's Lake
- ▲ Sepulveda Reservoir
- San Fernando Reservoir
- ◆ Rio Hondo
- * Cameron Canyon
- ▣ Blue Moon Ranch
- Other known Tricolor breeding sites
- Tricolor sites reported in literature

betulafolia), wild grape (Vitis girdiana), clumps of introduced Asian bamboo (Dendrocalamus membranaceus) and additional willows in damp parts. Within this woodland, small marshes had developed at several spots, consisting mostly of cattails (Typha sp.) and sedges (Carex sp.). Landscape adjacent to the woodland formed a mosaic of residences, farms and pastures. Redwings, a few Brewer Blackbirds (Euphagus cyanocephalus) and Cowbirds (Molothrus ater), roosted in the marsh and woodland vegetation.

Flood-control measures converted the river bed into a concrete drainage channel to a point just south of the study area, and a County Public Golf Course now occupies the former woodland-farmland-residential area west of the river. Although the habitat has been altered from its former semi-natural condition, cattails and willows survive along sluggish accessory streams lateral to the concrete channel.

Failure of Redwings to initiate breeding in this woodland during spring, 1953, stimulated a search for another suitable undisturbed site with abundant Redwings. Lee Lake, Canoga Park, was a suitable site. It is a three-acre private lake in northwestern Los Angeles County (Fig. 5.), owned by R. V. Lee. It was formed in 1928 by placement of an earth dam across Chatsworth Creek, the outlet of Chatsworth Reservoir which is a few hundred yards north of Lee Lake. The latter is maintained by

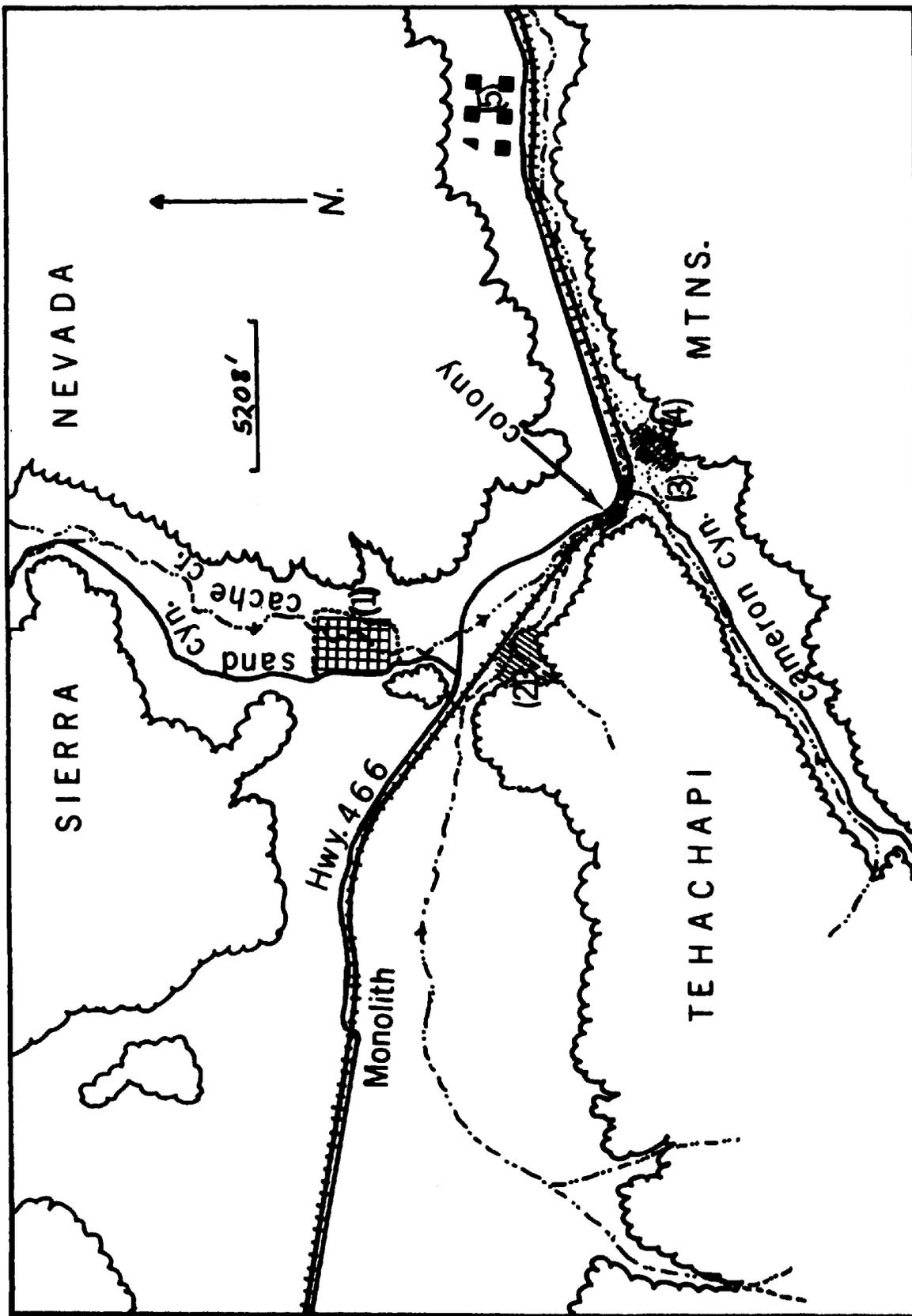
seepage from the reservoir dam (constructed in 1919) and by water pumped into it. Around the lake shore and its inlet grow abundant cultivated water iris (Iris orientalis), some cattails and numerous willows. The flat terrain immediately around the lake is covered with tall, Dallis grass and Rhodes grass (Paspalum dilatatum, and Chloris gayana); and it is also planted sparsely with various non-native shrubs and trees.

The vegetation of the local countryside was originally Coastal Sage Scrub on the hills, and oak parkland containing live oaks (Quercus agrifolia) and valley oaks (Q. lobata). Both oaks still persist on the reservoir property. Outside the reservoir property, most of this area was agricultural land and pasturage of large ranches until recently. Since 1955, these have largely been replaced with extensive real estate developments and industrial plants. Lee Lake, and the 200 acres around it, still remain; the land is devoted to casual cultivation of oats and alfalfa, and to occasional motion picture production. The lake has not been an intensive study area since 1954; but its condition and Redwing population were monitored regularly, 1956-1961.

In 1956, a search for Tricolor breeding sites began. One was located along on Cache Creek at the junction of Cameron Canyon Road and U.S. Highway 466 (Fig. 2.), 10 miles northwest of Mojave, Kern County. This lies in the

arid, desert-border of the eastern Tehachapi Mountains at an altitude of 3800 feet. The stream is intermittent, flowing heavily after storms which may bring snow or sleet even in April, but visible only as a trickle for a few hundred yards in spring and summer. This seepage supports some tall willows, mixtures of willow saplings and cattails near Cameron Canyon Road, and thick Tamarisk (Tamarix tetrandra) growth on the stream banks eastward. Within two miles of the creek, the steep surrounding slopes of the Tehachapis are covered with sparse Joshua Tree Woodland (adjacent), Pinon-Juniper Woodland (northwest), and Digger Pine Woodland (visible south). The flat drainage area of the creek, and the lower slopes are covered with rabbit-brush (Chrysothamnus paniculatus). The whole area is subject to intermittent livestock grazing. One-third mile southeast of the study area there is a damp, perennially green site (Fig. 2.) where Cameron Creek spreads out near its confluence with Cache Creek. The vegetation there consists of a few willows, low sedges (Carex) and reeds (Juncus spp.); and here shallow water often stands from late winter through early spring. This site supported larval insect food for blackbirds. The mountains descend rapidly to the east, where there is a quick transition to complete desert Creosote Scrub Community (see Munz, 1959, for descriptions of the capitalized plant associations used in text here). Westward

Figure 2 shows the Cache Creek Tricolor breeding in the eastern Tehachapi Mountains. The numbered (1-5), cross-hatched areas indicate main foraging sites adjacent to the breeding colony.

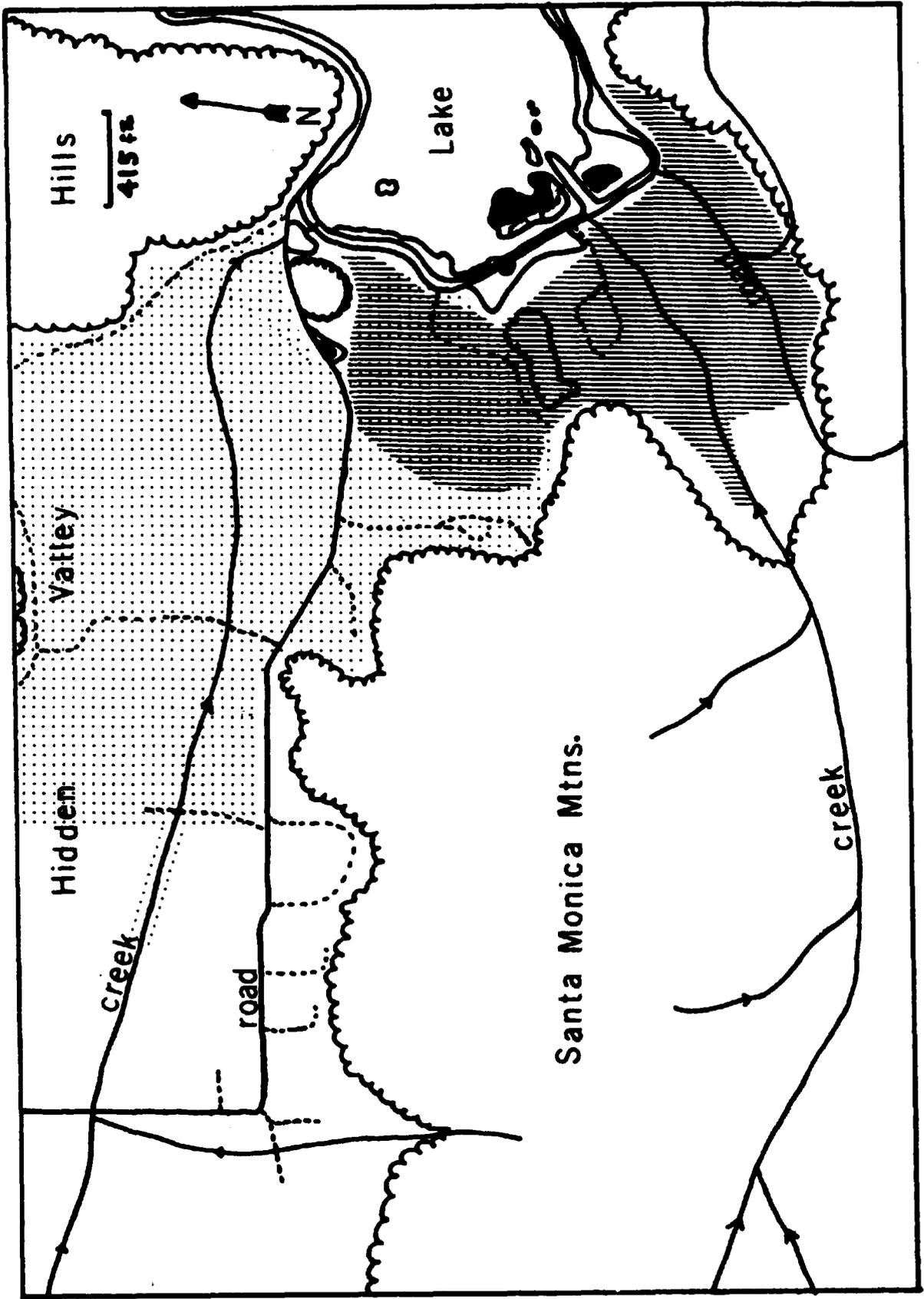


near the town of Monolith, and northwest up Sand Canyon (Fig. 2) irrigated cultivation occurs within three miles of the study area.

The most intensively studied area is Lake Sherwood, in the Santa Monica Mountains of eastern Ventura County, 25 miles east of the town of Ventura (Fig. 3). This is an artificial lake at 955 feet elevation, formed by placing a dam across Potrero Creek in 1905. It is about 400 acres in area, lying in a canyon bordered by chaparral-covered slopes and some adjacent oak parkland (*Q. agrifolia* and *Q. lobata*). The narrow valleys adjacent to the lake (except south) contain much cultivation and ranch pasturage, with scattered remnants of oak parkland. The lake's four main inlet streams are intermittent and support varying amounts of riparian vegetation along their courses, particularly where they enter the lake. Except at its relatively shallow west end with much marsh vegetation, the water of the lake margins is too deep to support emergent vegetation.

The major marsh subdivisions are: 1) west-central end (Figs. 3 and 8; abbreviated WLSM in the text), composed mostly of California bulrushes (*Scirpus californicus*) in deeper water and some cattails (*Typha latifolia*) in shallow-water marsh margins, surrounded by a few cottonwoods, many willows, and shrubby mule-fat (*Baccharis viminea*); 2) the southwest corner of the lake (Figs. 3

Figure 3 shows the western end of Lake Sherwood, and valleys and mountains west of the Lake. The vertically cross-hatched represents the main foraging area of the Tricolor colony in 1958. The stipled area represents this species' main foraging site during 1959. The black-colored portions of the West-end marshes, Lake Sherwood, and Hidden Valley Marsh show the locations of the Tricolor breeding colonies in 1957-1959. Compare to more detailed Figure 8.



and 8; designated SWLSM) composed predominantly of cattails with a few bulrushes. The area of each of these marshes is about two and one-half acres; they are separated by a 300-foot east-west land bank. Just west of Lake Sherwood were several small marsh areas and a pond which have been destroyed gradually by human activities since 1960.

Hidden Valley Marsh (Fig. 8; abbreviated HVM) is important in Redwing-Tricolor interactions. It is a quarter-acre cattail marsh 150 yards west of Lake Sherwood, and separated from the latter by a low hill. It lies at the eastern end of Hidden Valley, ca. two and one-half square miles in area, occupied by large livestock ranches with associated cereal-grain cultivation (oats and barley). This cultivation is unirrigated and in years of severe drought, such as 1961, the crops failed.

Lake Sherwood is a private lake, owned by J. R. Canterbury, who operates it as a fishing resort during spring and summer; and the Lake Sherwood Mutual Water Company manages it as a water supply for local residents. The lake level gradually recedes during the rainless summer and fall; but in years of normal rainfall, only part of the west end becomes dry. Since 1958 precipitation has averaged below normal, with the result that the lake has not been completely filled. By 1961, after three seasons of drought, the whole west half was dry. Employees of the Ventura County Fire Department have stated that the lake

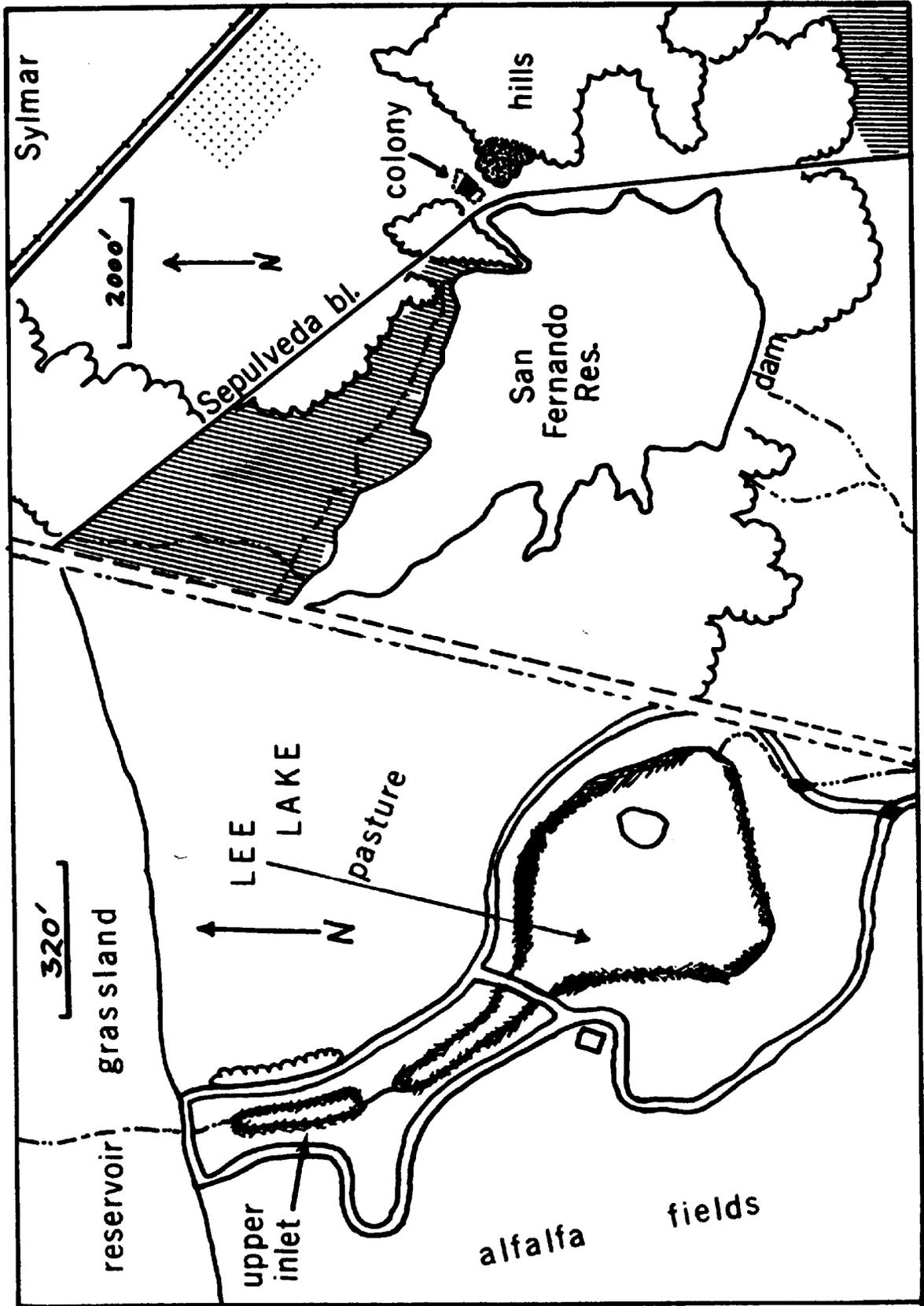
may refill at the rate of two feet an hour during heavy rainstorms, and has completely refilled in a single day when its level was 25 feet below normal.

Intensive study at Lake Sherwood was carried out from April 1957 through early 1960. Tricolor desertion in the latter year resulted in less frequent visits to the site.

Other locations, under casual observation early in the study, increased in importance for observation of blackbird breeding as a result of continued drought during 1959-1961. First observed in 1958, the dense expanse of 10 acres of nettles (Urtica holoserica), mule-fat, willows, and a few clumps of cattails bordering a small pond on the east side of State Highway 7 at San Fernando Reservoir (Fig. 4), then supported both breeding Tricolors and Red-wings. At an elevation of 1125 feet, the site is located in the town of Granada Hills, at the northern edge of the San Fernando Valley in Los Angeles County. It forms a small basin draining the surrounding hills that are covered with Coastal Sage Scrub Community; here it is chiefly black sage, Salvia mellifera. The adjacent hills are sporadically grazed by livestock. West of the pond is a broad area composed of the reservoir, surrounding rolling grassy slopes, and riparian growth. The pond area has been dry since early 1959. West and south of the pond area are the expanding outskirts of the town of San Fernando and some vestiges of vegetable and citrus cultivation.

Figure 4 is the upper diagram, showing the Tricolor breeding site at San Fernando Reservoir. The vertically hatched areas indicate main foraging sites of this species 1958-1960. The stippled areas are sites where Tricolors foraged additionally in 1960.

Figure 5 shows the Redwing breeding site and adjacent fields at Lee Lake. The cross-hatched portions around the lake and inlet indicate nesting area of the species 1953-1961.



In the Sepulveda Flood Control Basin (Fig. 1), Sherman Oaks, Los Angeles County, between Balboa Boulevard and Hayvenhurst Street, the Los Angeles River and small tributary streams have supported populations of Redwings only. Observations were made there during 1959-1960. The sluggish streams in this area contained thick cattail and bulrush growths, with willows along the banks. Immediately north and south of the stream channel cultivated grain has grown in the spring. Farther to the north is a County Golf Course, and farther to the south lies the Ventura Freeway. The Sepulveda Basin has held little water since the construction of its dam in 1941.

The San Fernando Valley has undergone great change in the last 20 years from an area covered by vast acreages of cultivation, ranches and grazing lands to one which is nearly filled with human habitation. In addition, with increased pressure for mosquito control, marshy areas continue to disappear at a rapid rate.

Several localities were visited in the southern San Joaquin Valley, a center of intensive agriculture, abundant marshland and riparian growth. Both species of blackbirds bred in a field at the Blue Moon Ranch, on Lerdo Highway, 17 miles west of Shafter, Kern County, in April 1960. The study area was a 10-acre barley field, substantial portions of which were heavily infested with tall, wild mustard (Brassica nigra). Surrounding the field on three sides

were areas where barley, cotton and alfalfa were grown. Blue Moon Ranch proper extends north of this field. It consists of cattle feeding pens, partly flooded pastures, and a network of marsh-bordered drainage ditches. In this region the agricultural mosaic changes annually; and in 1961 the previous year's barley field was but a barren, plowed site, surrounded by cultivated fields. The flat valley there is dissected by a myriad of marsh sloughs and drainage canals, and is dotted with countless small irrigation reservoirs with marshy margins.

Other blackbird breeding and roosting sites in Kern County where observations were made have been: Near Wasco, Buttonwillow, Buena Vista Lake, and Poso Creek at State Highway 65 in the San Joaquin Valley, and at Lake Isabella and Walker Pass near Weldon in the Sierra Nevada Foothills. These were all marsh or riparian localities. In addition, several blackbird colonies were observed along palustrine and riparian portions of the San Diego River, San Diego County, California during 1962-1964.

As an adjunct to these searches, museum specimens, egg collections, published reports, and the observations of reliable observers have been studied to determine particularly the distribution of the Tricolored Blackbird in southern California during recent years, and over the last half-century (Fig. 1).

III. METHODS AND MATERIALS

A. Field Observations

The survey of Tricolor breeding made at Cameron Canyon in 1956 was cursory, with the comparative study beginning during spring 1957. Preliminary observation and experiment on Redwings, employing stuffed specimens and playbacks of recorded vocalizations, were also undertaken during summer 1956 in western Montana. Earlier studies in 1953-1954 on southern California Redwings established a basis for later comparative studies.

The primary method employed has been field observation of the full spectrum of annual cycles in both species. Watching the birds at a distance was facilitated by binoculars and a spotting telescope, and close-up observation was afforded by the use of blinds and a 14-foot tower at the Lake Sherwood Tricolor site in 1959. Observations were recorded in a field notebook, and included accounts of behavior, environmental conditions, nest surveys, and interpretations of situations encountered. Throughout the study particular emphasis was placed upon the dynamics of behavioral interactions and their consequences.

Rainfall data were obtained from U. S. Weather Bureau records, and from the Ventura County Fire Department weather station maintained at Lake Sherwood since 1880. In addition, during 1959-1960, continuous temperatures were measured on the lake shore and in central WLSM. These were

taken in an identical manner, 24 inches above the substrate.

During the study 200 adults and 75 nestlings of both species were marked. The majority were banded with U. S. Fish and Wildlife Service numbered aluminum bands; and during the breeding season many adults were also marked with combinations of three different colored plastic bands, to which each color was assigned a number (e.g., orange-pink-orange = "535"). This permitted precise identification of many birds during the nesting cycle. Unusual plumage markings and distinctive individual vocalizations provided identification for additional individuals. Birds banded were caught in mist nets at roosting or nesting sites. Any external indications of breeding condition such as brood patches were noted in examining trapped birds.

Analysis of the displays conspicuous in the black-birds' behavior followed a functional classification. These stereotyped, species-specific patterns (see Dilger, 1956: 314) are designated by names previously assigned and established in the literature (Lack and Emlen, 1939; Beer and Tibbits, 1950; Nero, 1956a and b; Selander and Giller, 1961); or, for those newly described nomenclature is applied on the basis of the prevalent motor activity involved in the display, or with reference to the function of the behavior in the bird's life. Similarly, vocaliza-

tions are designated according to the context in which they occur, or with which they are correlated. The association of display and vocalization combined in the same functional behavioral pattern is recognized in applying names to such patterns.

Allied to description of behavior is the problem of motivational analysis. In this connection, hundreds of observations on events preceding, during, and immediately following any single behavior pattern, have aided in classification.

As an adjunct to field interpretations of behavior, the study of still and motion pictures and field sketches has contributed to the analysis of displays. Taped recordings and sound spectrographs made from a Kay Electric Company Model Recorder Sona-graph, have made possible an objective analysis of blackbird vocal repertoires. Sona-grams were made with a narrow band filter for an accurate portrayal of sound frequencies included in the vocalizations, and in most cases also with a wide band filter which furnished precise records of time sequences and relationships in the sounds uttered. This latter technique is valuable in analysis of highly segmented sounds, typical of the terminal portions of many male blackbird songs. Sound spectrographs have been used for comparison and analysis of vocalizations presented to birds in recorded playbacks.

B. Determination of Breeding Condition and Diet

Blackbird populations were sampled by shooting and netting at various times of the year. Heaviest sampling was done during February-March, before and during initiation of breeding. These furnished information on reproductive condition, diet, and several mensural characters such as weight, wing and beak sizes.

Gonad samples were taken from birds of both species for several weeks prior to the onset of breeding activity. The primary objective was to find out when Tricolors had reached an effective reproductive condition in relation to the date on which the species started nesting in different geographic regions. Where possible, both Redwings and Tricolors were collected in the same area for comparison with each other and with data previously obtained on the former (Wright and Wright, 1944). Testes and ovaries were fixed in 10% formalin or Bouin's solution. Ovarian material has only been examined grossly to ascertain when females were ready to ovulate. Testes were prepared histologically by embedding in paraffin, sectioning at eight to ten millimicrons thickness on a microtome, and staining with Mayer's Haemalum and alcoholic Eosin. Status of spermatogenesis and stages of testicular development were compared to those presented in the classic work of Blanchard (1940) on White-crowned sparrows (Zonotrichia leucophrys).

Crop and stomach contents were preserved in 70% alcohol, and examined under a dissecting microscope to determine the kinds and proportions of animal and vegetable foods consumed by each species at different times of the year. Emphasis was placed on feeding habits during the weeks prior to commencement of breeding and on the kinds of food delivered to the young. Food dropped by netted adults returning to feed young at the nest was collected. Samples of insects were taken at sites heavily exploited by adults gathering food for nestlings. The diet analysis complements earlier food-habit studies on these species, and provides a comparison with field observations of foraging habits.

C. Field Experiments

Full advantage was taken of natural experiments provided by environmental alteration through fluctuations in weather and human interference. These have been of special significance because of their correlation with the intensity of species interactions.

Field experiments presented taxidermically mounted specimens, and used tape recorded playbacks of song vocalizations to males of both species. Mounted specimens will hereafter be referred to as dummies. These were prepared in postures modelled after those shown by the birds in social, sexual, and aggressive activities. Experiments were aimed at discovering what cues the Redwing and Tri-

color use in distinguishing each other.

Dummies were placed at specified points outside and inside territories of both species and their distance from a nest was noted, when such was present. The techniques employed have followed in modified form those used by Noble and Vogt (1935) on Redwings, by Dilger (1956) on Thrushes (Catharus and Hylocichla), Weeden and Falls (1959) on Ovenbirds (Seiurus aurocapillus), and Falls (1963) on White-throated Sparrows (Zonotrichia albicollis).

Females were tested in the immediate vicinity of the nest, or on an apparent nest site prior to nest construction, and whenever possible in the absence of the mate. Tests were conducted throughout the breeding season to detect seasonal shifts in responses and their correlation with phases of the reproductive cycle. An individual was not tested at intervals closer than 10 minutes and never on two days in succession or more than twice a day.

As Dilger (1956) points out, ideally one should test a bird only once. But to obtain enough results (especially with a small number of marked birds available) to draw conclusions, the same birds were tested several times. A dummy was left in the experimental situation for 10 minutes or until the test bird had left without overt reaction, each being treated as a single test experience. The ideal situation is one in which the potential test bird is initially absent, in which case the experimental period begins

upon its return.

Vocalizations were recorded with a battery-operated portable tape recorder, "The Port-Able Tape Reporter" (made in England) from the Recorders Distributors Company, Hollywood, California. Tapes were made at a speed of seven and one-half inches per second (ips). An Electro-voice No. 655 multidirectional cardioid microphone was attached to the recorder, and was placed near the bird, or connected to an 18-inch parabolic reflector aimed toward the bird.

Playbacks were made with the same portable recorder, using a specially constructed small portable amplifier-speaker to carry the sound. The latter was camouflaged and placed at a specified point inside or outside the bird's territory, or in a particular relation to a nest. Some playbacks were made with a Revere T1100 tape recorder at seven and one-half ips, connected to a Powercon Vibrator Power Converter powered by a six-volt car battery for field use. This equipment was awkward and cumbersome in the field unless it could be operated from a car, which served as an excellent roadside blind at several sites.

A convenient interval for song sequences, where more than one of the same song was played back, was one per 20 seconds. A sequence of more than four calls was never played back at one test to any individual. Combined dummy-playback tests followed experimental procedures similar to

those outlined above. If no response was elicited after a four-call sequence, dummy and speaker were removed.

Test results were recorded on data sheets, which were then tabulated and analyzed. Responses were scored according to the type of reaction, the intensity of reaction, and its frequency. This ranged from zero response to overt attack or copulation with a dummy; gradations of incipient aggressive and sexual behavior between these extremes were noted. With playbacks, the degree of reaction was determined by the intensity of display and vocalization, and approach to the hidden speaker. By these methods it has been possible to quantify responses of birds to test stimuli, or at least to gain impressions of relative tendencies to react. Tentative conclusions are drawn concerning the stimulus or signal value of the displays and calls tested, and these are integrated with field observations on behavioral interactions and concepts of behavioral isolating mechanisms.

IV. GENERAL BIOLOGY

A. Distribution

The Redwing is found from Central Canada, throughout most of North America, south as far as northern Costa Rica (A.O.U. checklist, 1957: 526). Populations in the northern portions of the species' range are migratory, while the southern forms in generally warmer regions, including those in California, tend to be resident and move only locally in fall and winter.

The Tricolor has a much more restricted range. As summarized by Grinnell and Miller (1944) from numerous sources, it extends from southern Oregon and the Modoc Plateau of northeast California through most of the Californian lowlands west of the Sierra Nevada (occasionally into its foothills), cismontane southern California, and into northwestern Baja California. The two species are thus sympatric over the total range of the Tricolor. The major population center of the Tricolored blackbird is the Sacramento-San Joaquin Valley, with moderate occurrence in coastal drainages and flood plains farther south. The species is nomadic and highly colonial within its range.

B. Morphology

The plumage of the two species is quite similar. Color descriptions used adhere to those suggested by the color standard published in the A.O.U. Handbook (Palmer, 1962: 4). The male Redwing is a dull black, whereas the

Tricolor male has a metallic bluish luster to its black plumage. The most striking difference between males is the color of the lesser wing coverts (epaulets) and the marginal middle wing coverts. The former are reddish chestnut in the adult male Tricolor, bordered by rows of sharply contrasting white middle coverts. This combination of red, white and black have given the Tricolor its common name. The Redwing's lesser wing coverts are bright scarlet, usually with three marginal rows of buffy yellow coverts. Immature males of both species show paler lesser coverts than adults, with indistinct buff or dingy white margins in the Redwing and Tricolor, respectively. In the central valley and central coastal ranges of California, male Redwings show heavy black tipping on all the middle coverts, with a more extensive covering of their basal portions by the scarlet lesser coverts (esp. A. p. californicus and A. p. mailliardorum). This results in an obscuring of the usual buff border, producing a "bicolored" effect in the males (Van Rossem, 1926). Redwings in southern California show variable tendencies toward this condition, and like the central Californian birds they are often sympatric with breeding Tricolors.

Coloration is even more similar in the females of these species than in the males. They both exhibit heavy alternate streaking with dusky medium brown and whitish grey. However, female Tricolors are more uniformly sooty

brown with contrasting streaking most apparent on the throat, merging into an obscured streaking on the underparts. Female Redwings are quite variable in dark and light coloration; and in areas of major distributional overlap, such as central and northern California, they are actually the darker (sooty brown) of the two species. Southern California Redwing females are generally lighter colored than those in such northern populations. The rusty brown terminal margins of back and nape feathers in the female Redwing, most conspicuous in fall and winter soon after molting, serve to distinguish them from Tricolors in areas where the two are most easily confused. Female Tricolors never show this character, though their brown feathers are faintly edged with greyish white.

One of the most consistent characters for distinguishing Redwings and Tricolors is culmen length and depth of the bill at the base. Tricolors have a longer, more slender bill than Redwings. While the latter shows much variability in this character (Van Rossem, 1926), bill proportions for the two species always differ.

Sexual dimorphism in size is great in both, but is relatively less in the Tricolor. In specimens collected from the southern San Joaquin Valley, Cache Creek, and Lake Sherwood, weights were variable but Tricolor males and females were on the average heavier, respectively, than Redwing males and females (Table 1). The size differential

Table 1 shows mean weights in grams of male and female Redwings and Tricolors in all populations collected, 1958-1961. "N" indicates the number of specimens in each sample. Non-overlap of twice the standard error between the means of two samples indicates a significant difference between them. Individual populations from which these totals were accumulated showed the same significant interspecific weight differences, but no significant differences among intraspecific populations. The two columns at the right side of the table show the differences between males and females of the same species in terms of weight in grams, and the percent of the females' average weight which that difference represents.

	N	Mean	Standard Deviation	Standard Error	Male-Female Difference of Means	Male-Female Percent Difference
Redwing males; 1959-1961	31	62.5 g.	3.65	0.66	20.9 g.	50.0
Redwing females	12	41.6 g.	1.41	0.41		
Tricolor males; 1958-1961	36	67.0 g.	3.97	0.66	18.5 g.	39.1
Tricolor females	46	48.5 g.	2.54	0.37		

between male and female Tricolors is seen to be smaller than in Redwings. This agrees with Selander's (1958) findings correlating size dimorphism with degree of polygyny and promiscuity in the Icteridae.

Mailliard (1910) was the first to mention the difference in wing shapes between Redwing and Tricolor, which he presented as a key character for better distinguishing the two species. He found that the fourth primary was always much shorter than the first in Tricolors, while they are of the same length in Redwings. Comparative wing lengths in the two species are similar, with those of Redwings averaging slightly longer and with greater maximum width. The shortening of its proximal primaries indicates that the Tricolor has a more pointed wing. Comparing the two species in roosting populations in the Sacramento Valley, California, Orians (1961) showed that Tricolor males and females weighed slightly more than respective Redwing sexes. Measuring wing area, he found that the wings of male Tricolors average about 10 percent less in area than the blunt, rounded wings of male Redwings. A similar condition exists between the females of the two species, but area in Redwing females is only about seven percent larger than in Tricolors. By dividing the body weight into the wing area, Orians found that Tricolors carried about ten percent more weight per unit of wing area, indicating a greater wing-loading in that species. Similar

measurements have been made in this study; and the data agree with the above, except that male Redwings weigh less than Tricolors (Table 1). Storer (1947) has shown more pointed wings are characteristic of fast-flying birds, which observation in this study suggests is the case in Tricolors.

V. ANNUAL CYCLE

The annual activities of the Redwinged and Tricolored blackbirds, as with those of most north temperate passerine birds, are conveniently divided into a non-breeding period beginning in early summer, and a breeding period beginning in early spring. The difference in behavior of the birds between these two seasons is marked, as are the differences between the two species during certain phases of this annual cycle.

The Redwing and Tricolor must be considered together in various situations because of their frequent close association, especially during the non-breeding season. Discussion of both species, as well as other icterids and associates, has been combined to indicate the effects of the presence of another species and to outline common characteristics of mixed-species aggregations. Unique characteristics of Redwing and Tricolor during the non-breeding period are treated separately.

A. The Non-breeding Season

Mixed Roosting Aggregations

It is well known that blackbirds are quite gregarious during this time of the year. Redwings and Tricolors may be found roosting in favorable habitat, usually but not always over water, in flocks numbering from a few birds to several million individuals. The latter situation was observed on large marshes in the Sacramento Valley,

California, during early November, 1959.

In this study, the most extensive observations on non-breeding flocks were made at Lake Sherwood. Table 2 shows the numbers of roosting birds there for three years of study. The roosting population was always far more modest in size than those described from certain other areas (Emlen, 1952; Orians, 1960); this situation facilitated the estimation of numbers present and determination of distribution of species over the lake site.

The predominant species roosting at Lake Sherwood was the Redwing, which occupied the area in association with Tricolors, Cowbirds (Molothrus ater), Brewer Blackbirds (Euphagus cyanocephalus, subsequently designated Brewers herein for the sake of brevity), occasional Yellowheaded Blackbirds (Xanthocephalus xanthocephalus) and European Starlings (Sturnus vulgaris), in order of decreasing relative abundance.

The total roosting population at Lake Sherwood during three seasons markedly decreased each successive year (Fig. 6). This correlated with increasingly acute drought conditions each year. Each year beginning in mid-summer, at the end of the breeding period, the population of birds on the lake decreased sharply, and then increased rapidly to a relatively stable fall-winter plateau of numbers which did not decrease significantly until the following spring, shortly before breeding commenced. Usually the blackbirds

Table 2 shows the estimated roosting populations of Redwings (R), Tricolors (T), Cowbirds (C) and Brewer Blackbirds (B) during fall, winter and spring at Lake Sherwood, 1958-1961. The months in which estimates were made are indicated on the table. Compare with Figure 6.

1958-1959

October

R 3800
T 2000
C 800
B 200

Oct. -Nov.

R 4500
T 2500
C 1000
B 300

Jan. -Feb.

R 4000
T 2200
C 1000
B 300

March

R 2000
T 2500
C 600
B 200

April

R 400
T 2200
C 100
B few

1959-1960

August

R 600
T 75
C 200
B 100

August

R 1000
T 100
C 200
B 100

September

R 2800
T 1500
C 750
B 250

September

R 1800
T 1000
C 500
B 200

December

R 2200
T 1500
C 600
B 250

February

R 2300
T 1500
C 500
B 200

March

R 1500
T 1500
C 400
B 100

April

R 300
T 100
C 300
B few

1960-1961

September

R 250
T 50
C 100
B 50

September

R 400
T 150
C 150
B 100

October

R 2000
T 600
C 350
B 150

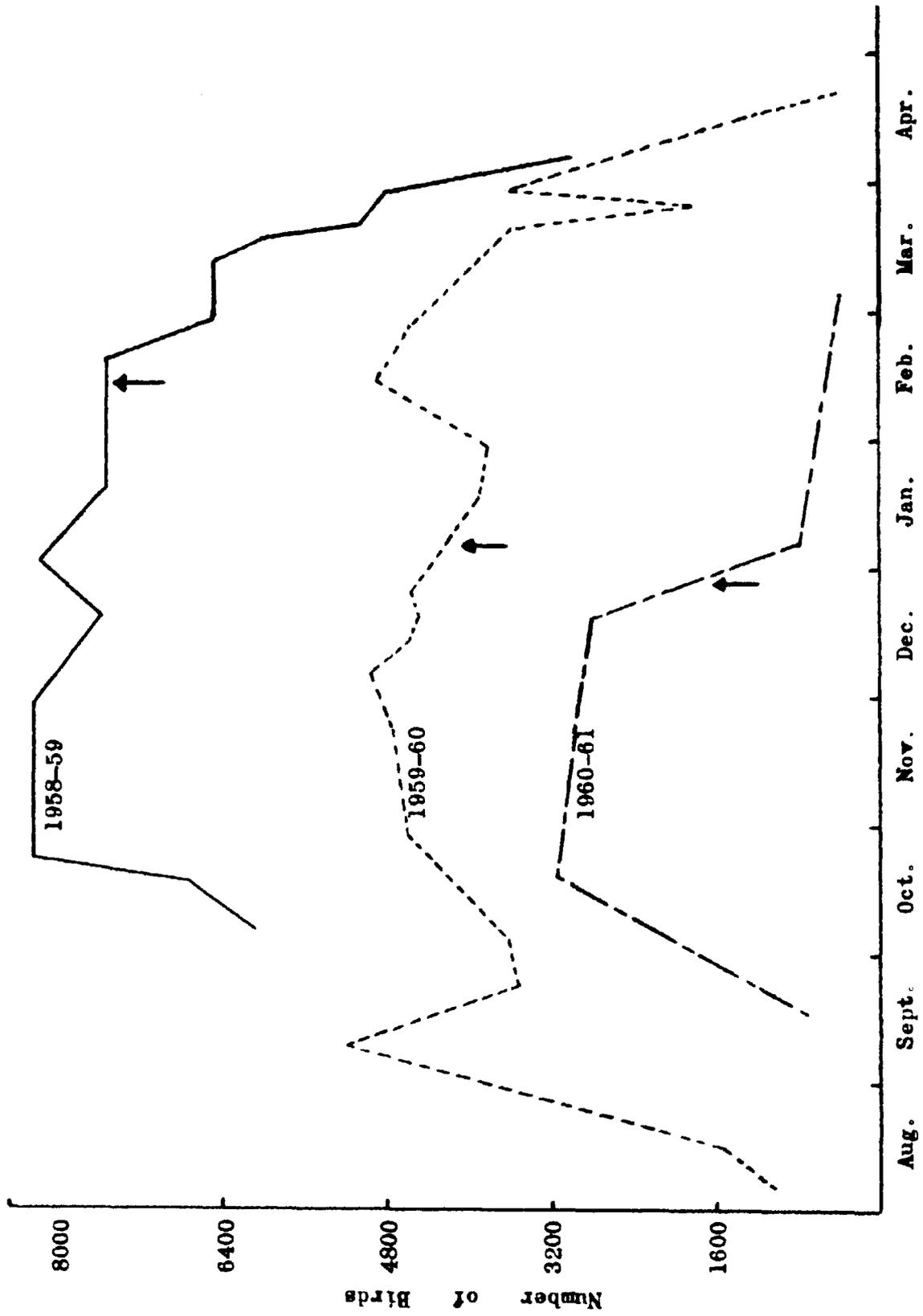
March

R 200
T 150
C 50
B 50

April

R 200
T few
C few
B few

Figure 6 shows counts of total blackbird and cowbird roosting populations at Lake Sherwood for three seasons, August-April, 1958-1961. The vertical arrows show the date when WLSM (West Lake Sherwood Marsh) was burned each year. Compare with Figure 8.



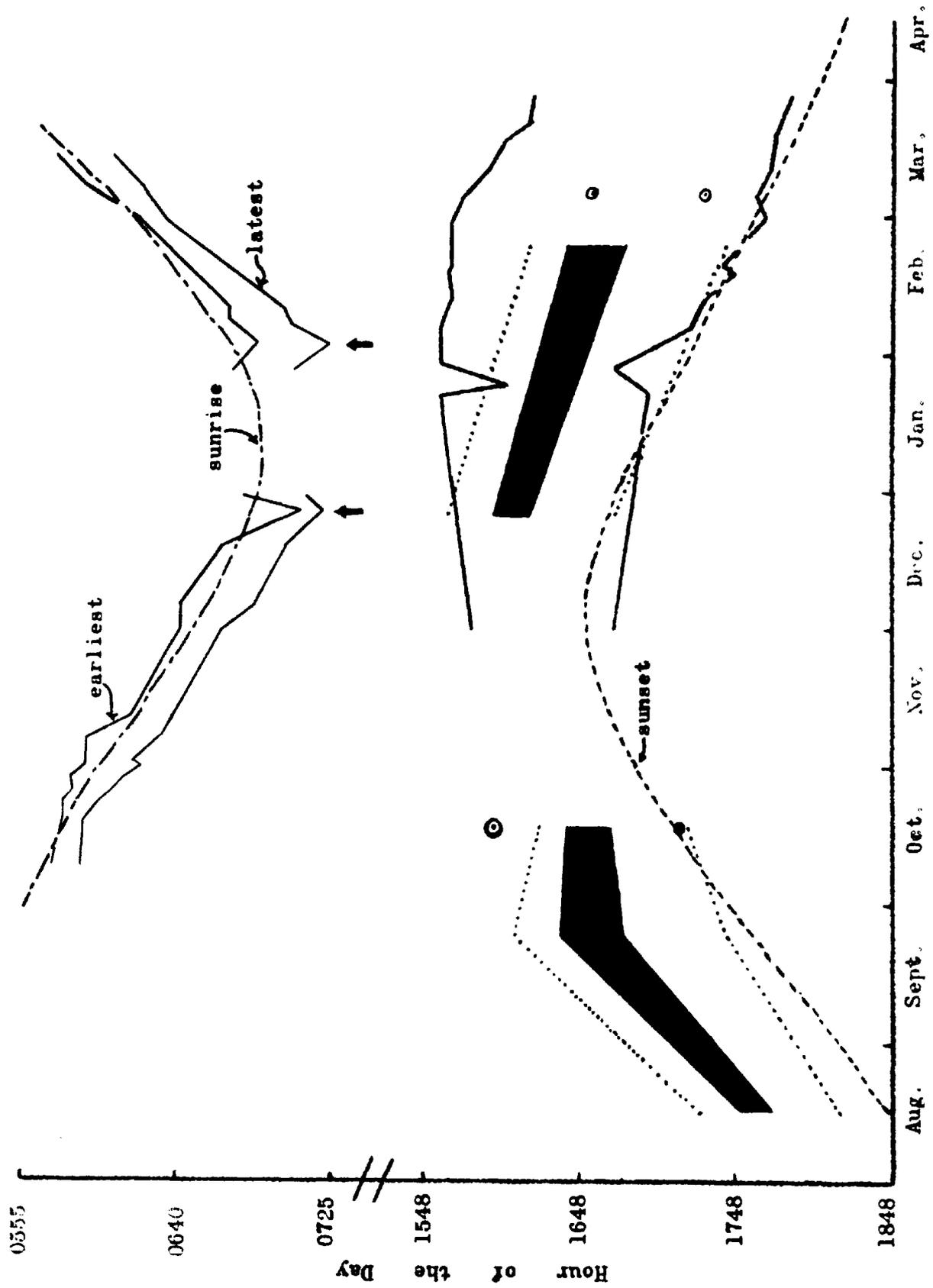
and their associates avoided or deserted sites such as HVM, the bulrushes of the intermittent pond west of the lake, and some vegetation at the northwest corner of the lake when these sites had dried up in late fall. Nevertheless, even in extreme drought conditions, the birds continued to occupy much of the vegetation on the western half of the lake. Partial burning or cutting of roosting vegetation did not appear to cause reduction of the blackbird population (Fig. 6). Rather, the birds seemed to crowd into other nearby vegetation. Likewise, flooding of some marshes, such as HVM in 1958, during winter appeared to stimulate their re-occupation by roosting flocks.

Observations at Lake Sherwood on arrival at the roost in the evening and departure in the morning revealed consistent patterns of behavior in the blackbirds and other roosting species. Evening arrivals began with the appearance of small flocks which circled the west end of the lake "cautiously" for several minutes before alighting in a chosen clump of cattails or bulrushes. This evening influx began from 42 to 114 minutes before sunset; and, within a few minutes before or after sunset, last arrivals coincided with local sunset (Fig. 7). From mid-January, 1959, first roosting arrivals occurred progressively earlier than sunset as the sun set later each day. This tendency lasted until early March, after which arrivals each day appeared slightly later (Fig. 7) as the photo-

Figure 7.

The bottom graph, shows time of sunset (dashed line) plotted against month of the year at Lake Sherwood, 1958-1961. The upper thin lines indicate the times of earliest roosting arrivals, the lower lines the times of latest arrivals. Of these, the solid lines are for 1958-1959, the dotted lines for 1959-1960, and the circled dots for 1960-1961. The darkened central portions represent the period during which half the roosting population arrived, 1959-1960.

The top graph shows the time of sunrise at Lake Sherwood for the same years. The upper and lower solid thin lines respectively represent times of earliest and latest morning departures from roosts at the lake, 1958-1959. The vertical arrows indicate dates when there was a heavy overcast.



period continued to increase. Peak arrivals, and the largest flocks, were observed during a short time span of 11 to 23 minutes during 1958-1959, when half the birds came to the roost. The birds tended to arrive slightly earlier on cloudy days, which agrees with the work of Jumber (1956) on roosting Starlings in the eastern United States, where arrivals correlated more closely with actual light intensities measured rather than the time of local sunset.

Birds at Lake Sherwood arrived mainly from the northwest through Hidden Valley, and the large numbers present in 1958 and 1959 indicate that birds came from many miles around, probably from as far west as 15 miles on the agricultural lands of the Oxnard Plain, and several miles north from the large ranches along U.S. Interstate Highway Ten. Lake Sherwood is the only site for miles around where large, protected marshes sought by blackbirds occur. This resulted in at least 20 times as many roosting Redwings than actually bred there in any year of the study (Tables 2; 4).

As the flocks on the top of the marsh vegetation on the lake built up and birds covered it like great black canopies, flocks alighted more and more readily, and a gigantic pre-roosting chorus rapidly developed --- a melange of Redwing, Cowbird, Tricolor, and Brewers calls. A few minutes after sunset the flocks began to exhibit

restlessness, with much local shifting and rearrangement of birds occurring. This signified the beginning of true "roosting behavior" (Jumber, 1956) as the birds began to descend to their ultimate sleeping sites. In accordance with Jumber's terminology, arrivals, perching high in marshes on adjacent trees and electric wires, and chorusing were designated "pre-roosting" activity. The birds either flew to another nearby spot to roost after arriving, or they descended to roost in the immediate vicinity of the initial landing place. The vocal chorusing continued until about 30 minutes after sunset, when the colonies rapidly became silent.

Evening arrivals at Lake Sherwood varied in number from one to more than 1000 individuals at a time. Initially, small flocks came at wide time intervals, steadily increasing in size and frequency; and after the peak of arrivals, flock size decreased rapidly with only scattered individuals appearing as darkness approached. Such patterns of flock size and frequency were generally consistent regardless of the variable annual sizes of total roosting population. Observations here are similar to those by Miskimen (1960) on captive male Redwings in Ohio. She found pre-roosting restlessness and final roosting behavior clearly related to light intensities, and on the average, correlated with local sunset.

Morning arousal and departure at Lake Sherwood fol-

lowed a pattern similar to that of the evening arrivals, but reversing in sequence of events. As dawn approached, scattered songs of Redwing males began. They were always the first of the roosting birds to vocalize at that hour. This commenced 30-40 minutes before sunrise and signaled initiation of morning arousal. Within 15 minutes individual calls had merged into a continuous chorus. Calling began with the birds still hidden in the roosting vegetation; and the first birds emerged to the tops of vegetation about 15 minutes before they departed, by which time it was quite light. Just prior to this emergence of the roosting birds, there developed a predeparture assembly in which blackbirds flew rapidly from other points in the west half of the lake into an irregularly shaped clump of bulrushes about 10,000 sq. ft. in extent near the northwest corner of the lake (Marsh "D", Fig. 8). This was the main staging area for thousands of the blackbirds immediately preceding morning departure. By no means did all the birds roosting at Lake Sherwood gather on this bulrush site; but it did become literally covered with a canopy of chorusing blackbirds. Far more than the number of birds actually spending the night in this small marsh gathered there during the morning assembly. The vocalizations of birds during this morning chorus generally formed a nearly indistinguishable mixture of several species. However, with close listening from several vantage points, distinctive calls of the

individual roosting species were recognizable. Figure 7 shows the departure times of blackbirds at Lake Sherwood compared to local sunrise during winter 1958-1959. This pattern was followed closely in other years of the study. The essential features of morning departure were that it occurred usually within a very few minutes of local sunrise (within one to two minutes on clear days), it was of very short duration (ordinarily 10-15 minutes, but as short as five minutes), and nearly all the birds departed northwest through Hidden Valley (Fig. 8). Similar to evening arrivals, flights of small flocks commenced and ended departures, with massive larger ones of as many as three thousand birds per flock leaving during the middle peaks of the exodus. At the peak of departures birds were often leaving in an almost continuous flow, so that it was difficult to separate them into flocks; and most of the roosting birds departed within one or two minutes. Once airborne, the birds in a flock ceased song chorusing and individuals began to utter single, species-specific calls. Thus, it was possible to estimate the composition of a flock passing overhead by the vocalizations coming from it.

The patterns of activity described for roosting birds at Lake Sherwood applied generally to all species occupying the area during the study, and particularly to Redwings and Tricolors. The patterns outlined above are applicable to most roosting blackbird flocks, and differences in arrivals

and departures are primarily related to size of roosting population. The millions of roosting blackbirds observed in the Sacramento Valley in November 1959 required longer to gather at the roosts in the evening and to leave in the morning than the birds at Lake Sherwood. In other study areas such as Rio Hondo and Lee Lake, where large roosting flocks were not characteristic, any roosting birds tended to arrive quickly and quietly late in the evening and to leave similarly about sunrise.

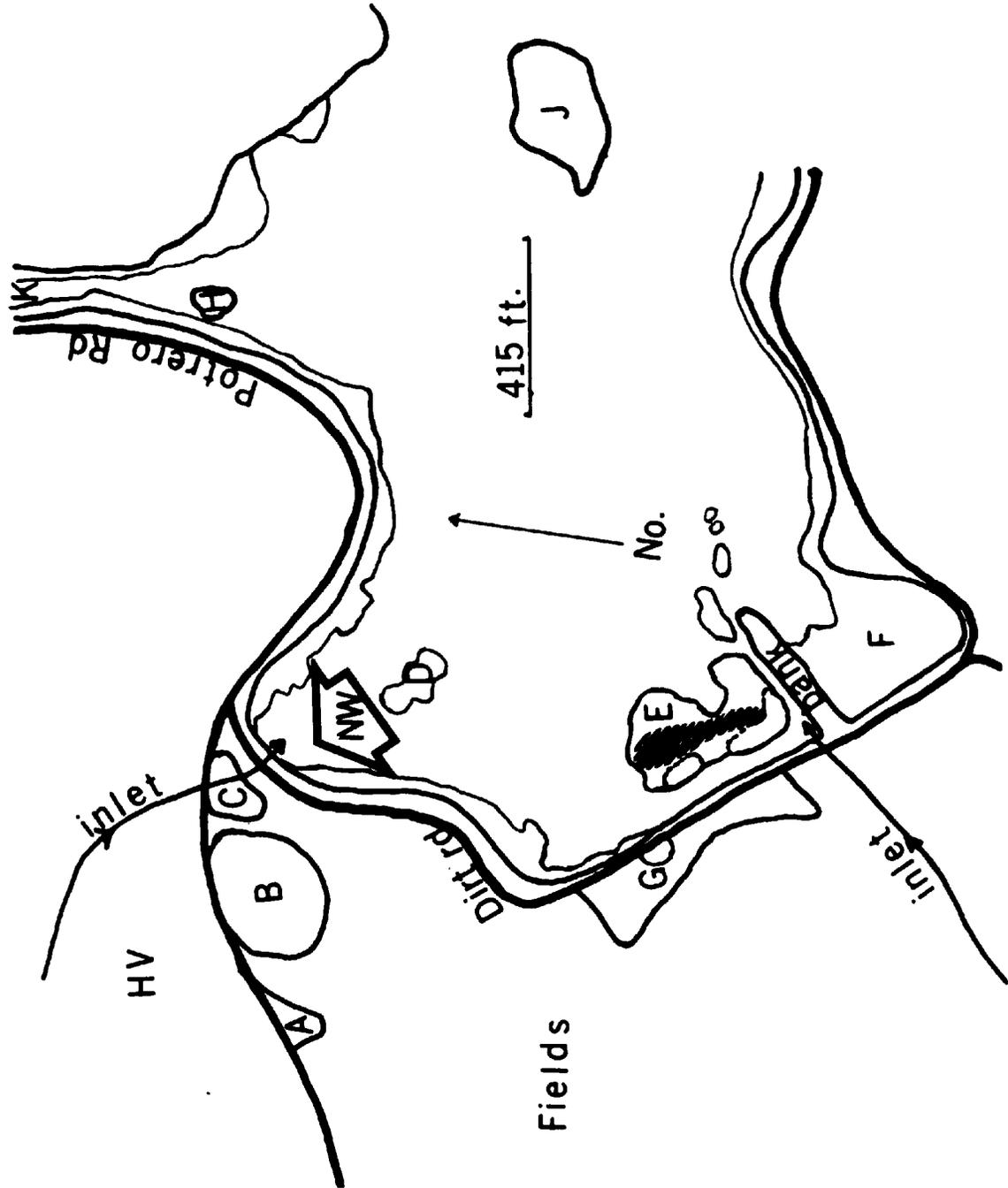
There were no observable fall and winter differences in arrival-departure times or direction between Redwings and Tricolors. The most distinctive species was Brewers, which tended to linger in small flocks on electric wires at the northwest corner of the lake after most of the other birds had departed. This area tended to be the gathering site for that species.

Roosting Distribution of the Species

The Redwing

The Redwing was distributed over most of the occupied roosting sites at Lake Sherwood, being most heavily concentrated in the north and northwest lake margins, the north center cove area, and north WLSM (Fig. 8). Both sexes were present; but females generally outnumbered males by a ratio of five to one during fall and winter 1958-1959, and 1959-1960. Females were in greatest abundance in north and west parts of WLSM, and along the northwest shoreline

Figure 8 is a diagram of the west half of Lake Sherwood. The capital letters represent Hidden Valley (A), Robinhood Hill (B), Northwest Pond (C), Northwest-corner Bulrushes (D) just below "NW" arrow, West-Lake-Sherwood Marsh (E), Pond Bulrushes west of Lake (G), Bulrushes (H) in north-center inlet (K), and an island (J). The cross-hatched part of WLSM (E) indicates the main Tricolor roosting area. The large arrow marked "NW" shows the main direction of exodus during morning roost departures. Compare to Figure 3.



vegetation; while males predominated in the north-center and southwest corner of the lake. Allen (1914), and Nero (1956a), and others, have also reported such tendencies for roosting separation of the sexes. Flocks of thousands of Redwings roosting along drainage ditches at the Blue Moon Ranch in mid-October 1960, showed a reverse trend being about 85% males.

After the morning departure of roosting birds at Lake Sherwood, varying numbers of Redwings returned to roosting sites on the lake later in the morning. There was an irregular shuttle of this species to and from feeding sites west and northwest for the rest of the day, until evening arrivals of roosting birds commenced. A conspicuous daily pattern at Lake Sherwood was its almost complete silence by 20 minutes after the morning exodus, once lingering male Redwings had left. It remained so for at least one hour, and then small Redwing flocks, mainly males, drifted back to the lake. There were never more than 500 of these diurnal returnees in the non-breeding season, even when the peak Redwing population was about 4500 in 1958 (Table 2). These birds and others shuttled back and forth between foraging areas and roosts all day. At HVM, males were the only returnees, appearing mainly in the morning and afternoon during winter 1958-1959. Individuals shifted in and out of the marsh, often reaching 35 in number.

In areas west of the lake flocks of many sizes were observed, the largest with 2500 blackbirds. Redwings usually were the most numerous species in observed feeding flocks; and some flocks of this species alone were noted at various times. Consistent, but incomplete, division of the sexes into separate flocks was again the rule. Flocks feeding around the Hidden Valley ranches were composed mostly of males; but flocks of hundreds of females were frequently seen in the areas west and northwest of that Valley. Redwings, and accompanying Tricolors and Brewers, were observed feeding in a wide variety of situations. They were usually in flocks of a few hundred, and frequented recently tilled fields, and pasturelands. They foraged under a great variety of conditions; and several times they were seen scurrying over completely frozen fields on very cold mornings at sunrise.

Redwings, like their avian roost associates, appear to be opportunists in foraging activities; they feed upon whatever is available in the way of seeds, insects and other arthropods. They attack vigorously broken earth in plowed fields, livestock excrement, matted plants, erect plant stems (which they may split to obtain insect larvae: Fischer, 1953), or moist flatlands such as shallow-flooded pastures.

Redwings, and their icterid allies with which they roost, are well adapted for inserting the beak into openings

and prying forcefully by opening the mandibles in attempts to split open the potential food-containing object. They may also push forward and upward vigorously to overturn objects, even small stones estimated weighing nearly as much as an individual bird. By such behavior, they obtain food that is clearly unavailable to large numbers of other avian species feeding in the same sites. Beecher (1951) has discussed morphological details of such feeding adaptation in icterids; and Lorenz (1949) has elaborated on the skull modification attendant to this type of feeding in both Icteridae and Sturnidae (starlings). This involves a sharp, posteroventral bend in the buccal cleft ("corner of the mouth"), positioning the eyes behind it in such a way as to enable them to peer anteriorly between the opened jaws into any pried-open crevice. The feathers of the skull between the eye and the buccal cleft are rather flattened and dull in contrast to the rest of the plumage, and presumably reflecting little light, which Lorenz pointed out for sturnids but not for icterids.

During the non-breeding season, food was primarily seeds, especially cereal grains in the vicinities of livestock ranches and cultivated areas. Occasionally insects appeared in the diet, and a few birds collected around pastures had eaten numerous dipteran larvae or pupae, probably obtained from livestock feces. This was particularly evident in a dozen stomachs examined from the Blue Moon

Ranch on 15 October 1960. Most contained nearly ripened milo maize grains, but two had only insect remains apparently from cattle feedyards. These are expected results, as it has been long known (Bent, 1958) that non-breeding Redwings have fed almost exclusively on plant materials, whether they were wild seeds or cereal grains.

One clear ecological correlation should be mentioned. While the areas of extensive marsh described provided ample roosting sites for many thousands of Redwings, their limited area did not provide food for such flocks. The marsh roosts were situated close enough to large cultivated areas, pastures, or livestock feeding sites that the hordes of blackbirds could reach them for adequate foraging.

Feeding flocks of Redwings and associates exploited foraging locations in what appeared to be a quite unsystematic and random manner. Flocks shifted erratically from one part of a field to another. Frequently members on one side of a given flock flew up and over to another side of the flock, as it appeared to be moving in a particular direction over the field as noted by Scott (1958). Under such conditions, aggressive interactions among individuals were infrequent, even though new arrivals alighted close among individuals of a feeding flock. Generally, flock members maintained a few inches distance of tolerance from one another, as noted by Emlen (1952). Occasionally two or more birds expressed interest in a food item, resulting

in one dominant individual (usually a male) obtaining the item by pecking at or charging one or more competitors. Such an encounter resulted in the displacement or supplanting of the unsuccessful contestants a short distance, and it failed to affect the remainder of the flock.

Hostile interaction of a higher intensity in males resulted when an attacked individual Redwing resisted the attack. This usually included a "joust", similar to the beak-to-beak fighting seen among male domestic fowl. A vanquished male again was usually displaced only a short distance within the flock. Such jousting has been observed rarely in female Redwings, but not in other blackbirds. It tended to resemble an aerial fight often seen between breeding, territorial Redwing males. Occasional aerial chases represented the most intense type of aggressive encounter seen among winter flocking Redwings. This was most often an adult male pursuing a female or immature male. Despite the fact that independent foraging or hostile interactions did not generally alter actions of the rest of flock, a sudden flushing or scaring-up of such a flock resulted in a united flight response by all its members. In this way, the group catapulted aloft as a single, compact unit, which loosened the formation only after becoming well airborne. All manner of gradations were observed leading to the complete flushing of the flock from the ground. Often a flock started to fly up, but the

result resembled a false start in which, starting at one point, the birds rose off the ground in an undulating fashion, immediately returning to nearly the same position they had held moments before. The signal triggering a true flight seemed visual, as no auditory cues were detected by the observer. The signal may have been related to the precise manner in which one or more birds initially left the ground. A fluttering flight seemed to indicate intent of changing position in the flock, as opposed to the swift dart into the air of a startled bird intending to continue airborne. Sudden flight and flock compactness has also been noted in the European Starling (Tinbergen, 1951:171) in apparent visual response to raptorial predators. A similar flock reaction to a Redtailed Hawk (Buteo jamaicensis) was noted in roost-arriving blackbirds at Lake Sherwood in 1960.

The Tricolor

The Tricolor exhibited habits quite similar to those of the Redwing during fall and winter, especially with reference to roosting, arousal and feeding activities. The former usually roosted in large numbers in habitat identical, or very similar to that ascribed to Redwings. Again, most of the observations on this subject took place at Lake Sherwood, where the Tricolor roosted consistently, and usually bred in the spring. Tricolor actions at Lake Sherwood have been taken as representative of that species

during non-breeding, since they were closely paralleled by those in localities less well studied.

Figure 8 indicates that roosting Tricolors tended to concentrate on WLSM, the exact site on which more than a thousand of them annually nested from 1957 through 1959. During these years roosting numbers of this species slightly exceeded those ultimately attempting to breed there. Observations of arrivals and arousals showed that the Tricolor followed the same patterns as Redwings until the last week of March (Figs. 7; 15). Most Tricolors proceeded directly to their roosting site upon evening arrival; and most of them joined the "pre-departure assemblage" in the northwest corner of the lake at dawn prior to the mass morning exodus. The total numbers of Tricolors inhabiting the lake area followed the trends of dwindling roosting populations there during the study years (Fig. 6; Table 2). From a few hundred to several thousands of them roosted there, shifting sites only with complete destruction of the preferred marsh, as in January, 1961 (Fig. 6).

Sex ratios appeared to vary from nearly equal to about three to one (females predominating), but in an inconsistent pattern throughout the non-breeding period. Although females seemed more numerous than males, it was clear that the disparity in the ratio of the sexes never reached the magnitude of that found in the Redwing. Most males and females tended to roost together in WLSM (along with many

Redwing females, fewer Cowbirds and Redwing males), so that the degree of separation of sexes in roosting Tricolors was less than in Redwings (Nero, 1956).

Chorusing in roosting and arousing Tricolors consisted in the gradual buildup of a steady droning of nasal "growls", with the initiation and augmentation of the chorus similar to the Redwing pattern. Tendencies for roosting segregation of Tricolors from other species were reflected in the situations at Blue Moon Ranch and other San Joaquin Valley sites, and on Cache Creek in Kern County. This species has consistently shown a gregariousness and preference for flocking and roosting with individuals of its own species throughout the winter.

At Lake Sherwood many Tricolors also returned characteristically to rest in vegetation on the lake during late morning and midday hours. However, rarely more than 300 or 400 of these individuals appeared on the lake at one time during that period before the commencement of evening roosting arrivals. Certain trends were clear in this activity. Small flocks of returning birds gradually augmented these midday resting flocks; but they varied daily in number and location at the west end of the lake. These flocks of morning revisitants formed a typical chorus of droning vocalizations. Although the droning songs were uttered only by males, some females were always included in the flocks, their numbers fluctuating greatly.

Aggression among individuals of Tricolor roosting flocks was extremely low, although they roosted more densely than they occurred in nesting situations. Tricolors engaged in typical pre-roosting activities noted for Redwings. Hostility was related to shifting of positions in the roosting flock and was most often exhibited by male birds uttering a characteristic threat (annoyance) call which has been phonetically rendered as "Kraah" (see below under Tricolor Vocalizations), and occasionally pecking at one or more nearby birds. Although the nature of the vegetation and the presence of large, mobile numbers of Tricolors, precluded determination of whether a particular bird roosted in the same spot all winter, the Tricolor flocks tended to maintain relatively stable numbers and a constant roosting site throughout fall and winter of a given season at Lake Sherwood. However, most of them had disappeared from the lake by August, 1959; and subsequently there was a buildup to the peak levels seen during the following fall and winter (Fig. 6). As shown in Figure 6, this late summer fluctuation in numbers was proportionately greater in Tricolors than any other roosting species. The Tricolor population did not decrease again at Lake Sherwood until the following March, 1960, when Tricolors began a complete desertion. In 1958-1959 the relatively high numbers of Tricolors remained in the marshes all winter; and it appeared that small total numbers deserted the lake, so

that the breeding population numbered slightly less than the previous winter roosting population (Fig. 6).

G. L. Hutson, of the Encephalitis Laboratory at the Bakersfield General Hospital, (Pers. comm.) has stated that by marking Tricolors with colored dyes during the winter of 1952, he found a high rate of turnover of individuals in roosting populations of the southern San Joaquin Valley, since most of his marked birds disappeared after intervals of three to four weeks and unmarked individuals replaced them. Neff (1941) also documents winter wandering of the species in the Central Valley of California. The Tehachapi Pass-Cache Creek area becomes climatically most inhospitable in winter with occasional snow and freezing night temperatures. Tricolors never roosted there between September and the following March. In contrast, the San Joaquin Valley features a relatively more equable climate, an intensive year-round irrigated agriculture, as well as extensive areas devoted to feeding of beef cattle. The Lake Sherwood area tends to parallel the latter region in these conditions. The mosaic of these ecological conditions is variable, however; and the Tricolor population mobility recorded by others, and suggested even by the moderate changes in Lake Sherwood winter numbers (Fig. 6) probably reflects adaptive responses to localization of food resources.

Tricolor stomach contents during fall and winter

indicated that the diet was nearly all plant material, and correlated with the types of plants which were in fruiting stage around the roosting regions during those months. At the Blue Moon Ranch, Tricolors fed almost exclusively upon ripening milo maize, as noted for Redwings, prior to roosting in mid-October, 1960. Elsewhere, weed seeds (particularly Erodium cicutarium), and cereal grains (such as those found in prepared cattle feeds) comprised most of the diet. By March, Tricolors showed an average increase in insect food (Fig. 13), which correlated with environmental conditions reflected by insect abundance during the period of late winter and early spring rains (Fig. 11).

Foraging habits were not observed to differ between the two species. However, Tricolors were often found in flocks separate from all other birds, particularly in the Lake Sherwood area. In such instances it was not determined whether the birds were eating different foods.

Composition of Tricolor feeding flocks was recorded on several occasions and males usually predominated, especially in the Lake Sherwood vicinity; but again, proportionately more females were present in such flocks than there were in similar Redwing flocks. In foraging Tricolor flocks aggression seemed to be at least as low as in Redwings under similar foraging conditions.

Species interactions between non-breeding Redwings and

Tricolors did not appear decisive in determining the success of either species. There was no clear evidence of actual physical competition or struggle over food or space between members of the two species. Compared to Tricolors, Redwings roosted in proportionately greater numbers and density than they nested during the breeding season. As a result, Tricolors at Lake Sherwood occupied little more area during the non-breeding season than they did during the nesting period. Doubtless each of the two species occupied roosting space to the partial exclusion of the other, and foraged in areas where each obtained food at the potential expense of the other. Difficulty in quantification of these relationships within highly mobile blackbird flocks, has left the impact of such a condition as yet unresolved. It did appear that at Lake Sherwood and in the Central Valley both species possessed the capacity of foraging widely enough to avoid each other, depending upon the roosting site only for shelter. Also, exclusion of one another from any portion of this shelter site was not due to any measurable aggressive tendencies by either species. Fluctuations in roosting blackbird numbers at such sites as Lake Sherwood and Cache Creek seemed clearly attributable to favorable or unfavorable habitat conditions, both shelter and foraging, than to any ability of one species to displace or prevail over the other by aggression. Thus, apparent winter movements by portions

of either Redwing or Tricolor populations could not be attributed directly to the influence or impact of one species on the other.

B. Breeding Season

The Redwing

Territoriality

While actual procurement and fertilization of a mate signal the start of Redwing breeding, aggressive activities by males exhibited ostensibly in the non-breeding season, herald the onset of reproduction. Males which successfully engage in these activities are placed in the most favorable situation to reproduce. Such behavior forms an integral part of breeding chronology, resulting in the absence of a sharp demarcation between non-breeding and breeding phases of the annual cycle. The ensuing account considers spatial and temporal aspects of development and maintenance of territory, the initial manifestation of the transition to a breeding period.

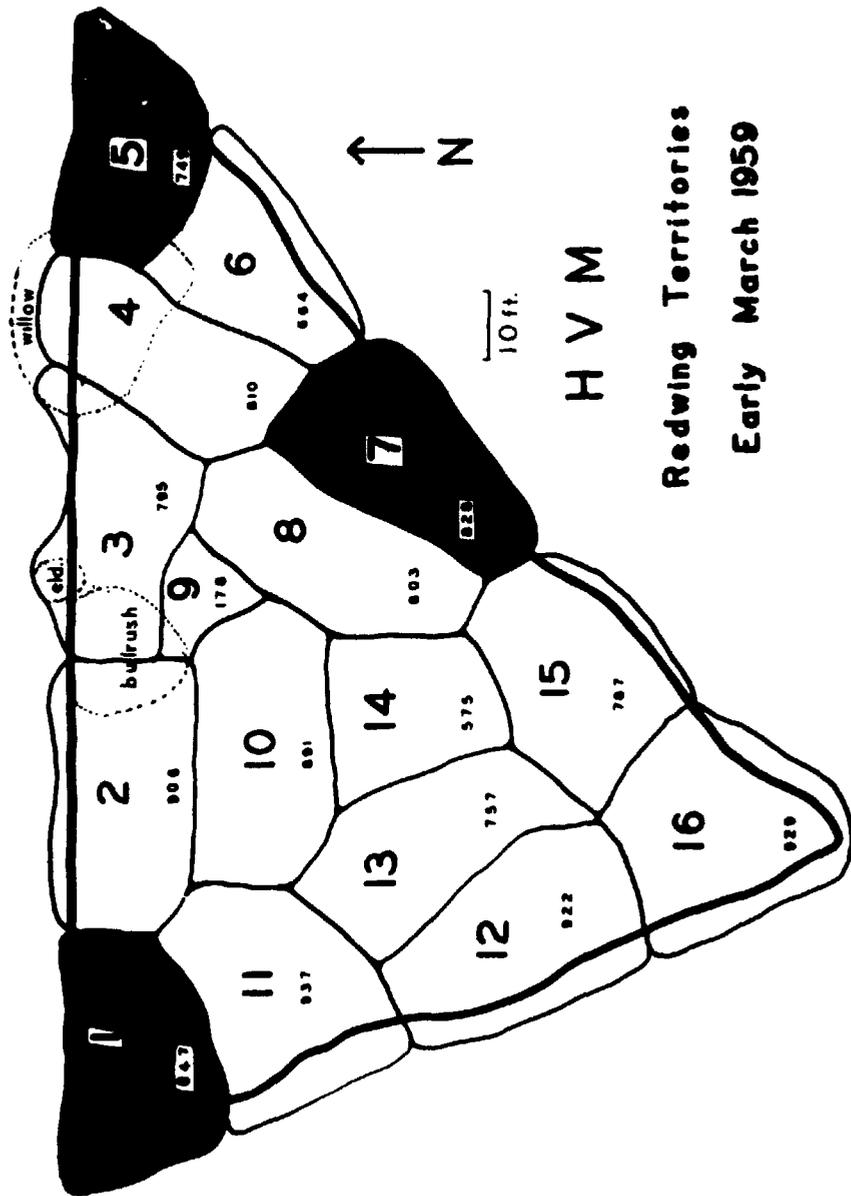
Each male so capable occupies and defends a well-defined space exclusive of other Redwing males, within which a nesting cycle develops when the owner acquires one or more mates. Persistent inter-male contests occur, resulting in a relatively wide spacing among successfully territorial males.

Southern California Redwings reside continuously on breeding sites throughout the year, or move only locally to

roost in protected areas during fall and winter. This contrasts with the more mobile, highly migratory populations of this species in much of North America, which spend the non-breeding period great distances away from territorial and nesting sites (Beer and Tibbitts, 1950; Nero, 1956a). Such perennial resident males at Lake Sherwood were observed to manifest significant territorial site tenacity outside the breeding period. In a few cases these males were recognized (Figure 9) on incipient territories by early January, 1959 (Table 3) at sites occupied the preceding breeding season.

Lake Sherwood further afforded abundant examples of measurable early Redwing territoriality. Aggressive encounters had clearly begun on HVM during the mornings by mid-January, 1959, fully seven weeks prior to the first recorded pair formation there (Table 3). The most vigorous and intensive interactions occurred among the potentially breeding adult male residents, as monitored between January and late March (Figures 9 and 16). The several hundred other roosting cohabitants mentioned earlier were usually only involved incidentally in such interactions, as also occurred on Lake Sherwood proper. Most of these individuals seemed merely to disrupt and obscure Redwing territorial ontogeny by their presence during morning arousals and evening arrivals without engaging in vigorous territorial conflicts. During late March, when Redwing territorial

Figure 9 shows a scale diagram of Hidden Valley Marsh during the first week of March, 1959. Male Redwing territories are outlined and numbered (1-16) in heavy black. The small numbers in each territory indicate the area in square feet. The stippled territories (1,5,7) are those of identifiable, but unbanded males. Territory 9 is that of banded male "532". Abbreviation "eld." means elderberry tree. Compare Figures 3 and 8.



H V M
Redwing Territories
Early March 1959

Table 3 shows the dates of commencement of successive phases in the Redwing breeding cycle, 1953-1960, at three study sites. In order, the phases for each year are as follows: First territorial defense; Arrival of first females; First sexual chases; First female pre-coital display; First nests built; First copulations; First eggs laid; First hatchings of young. The dates list the month first, the day of the month second. Question marks mean no observations, or estimated dates. For HVM, dates in parentheses represent estimated dates of breeding start; Tricolor invasion subsequently delayed effective Redwing breeding for two weeks (see text).

Table 4 (lower) shows sex ratios and population sizes of Redwings for the localities and years listed. Total population is the first number, followed by the number of breeding males. Dashed lines mean no observations; "X" means no counts made during observations; question marks mean undetermined numbers of birds; an asterisk means no observed effects of interference by shifting Tricolor flocks; and superscript "a" means breeding occurred adjacent to a Tricolor colony.

Redwing Timing

<u>Lee Lake</u>	<u>1953</u>	<u>1954</u>	<u>1956</u>	<u>1960</u>
Territory	--	1/20	--	est. 1/21
Females	--	3/1	3/17	ca. 4/1
Arrival				
Sexual Chases	--	3/1	3/17	4/2?
Precoition	--	3/8	--	4/3-5
Nests built	3/19-20	3/11	3/23	ca. 4/5
Copulations	--	3/14	3/25?	4/7-8?
Egg laying	3/25	3/17	3/29?	4/11
Hatching	4/8	4/12	4/11?	ca. 4/25
<u>WLSM</u>	<u>1958</u>	<u>1959</u>	<u>1960</u>	
Territory	1/15	1/15	1/20-21	
Females	--	3/4	ca. 3/7	
Chases	3/7	3/5	--	
Precoition	3/7	3/8	3/11	
Nests	3/15	3/12	3/17	
Copulation	3/20	3/16	3/24	
Eggs	3/26	3/22	4/1	
Hatching	4/9-10	4/6	4/14-15	
<u>HVM</u>	<u>1958</u>	<u>1959</u>		
Territory	1/15	1/15		
Females	3/1	3/5		
Chases	3/5	3/8		
Precoition	3/8	3/18		
Nests	3/13	(3/28?); 4/7		
Copulations	3/20	(3/30?); 4/10		
Eggs	3/26	4/12		
Hatching	4/11	4/26		

Redwing Populations

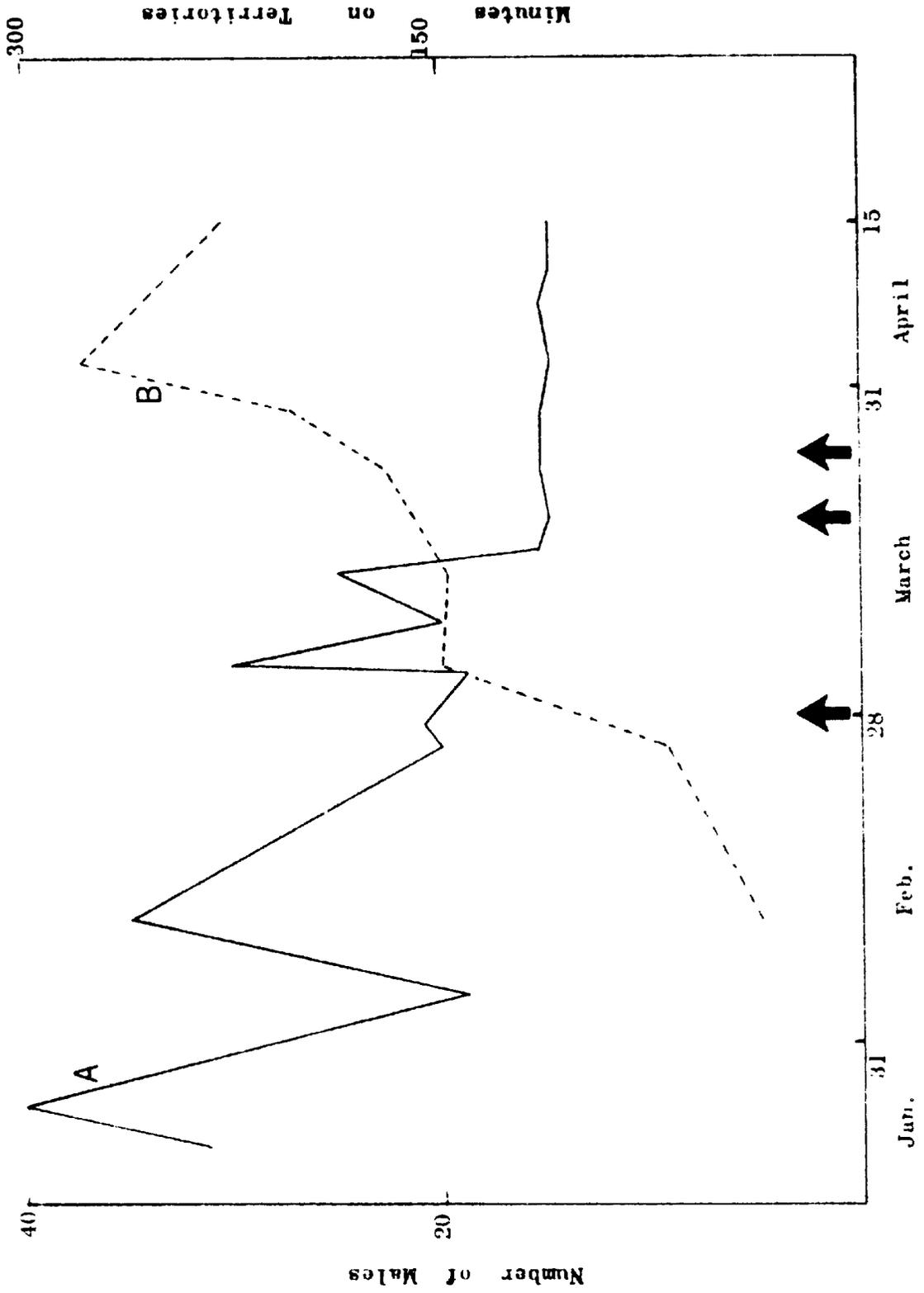
	<u>Rio Hondo</u>	<u>Lee Lake</u>	<u>Lake Sherwood</u>	<u>Sepulveda Dam</u>	<u>San Fernando Reservoir</u>
1953	none	200/48	--	--	--
1954	40(?)	180/62	--	--	--
1957	X	170/68	175/58*	--	--
1958	60/15	200/?	350/80*	--	^a 25(?)
1959	X	180/67	400/85*	200/60	^a 20/6
1960	50/12	180/66	200/65*	200/61	^a 15/4
1961	50/?	--	100/27*	Habitat destroyed	11/3

activities approached a stable level (Figure 10), such transient winter roosters were rapidly disappearing (Figure 6), as these birds presumably departed in search of their own breeding areas.

January territoriality was temporally sporadic, being exhibited only for brief periods during the day. As the season progressed, males on HVM in 1958 were observed to spend more time daily on individual territories (Figure 10). There was further a gradual, irregular decrease in recorded male Redwing numbers actively trying to occupy territories on HVM. The greatest amount of fluctuation in territorial male numbers occurred prior to March 1, which again was probably in part related to interactions with males in the transient winter roosting population present. The general trends were reduction in numbers of territorial Redwings, increase in mean territory size (Figure 9), and increase in time spent by a male within its confines. The first two trends are in direct contrast to that reported in regions where Redwings are highly migratory. In Wisconsin and New York, for example, spring migrant arrivals produce increases in numbers of competing territorial males and decreases in mean territory size (Allen, 1914; Nero, 1956b; Case and Hewitt, 1963).

Although the territorial male population on HVM had stabilized by the third week of March, 1958, a few days before first observed copulations (Table 3; Figure 10),

Figure 10 shows the maximum number of males observed on territories at HVM, 0800-1000 hours, February-April, 1958, in the solid line "A". The dotted line ("B") indicates the estimated mean amount of time spent on a territory by individual males, 0700-1200 hours, during the same period. The vertical arrows indicate, from left to right, arrival of first females to prospect the marsh, first observed copulations, and first eggs laid.



vigorous encounters continued between established and un-established males at least until mid-April. Achievement of a relatively stable population did, however, additionally correlate with an apparent slackening of intensity of physical encounters among established HVM males. During January and February such encounters had at least increased in frequency as males increased time occupying territories. Vocalization, moving and stationary display, and fighting represent the range of increasing intensity of interactions observed among territorial Redwings; and by mid-March the first two (milder) categories of encounters prevailed.

Contests typical of both established and unestablished males were engaged in by a banded Redwing (orange-pink-white = "532") on HVM during February-March, 1959. During February, male 532 roosted in the marsh, and persisted in attempts to gain a territory at its south end in conflicts with male 16 there (Figure 9). Unable to establish himself in south HVM, by March 1 male 532 had moved to the north side of the marsh where he similarly attempted to insert himself in contests with males 3,4 and 5 (Figure 9). In all of these attempts, male 532 undertook flight displays, song, and sporadic attack; but only subsequent to capture and removal of an unbanded established male in north-central HVM on March 5 did male 532 establish himself in a territory (male 9, Figure 9), defending one of the smallest Redwing territories yet on record. The space seemed re-

duced in area compared to that of its previous occupant, and male 532 was constantly engaged in displays and boundary fights with his neighbors.

The above and other observations suggest the presence of extra, peripheral adults, both resident and transient, which represent a competing, potential replacement reservoir in contention with the established male population. Although the preceding seems widespread among Redwings (this study; Nero, 1956b; Orians, 1961), an unusual sequence of events at HVM in 1959 suggested that the apparent surplus of male Redwings was most abundant, and exerted greatest pressure upon the established males before and during the early part of nesting in the species. An invasion of the marsh by prospecting Tricolors occupied central HVM until mid-April (Figure 16), when most of that species departed apparently in favor of other nesting habitat. Tricolor evacuation was not followed by a return or replacement (by peripheral males) of any of the nine originally evicted Redwings. Instead, the remaining seven resident Redwing males simply occupied the vacated marsh portion (compare Figures 16 and 26). During this period of readjustment on HVM, two to three weeks after most Lake Sherwood Redwings commenced breeding, no unestablished males, adult or immature, were found attempting to obtain territories in central HVM.

Numerous studies in diverse geographic areas and vege-

tational substrates have shown great size variation among individual Redwing territories. Table 5 illustrates substantial territorial size range in the present study. Grouping of these territories into particular habitat categories causes the size variations to assume a consistent pattern. These habitats were: 1) Marsh-edge; 2) Medium to large open marsh; 3) Open field. In the same numerical order, mean territory size increased through category 3. Table 5 shows 308 territories in category one averaged 2306 sq. ft.; 171 in category two averaged 2.7 times the mean of category one; while the mean for 137 territories in category three was 3.5 times that of category one. Although there was overlap in territory sizes among the three habitat categories listed, most of them fit the correlation of the larger and more uniform the habitat, the larger the territory. A non-parametric, two-sample rank test (Goldstein, 1964:55) of the territory means in Table 5 showed significant differences between categories one and two and between categories two and three at the one percent level.

Besides the above categorical distinctions, numerous other examples of intraseasonal and annual variation in Redwing territory size were observed. The simplest trend during a season was that of size increase, correlating with the previously described intense territorial competition and accompanying decrease in numbers of competing males during prebreeding activities. This condition was compli-

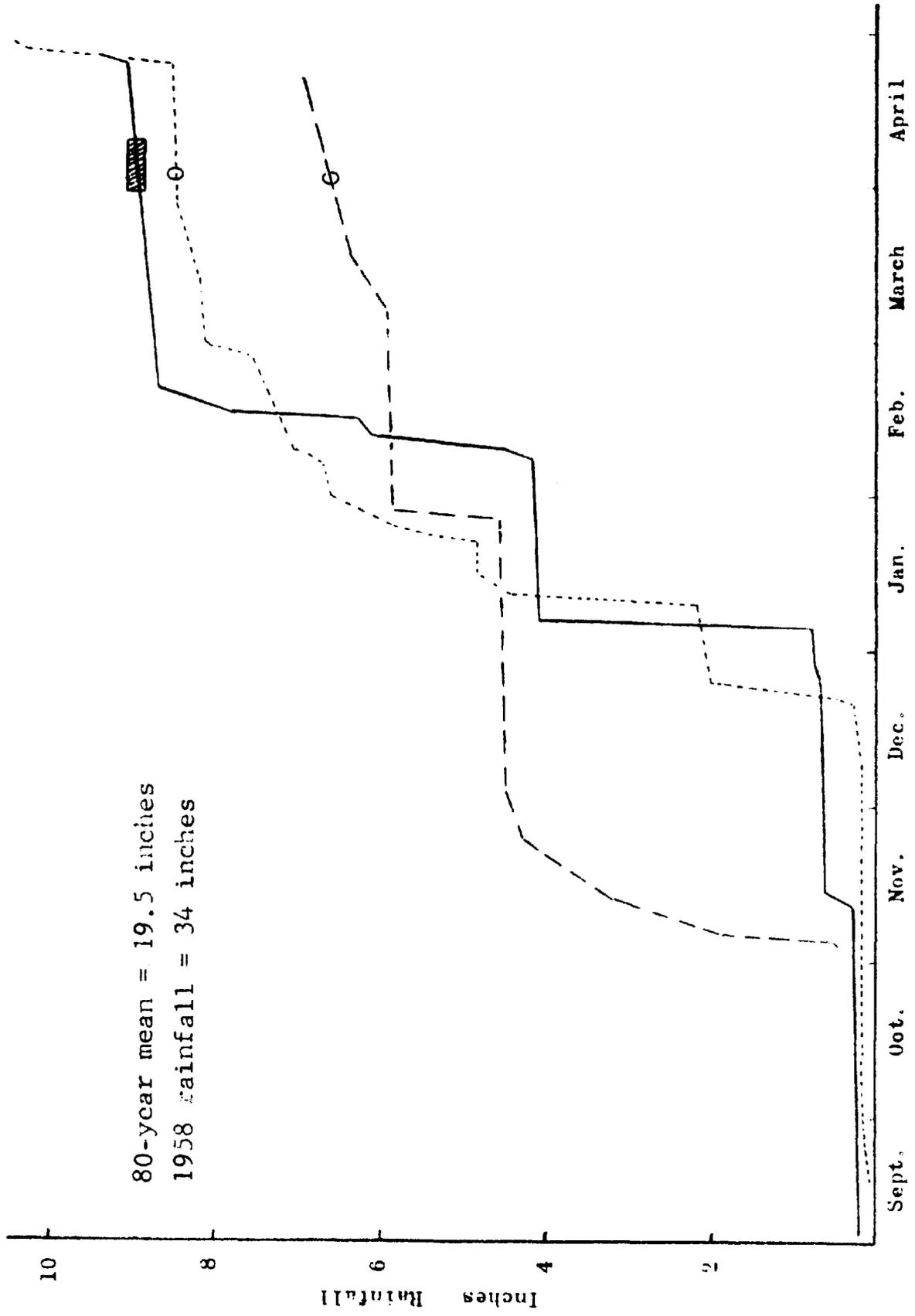
Table 5 summarizes data on mean square footage of Redwing territories versus number of males holding territories (e.g., 2000/6) in three different types of habitat measured. A dashed line means no observation was made. An "X" means no measurement was made during observations. A zero means the species was absent from a habitat. The presence of an asterisk next to the number of Redwing males indicates they bred adjacent to a Tricolor colony. Mean territory size is included for each category. Edge-foot refers to ratio of ecotonal perimeter present adjacent to the habitat (see text).

1) Edge habitat		Mean size = 2306 sq. ft. (N = 314)							Areal Square Feet/ Linear Edge-foot	
	1956	1957	1958	1959	1960	1961	1962	15 [along creek]	a10; b20 [marsh edge]	
Cache Creek	X	800/6	0	774/16	b2000/5	2000/5	2000/5			
HVM				720/7*						
				1571/7						
Lee Lake	X	--	--	1200/15	1200/15	1400/14	--	40 [on lake inlet]	a30 [riparian marsh]	
Rio Hondo	a3000/4	--	--	--	X	b3878/10	X	b13 [narrow stream]		
L. A. River tributary	--	--	--	a3000/15	b2080/61	X	X	a20; b29 [stream]		
S. F. Reserv.	--	--	3000/6*	a2500/2*	b4500/3*	--	--	a30; b35 [marsh edge]		
W. L. Sherwood (lake edge)	X	X	be3600/5*	f3000/21	4000/19	X	X	be25; f40; g45 ["be" = Figure 28 diagram]		
Blue Moon Ranch (drain ditches)	--	--	--	--	3000/30	X	--	30 [marsh borders]		
2) Large-marsh habitat		Mean size = 6193 sq. ft. (N = 171)								
W. L. S. (not lake margins)	X	X	3000/15	4000/15	5000/40	6540/52	X	All	> 60	
"Nigger Slough" Torrance (Livingston, 1949)	--	10000/20	--	--	--	--	--		> 100	
Santa Clara River	--	--	--	--	--	7000/18	--		> 70	
San Diego River (impoundments)	--	--	--	--	--	--	8000/11		> 70	
3) Open-field habitat		Mean size = 8121 sq. ft. (N = 137)								
Hidden Valley	X	X	7000/50	8000/50	7300/12	0	X		> 100	
Blue Moon Ranch	--	--	--	--	11000/25*	0	--		> 175	

cated by Tricolor interference on HVM in 1959. A stable mean territory size of 774 sq. ft. in early March (Table 5, Figure 9) decreased to 720 sq. ft. during early-April Tricolor invasion (Figure 16), but more than double to 1571 upon Redwing reoccupation of vacated habitat by mid-April. Only instances of conflict with Tricolors led to observed reduction of mean territory sizes during a breeding season among southern California Redwings.

Annual fluctuations in territory sizes usually coincided with climatic variations or habitat modifications. Post-1953 increase above 900 sq. ft. in territory size at Lee Lake (Table 5), in conjunction with decrease in numbers of territorial males from 20 to 15, followed removal of adjacent open grassland. Similarly, climatic and habitat adversity resulting from low rainfall (Figure 11) were followed by reduction of the territorial male population and a corresponding rise in mean territory sizes from 1959 onward (Tables 4 and 5) in large marsh situations and in some open-field habitat. Climatic change had two effects in the Lake Sherwood area. First, marshy area on the lake increased conspicuously during 1960 and 1961 with lowering of the lake level. Concomitantly, the number of males and mean territory size rose (Table 5). Second was the effect upon open-field habitat between 1958 and 1961. During 1958 field growth was the most luxuriant of any year observed, and largest numbers of territorial males were present.

Figure 11 summarizes rainfall data at Lake Sherwood for the dry seasons, 1958-1961. The solid line indicates 1958-1959, the short-dashed line 1959-1960, the long-dashed line 1960-1961. The cross-hatched bar shows the dates of commencement of initial Tricolor breeding in 1959. The two open circles show the dates when this species commenced colony establishment but deserted the site, 1960 and 1961. Mean annual rainfall, and the high for 1958, are listed in the upper left of the figure.



Mean territory size increased during drier 1959 with at most a slight reduction in territorial individuals (Table 5); but in the following year far fewer birds bred with smaller average territories in less extensive field habitat. In 1961, when fields in the area were extremely parched, and growth stunted, no Redwings occupied territories there.

The foregoing observations have indicated a correlation between habitat favorability and Redwing exploitation. It is implied that such favorability correlates with abundance of environmental resources. At this point it is profitable to quantify further a definition of edge habitat in relation to Redwing territoriality. Edge-habitat, or ecotone, is used here in the same sense that ecologists employ it (Odum, 1959:279), that is, an area of transitions between two kinds of vegetation or habitat. Such a transition is often abrupt, as the change from cattail marsh to grassy bank. A grassland-marsh "edge" was the typical condition observed in Redwing habitats. Expanding the description further, large marsh and field habitats were similarly bordered by edge situations.

Edge relationships in Redwing habitats were measured as follows. Total habitat area occupied territorially at each site was divided by the computed linear footage around the edge of the site, where the edge transition occurred. The derived ratios of square footage per linear edge foot

are included in Table 5. Edge habitat, category one is characterized by a low ratio, below 50:1; large marsh areas all showed higher ratios, usually between 50 and 100:1; and the few recorded open-field ratios measured above 100 to 1. These measurements basically reflect the occurrence of Redwing territories in habitat of variably limited extent, whose margins were readily distinguished from adjoining vegetation. The periphery of the above described habitats usually marked the approximate limits of the territorial Redwing population; but males consistently included such edge situations within their territories. For example, peripheral males on HVM (Figure 9) invariably defended the moist grassy vegetation at the margins of the marsh cattails. These findings agree with Beecher (1942) and Odum (1959) who show higher avian breeding densities in habitats with large proportions of edge habitat.

In this study the comparatively small territories of category one were the same size range as those of relatively small marshes measured by Thomsen (1944), Beer and Tibbitts (1950), and Nero (1956b) in Wisconsin, Strosnider (1960) in Kansas, and Orians (1961) in central California, all of which averaged between 2500 and 3500 sq. ft. Similarly, near Ithaca, New York Case and Hewitt (1963) found smallest territories in marshes and largest territories in upland field habitats. Among the largest territories reported for this species are those of Linford (1935) in

large marshes of the Utah Great Basin where average territory size was about 31,000 sq. ft.

Foraging behavior tended to vary according to habitat in territorial males observed in the study. All marsh inhabitants spent most of their time feeding outside their territories. For example, both centrally and peripherally located males on HVM (Figure 9) fed mainly in the grass and sedge borders of the marsh or in adjacent pastures and fields (see also Figure 3 and Table 11). In contrast, owners of open-field territories spent nearly all of their daily activity, including foraging, within their territories. Only occasionally were Hidden Valley males observed to cross Potrero Road (Figure 3) north or south to fields outside their territories. These observations agree with Nero's (1956a), who reported Redwings feeding in the "uplands" away from the breeding marsh. Birds studied by Linford on the other hand foraged almost exclusively within their large territories. Orians (1961) has also suggested a correlation between territory size and the amount of time spent feeding within it.

Fair Formation and Sex Ratios

While resident southern California Redwing males underwent conspicuous behavioral preparation for breeding during several weeks prior to acquiring mates, females showed no outward behavioral change. Although they often roosted with males in the same marshes at Lake Sherwood,

females defended no territories, seemed no more aggressive toward roosting fellows, and were typically absent during the day from marshes until early March.

Resident Redwings in southern California marshes thus had the entire winter in situ to influence one another. As a result, it is difficult to assign a precise date to actual forming of a pair in such individuals. However, females began to appear regularly, and in substantial numbers, only at the actual time they commenced to prospect potential breeding sites and establish recognizable pairing relationships with males. These dates ranged from 11 to 26 days before egg-laying (Table 3). This compares favorably with Nero's data (1956a) in which the mean period between the start of pairing and egg-laying was about 21 days. The suggestion of a slightly shorter period in southern California birds may again be related to the fact that potential mates roost together on breeding sites during the whole non-breeding period.

Entry of a female into a potential mate's territory during a given day (Table 3), and overt mutual interaction with him, signaled a change from the quiet and sporadic female presence during preceding weeks; these clearly constitute the onset of effective pair formation. The phenomenon, observed at both Lee Lake and the Lake Sherwood area, was striking. In these cases females appeared on the marshes, apparently quite tense, peering about intent-

ly, with closely appressed plumage. Some of them simply wandered through the marsh; while others seemed to go directly to a certain part of a territory --- as though they had made a prior selection, perhaps as a result of roosting there. Immediate male reaction to such intrusions was variable; but by the end of a day after initial female arrival males had begun to frequent "sexual flights" or "chases", a male pursuing a female generally within his territory. Occasional "group" sexual chases were observed, such as at Lee Lake in early March, 1954. Typically several males collectively chased a single female, often through the territories of several males. Such group interactions were unusual and occurred only during the early part of the pairing period when the resident males greatly outnumbered prospecting females.

Intensive sexual chases lasted about a week for individual females, soon being followed by initial copulations (Table 3). Unmistakable female readiness was signaled by the onset of frequent, loud precopulatory calls and attendant displays (Figures 20 and 21). By then, an individual female had come to occupy a distinct part of the mate's territory, which she maintained as a "sub-territory" (Nero, 1956a) when the male was polygynous. Other females were excluded from the sub-territory.

Subsequent to arrival of initial prospecting female contingents, most males acquired one or more additional

mates during the first two to three weeks of the breeding season. Males facilitated initial entry of later females into territories by driving away earlier established females, usually while alternately engaging in sexual chasing with the new female. This arbitration literally made possible the formulation of a stable sub-territorial organization within a polygynous mating system.

The Redwing males in this study were typically highly polygynous (Table 4), some acquiring as many as six mates. Since most of the breeding population was unmarked, the ratios in this study were determined by observation of male actions, and by counting simultaneous nestings in one territory. Data from Table 4 indicate that sex ratios usually averaged between two and three females per male, with an overall mean 2.7 per male. Sex ratios were approximately equivalent in comparing small, medium and large territories (Table 5), indicating increasing density of female population proceeding from large to small territories. Highest sex ratios occurred in the Lake Sherwood area during the 1958 and 1959 seasons when the Redwing population was largest, and environmental conditions appeared most favorable. Coinciding with increasing drought, female numbers dramatically diminished during 1960 and 1961 in the same area (Table 4).

Redwing ratios in this study averaged slightly higher than those reported by most authors, whose means ranged

between 1.6 and 2.8 females per male (Smith, 1943; Beer and Tibbitts, 1950; Nero, 1956a; Case and Hewitt, 1963). Several authors have noted higher average sex ratios between 2.8 and 4 females per male, (Orians, 1961; Strosnider, 1960); and Lindsdale (1938) claims ratios as high as 8 to 1 in Nevada Redwings. In all instances there were clearly individual, seasonal and geographic variations in sex ratios, with monogamy a rarity.

Nesting Substrate and Nest Construction

Preceding accounts indicate that choice of nesting vegetation was dependent upon male territory. Nests were built only in such areas and successful males were clearly those in whose territories females settled and reproduced. Table 6 compiles data on vegetation used in territory and nesting by southern California Redwings. Characteristic of the species, about half of the observed populations selected cattail marshes, and 80 percent occurred in some kind of marsh vegetation. The remaining examples of dry land nesting parallel a variety of published accounts on Redwing use of non-palustrine habitats (Dawson, 1921; Calder, 1926; Smith, 1943; Nero, 1956b).

In marshes, Redwings consistently showed a preference to place nests in vegetation with water beneath it, when such was available. However, they continued to occupy nests in drying marshes such as HVM and Lake Sherwood in 1959. Moreover, many nests were built in completely dry

Table 6 (upper) summarizes data on the types of nesting habitat utilized by Redwings in southern California. Breeding populations were divided into two groups: Group 1, those with a single male and mates; Group 2, those with two or more males plus mates. No breeding populations were observed adjacent to Tricolors in which only one male Redwing was present. Asterisked other marsh category means mulefat, knotweed, curly dock, sedges (see "Study Areas" above).

Table 7 (lower) summarizes data for clutch size of Redwings at the study sites listed. Total nests refer to number in population sampled. Numbers in 2 to 5 clutch-size column indicate nests actually sampled. Superscript "a" indicates nests censused only at the south end of WLSM (West-end Lake Sherwood Marsh). Superscript "b" indicates nest counts made only in the northwest corner of Lake Sherwood (see Figure 8), 1960. Superscript "c" indicates that nest counts were made only in the northwest corner of WLSM, 1961.

	Riparian	Cattails	Bul-rush	Other* marsh	Dry fields
Isolated males ¹	2	3	0	0	0
Small populations ²	11	27	6	3	10
Tricolors ² adjacent	2	5	1	1	1
TOTALS	15	35	7	4	11

Total nests	Sites	Year	Clutch size				Mean
			2	3	4	5	
160	Lee Lake	1953	4	44	39	2	3.44
120	"	1954	1	18	18	2	3.54
85	"	1956	1	13	11	1	3.46
70	"	1958	1	6	5	0	3.33
25	HVM	1957	0	3	3	0	3.50
45	"	1958	2	23	19	0	3.39
65	"	1959	2	10	12	1	3.63
50	WLSM	1958 ^a	1	7	4	0	3.25
60	"	1959 ^a	3	17	11	1	3.31
30	"	1960 ^b	1	3	4	0	3.25
25	"	1961 ^c	1	5	1	0	3.00
30	Rio Hondo	1960	1	12	9	1	3.43
70?	Hidden Valley fields	1960	0	5	2	1	3.50
50?	Blue Moon fields	1960	2	6	6	1	3.40
150	Blue Moon drain ditches	1960	0	13	15	2	3.63
75	L.A. River Sepulveda Dam	1961	4	17	12	0	3.24
1055	<u>TOTALS & MEANS</u>		24	202	169	12	3.42

(407)

marsh vegetation, consisting of isolated clumps of bulrushes and cattails, on northwest Lake Sherwood.

In both marshy and terrestrial habitats Redwings invariably preferred what observation lead to be described as the sturdiest vegetation available. Along the shores of Lee Lake, nests were commonly placed on the open-water side in dense clumps of water iris. Similarly, in stream-side marshes of the Sepulveda Basin, Rio Hondo, San Diego River, and elsewhere, nests were most often found on the open-water side of the thickest cattail and bulrush growth available.

In 1961 when all of the west end of Lake Sherwood was dry, with much of it covered by herbaceous growth of sweet-clover (Melilotus indicus) and curly dock (Rumex crispus), preferred vegetation was still clumps of dead bulrushes and cattails. In open fields Redwings chose stronger suffrutescent vegetation such as large wild mustard plants (Brassica nigra) growing among grain or forage crops (Hidden Valley, 1958; Blue Moon Ranch, 1960), or a dense firmer herbaceous growth of plants such as fiddle necks (Amsinkia intermedia) in Hidden Valley barley fields during 1960.

While Redwing avoidance of various habitats surrounding breeding areas at sites such as Lake Sherwood doubtless reflected their unsuitability for nesting, a single example of failure to complete a nesting cycle in a previously

favorable site was observed. During 1960, only five male Redwings established territories on completely dessicated HVM whose cattails had been reduced to low, broken and largely isolated clumps as a result of winter grazing by dairy cattle (Table 5). No more than a dozen Redwing females briefly prospected the marsh during the first week of April, without any apparent inclination to stay or any sexual responses toward the territorial males. The latter had deserted HVM by the end of April. This seemed clearly a demonstration of the requirement for males to select some minimally favorable form of vegetation to be successful in retaining nesting females. Among the territorial males present in 1960, one (number 7, Figure 9) had bred successfully there 1957 through 1959.

Male and female behavior in which the two wandered together through a sub-territory as though choosing a nest location, defined as "Symbolic Nest Site Selection" by Nero (1956a), and a few instances of "Symbolic Nest-building" (Nero, 1956a) during which the male manipulates bits of vegetation, were observed (see section on Redwing Displays). However, actual nest construction is performed by the female alone, after five to fourteen days of symbolic and sexual interaction with the male (Table 3). Time required to complete nests averaged about five days, rarely taking over a week early in the season at southern California study sites. Nests seemed to be built more rapidly

later in the season (May-June), as reported by Case & Hewitt (1963).

California Redwings built nests essentially like those described in the earlier excellent summary and accounts of Allen (1914), and more recently by Bent (1958). Kinds and consistencies of materials conformed generally to those typical of nests built in marshes. Nest structure is divided into three parts: 1) lowermost loosely woven base of coarse stems and leaves, cattails, bulrushes, or grasses ranging two to 12 inches in depth, usually anchored to three or four sturdy vertical stems of substrate, as previously described; 2) a middle, shallow concavity with a thin lining of initially moist bits of stems, leaves and mud, which hardens into a stiff shell of "papier mache" consistency up to a quarter-inch thick; 3) a finishing deeper cup of fine-stemmed grasses and similar plants, resulting in an upper structure ca two inches deep and three inches in diameter. Nest materials correlated with the apparently most readily available vegetation. For example, at Lee Lake, plants mentioned earlier, such as Dallis and Rhodes grasses, iris leaves, various decaying marsh debris including willow leaves, and slender grasses such as brome (Bromus sp.) and foxtail (Setaria viridis) predominated. In dry fields, nests commonly showed abbreviated bases and thinner or absent middle wet shell, the latter being obtained from nearby wet areas when included

in a nest. No females were ever observed to travel more than 300 yards from the nest site in search of materials.

Clutch Size and Incubation

In this study Redwing clutch size ranged from two to five eggs. These data are summarized in Table 7. All mean clutch sizes fell between three and four eggs. Small samples notwithstanding, means of Redwing clutches ranged from 3.0 to 3.63, with an overall mean of 3.42 (1953-1961). The smallest means were recorded during the driest year, 1961 (Table 7); while consistently higher averages occurred in apparently more favorable, wetter years prior to 1960.

Although most egg data were drawn from nesting situations in edge habitat (Table 5), comparable data from other habitats indicated no correlation between clutch size and habitat type or population size of Redwings, such as that reported by Case and Hewitt (1963) in which larger clutches were characteristic of more dispersed breeding populations in upland field habitats.

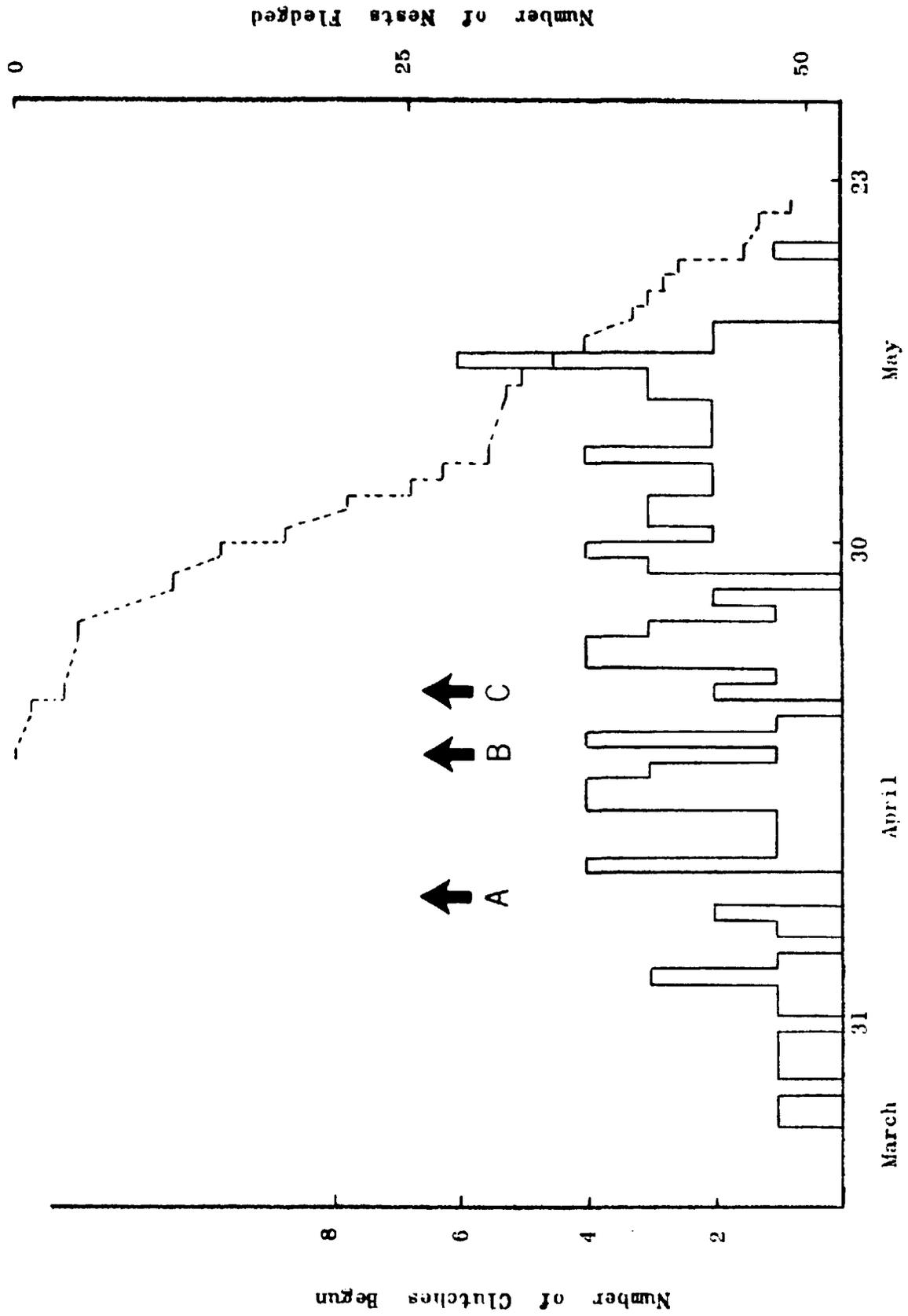
Long term averages in this study showed an expected correlation with latitude widely known for north temperate birds (Lack, 1954). Southern California Redwing clutches averaged typically smaller than those reported in various studies at more northerly latitudes (Case and Hewitt, 1963; Nero, 1956a; Smith, 1943); and they were larger than those reported in central Mexico by Hardy and Dickerman (1965). Intraseasonally, smaller clutches were laid early during

late March, with an increase in April (egg-laying often reached a peak by mid-April), followed by a variable condition in May: such as, continued increase in the mean shown at Lee Lake (1953) or a slight decrease (Lake Sherwood, 1958).

Numerical peaks reflecting simultaneous nestings seemed to be absent in Redwing populations studied. For example, at Lee Lake in 1953, (Figure 12) a daily record of clutch commencements reveals relatively continuous nesting activity from late March to late May. However, between April 9 and 19, twenty-four clutches were started, compared with only ten begun during the preceding ten days at the beginning of the nesting season. As nearly all new breeding females in a population appeared to have selected mates by early April, continued new nesting attempts, as late as June 15 in 1958, were attributed to re-nesting by the same females (see arrows, Figure 12).

Incubation was performed by the female Redwing alone. The male remained on his territory during much of the day, but rarely approached a nest except in times of potential danger, such as the arrival of an observer or a predator. The onset of incubation was accompanied by a sharp decrease in display and vocalization so loud and frequent in the female during courtship and nest-building. Females usually quietly left or returned to a nest with eggs, unless approached by an intruder or the mate.

Figure 12 compares the number of Redwing clutches begun per day at Lee Lake in 1953, with the cumulative number of nests that fledged during the same time. The bar graph indicates clutches begun; the dotted line shows cumulative number up to 50 fledged nests. Arrow "A" indicates the date of first hatching, arrow "B" the date the first clutch of eggs was recorded destroyed, arrow "C" the date of first fledging.



An incubation period of 11 to 12 days was determined for Redwings (Table 8), counting from the laying date of the last egg until all eggs had hatched. This paralleled reports of Beer and Tibbits (1950), Nero (1956a). No ten-day incubation periods were noted, as have been reported occurring occasionally in New York Redwings by Case and Hewitt (1963). Eleven-day periods predominated at Lee Lake in 1953-1954, where the most detailed accounts were obtained, a condition which appeared to prevail at all other study sites. Twelve-day incubation periods occurred only among the three- and four-egg clutches, ranging between 10 and 17 percent of totals observed in those two categories (Figure 12).

Foraging and Care of Young

The altricial Redwing nestlings were fed and brooded by the female, a condition long recognized for the species (Allen, 1914; and others). Foraging was consistently performed away from the immediate nest vicinity. All food was brought to the nestlings in the parent's beak, no regurgitation of swallowed food ever having been observed. Redwing food consisted of a variety of plant and animal material over a whole year, with insects and other arthropods usually comprising at least ninety percent of the intake during nestling life and most of the breeding season for marsh-inhabiting Redwings studied (Figure 13). Similar results were reported from central Canada by Bird

Table 8 (upper) shows Redwing incubation periods of 11 or 12 days, listed according to clutch size at three study sites, 1953-1959. Incubation was measured from laying-date of the final egg in a clutch. Two-egg and five-egg clutches all hatched within the 11-day period.

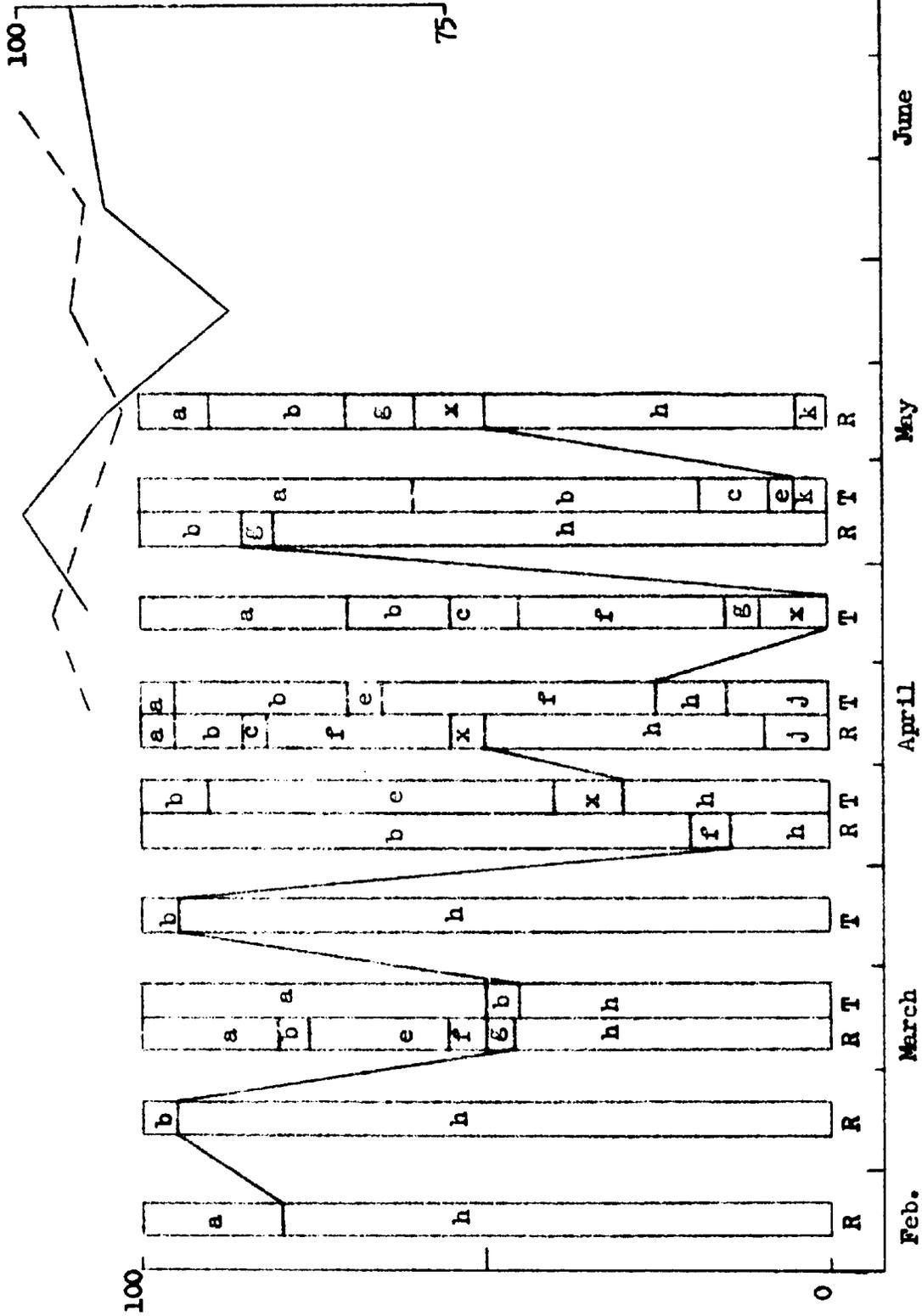
Table 9 (lower) shows Redwing nesting success at three study sites, 1953-1959. The categories of columns "A-E" include the following data: A) Total number of nests observed in which any fledging occurred (this number is calculated below in Category "C" as a percentage of total nests actually observed in a season); B) Percent of fledging from total hatched eggs in all nests observed; C) Percent of observed nests (Cat. "A") which fledged any young; D) Mean number of fledglings produced per successful nest (Cat. "A"); E) Mean number of fledged young per nest, when all observed nests ($\frac{\text{Cat. "A"}}{\text{Cat. "C"}}$) are included. Compare similar calculations for Tricolors in Table 19. Asterisk (*) for WLSM years indicates nest observations were made only at the south edge of that marsh.

	2-egg		3-egg		4-egg		5-egg		
	11 d.	12 d.	11	12	11	12	11	12	
Lee Lake									
1953	1	0	24	4	25	4	2	0	
1954	0	0	7	1	5	3	1	0	
Lake Sherwood									
1958	1	0	8	1	3	2	0	0	
1959	0	0	6	2	4	0	1	0	
HVM									
1958	0	0	5	0	3	0	0	0	
1959	0	0	6	1	2	0	1	0	
TOTALS	2	0	56	9	42	9	5	0	

	A	B	C	D	E	Total Estimated Population
Lee Lake						
1953	54	35.9	57.9	2.04	1.24	160 nests
1954	22	52.4	79.0	2.91	1.81	120
HVM						
1958	15	64.7	67.3	2.35	2.20	45
1959	25	18.8	63.1	2.40	0.67	65
WLSM						
1958*	6	60	60	2.0	2.0	50
1959*	11	50	60.7	2.0	1.82	60
TOTALS	127					500

Figure 13 shows a composite of data on Redwing and Tricolor food and feeding. The solid upper right line indicates food given young by Redwings on WLSM in 1959; the dashed line is the same year for tower bulrush Tricolors (see text). The vertical bars show proportions of food in Tricolor (T) or Redwing (R) stomachs collected 1954-1961, with months being divided into equal thirds. The "a-g", and "x" symbols mean respectively: Noctuidae, Coleoptera, Orthoptera, Odonata, Aphids, Homoptera, miscellaneous arthropods; and "h-k" refer to: cereal grains, Erodium seeds, and miscellaneous plant materials. See text for discussion. The diagonal lines connecting adjacent vertical bars indicate demarkations between animal and plant proportions.

Percent Nestling Animal Food



Relative Proportions of Animal and Plant Food in Adult Stomachs



and Smith (1964) for marsh-nesting blackbirds.

Small, scarcely visible food items were supplied to very young nestlings; but by the age of three days, nestlings received food items easily discernible from a distance of several feet.

As young Redwings grew in size, there appeared a tendency for the female to brood less during the day and to increase slightly the daily tempo of food delivery. The limited quantifiable observations on Redwings are summarized in Table 10 for several females at Lake Sherwood and Lee Lake. Feeding rates seemed to increase by 10 to 30 percent between hatching and one week of age; but this condition varied substantially for any individual female depending upon the hour or particular day, as was demonstrated very early by Allen (1914). The latter reported food delivery trips ranging from 40 to 55 per hour for nestlings whose ages he did not indicate. Birds observed by me for brief periods of 15 to 30 minutes at times returned to the nest at 45 to 150 second intervals; but most such trips involved activity other than food delivery. Often the parent peered into the nest, probed its lining, brooded or removed fecal sacs without feeding young. Nonetheless, delivery rates to Redwing nestlings were strikingly rapid at Lake Sherwood, reaching six to seven trips per hour with a range of one to 26 minutes per trip (Table 10). Feeding of young occurred throughout the 13 to 14½-hour diurnal

Table 10 shows some Redwing feeding rates to nestlings at three study sites. Column four from left lists the number of young per nest (number of individuals from column two) at a particular age. Data are totaled or averaged in appropriate columns at bottom of table.

Location	Number Individuals	Parent Sex	(Number) & Age of Nestlings	Number Trips Observed	Mean Trips/hr.	Time Range (mins.)	Month
Lee Lake 1953	1	F	(3) 1 day	8	12.1	1-11½	May
"	2	F	(3) 2 day	6	7.9	4-15	May
"	2	F	(2) 6 day	13	5.3	11-18	May
HVM 1958	2	F	(3) 3 day	17	5	3-20	May
"	5	F	(3) 7 day	41	7.3	2-26	April
HVM 1959	2	F	(2) 5 day	19	4.6	8-23	May
"	1	M	(2) 5 day	6	1.2	15-125	May
WLSM 1959	1	F	(4) 2 day	6	10.2	2½-18	June
"	2	F	(3) 4 day	8	6.9	3/4-16	June
TOTALS	18 parents		(50) nestlings	124	6.5 mean		

periods during the span of Redwing nestling and fledging life in southern California. Food lacks uniform availability for blackbirds; and the spatial distribution of most organisms, including nesting Redwings, reflects clumping of populations (Hairston, 1959; Slobodkin, 1963), points previously suggested in other habitat and behavioral aspects of this study. Most effective conceivable foraging schedule would involve regularly spaced trips, a parent bird returning with a beak full of insects at each effort. Since the parents failed to make regular trips, discontinuity of food distribution was doubtless reflected; and it was striking to observe the return of a parent many times with only one or two food items, ostensibly to supply three or four nestlings. Thus, Redwings returned from many foraging trips carrying less food than potential beak capacity. Such a fact was not conclusively correlated with observed nestling mortality, but theoretically it should be. At Lake Sherwood observations indicated that males were feeding nestlings more frequently during May, 1959 than in the same period of 1958. Male assistance rarely exceeded 25 percent of the total feeding effort at any one nest, usually being considerably less than that. In 1958 no males performed this activity at nests located along the south edge WLSM (Figure 27); while three of five observed there in late May, 1959, carried food often. Likewise, on HVM two out of sixteen males were observed

to supply food to nestlings in 1958; but at least three of seven did it consistently during early May, 1959. In all years, males were repeatedly observed to feed fledglings on their territories further assisting female parents, as reported by Nero (1956a).

Assuming a Redwing were able to fly 30 miles an hour --- a reasonable speed according to Poole (1938), a theoretical performance could be calculated as follows. The bird would leave the nest, arrive at the foraging destination, search 15 seconds, and return, traversing a maximum of 680 yards round trip during one minute elapsed time. Even if search time were zero, maximal one-way distance could not exceed a quarter-mile. Table 11 indicates nearly all foraging sites observed could be reached within such an "ideal" time span. Considering that most flights exceeded one minute, rarely attaining 1000 yards round-trip distance, 12 trips per hour were well within physical possibility. Frequent less-than-capacity food deliveries suggested either that females foraged a minimal amount of time, or spent a lot of time searching for the small amount of food gathered. Orians (1961) suggested that the latter condition prevailed regardless of food amounts obtained. Observations in this study, especially in the Lake Sherwood area, showed a consistently wide range of variation in length of trips (and necessarily in foraging time), and clearly in amounts of food procured per

Table 11 summarizes data on foraging sites of Redwings in feeding the young at three study sites, 1953-1960. Compare localities with Figures 3 and 5. A question mark indicates approximate distance.

YEAR	COLONY	FORAGING SITE	MAX.-MIN. DISTANCE TRAVELED
1953-1954	Lee Lake	Adjacent irrigated grass-land	1 - 50 yards
"	"	reservoir grassland and stream	50 - 250 yards
"	"	nearby alfalfa and grain fields, pasture E. and W.	150 - 400 yards
1958	HVM	adjacent wetland, grass and grain fields	2 - 440 yards
"	"	wet and dry pastures, north	50 - 250 yards
1959	"	adjacent fields, wetlands	2 - 440 yards
"	"	pastures, north and west	50 - 300 yards
1958	WLSM	adjacent dry pasture, grass and streamland west	25 - 500 yards
"	"	grass and grain fields N.W.	100 - 440 yards
1959	"	adjacent pasture (no cattle) and stream west	25 - 400 yards
"	"	NW grain fields	50 - 500 (?) yards
1959-1960	Hidden Valley Field	Cultivated grain fields in and out of territory	1 - 200 yards

trip.

Reproductive Success

A successful nesting effort was defined in this study as one in which one or more nestlings attained an age of eight days. Such an age was the earliest at which nestlings seemed to be adequately coordinated to depart independently from the nest. Young usually left the nest voluntarily between 10 and 12 days of age, and under duress at eight or nine days. Any successful nest departure changed the designation of the bird to that of fledgling. Unsuccessful nests included those destroyed or deserted containing eggs or nestlings.

Table 9 (see above) summarizes three ways of calculating nesting success, as follows: 1) Total percent of young fledged from total hatched; 2) Number of young fledged per nest in which hatching occurred; 3) Number of young fledged per successful nest. Such methods provide data on breeding success of whole populations, and allow broad comparisons with a variety of other studies. For example, total success for Redwing populations listed in Table 9 compares favorably with a range of 40-50 percent reported by Nice (1957) as typical for open-nesting passerine birds. The categories of fledging per individual nest indicated presence or absence of widespread mortality resulting from removal or disappearance of all nestlings from individual nests, which has been reported

as a typical effect of predator activity (Young, 1963; and this study). The category indicating number of young per successful nest affords an approximation of the average number of nestlings lost through starvation or accidental falling from the nest by comparing these figures in Table 9 with mean clutch size in Table 7.

Instances of high mortality among Redwings were mainly the result of two factors. The first was terrestrial predation, the second habitat destruction. On HVM in 1959 there was a high rate of predation on Redwings, resulting in total egg loss by at least 25 nests between April 17 and mid-May. This predation correlated with the drying of the marsh during late April; all nests were found abandoned with eggshell fragments present, often containing bits of dried yolk. Such a situation contrasted with late April, 1958, when the marsh was completely flooded and loudly vocalizing fledglings were abundant. However, successful nests produced similar numbers of fledglings (Table 9) during both years. Aerial predators on eggs or young were not seen in either year. Potential terrestrial predators were abundant in the area. Young opossums (Didelphis virginianus) frequented willows adjacent to HVM. Additionally, ground squirrels (Citellus beechyi), striped skunks (Mephitis mephitis), and feral cats were active in the area. All were seen as road kills from auto traffic. Over-water nest construction appeared

to hinder efforts of non-aquatic terrestrial predators. This is readily seen by comparing figures in column "E" of Table 9 for HVM in 1958 (wet) and 1959 (drying marsh). Smith (1943) has also reported progressively reduced Redwing breeding success in bulrush, cattail and Sparganium habitats respectively, representing increasingly dry nesting situations. Despite extreme predation in the desiccated marsh reported here, no similarly substantial predation occurred in the few nests observed near the margins of Hidden Valley barley fields during 1960. This may have been due to the more dispersed and unpredictable occurrence of Redwing nests in such habitat (as well as the sporadic distribution of the habitat itself), while nests in marshes studied were closer together. Marsh was the more typical nesting habitat for the species and may well have been more readily frequented by ground predators. The lake bed at Lake Sherwood dried out more slowly than HVM (where water was more shallow) in 1959 and total losses to predation were lower on the former. Nests at the west end of the cattails along the south edge of WLSM (Figure 27) showed greater mortality than those farther east, where water remained under the vegetation until the end of the breeding season. However, even on that marsh total success was comparable for 1958 and 1959 (Table 9). Nesting losses have repeatedly been recorded as more prevalent in marshes that dry up (Dawson, 1921; Bent, 1958) than in initially

dry land situations.

Differences in success between 1953 and 1954 at Lee Lake appeared unrelated to wet versus dry conditions, as the marsh never dried up and rainfall was similar in the two years. Nevertheless, total success was greater in 1954 (Table 9). Predator pressure seemed greater in 1953. Moreover, the fact that more young were reared per successful nests (2.91 vs. 2.04) suggests that ecological conditions in areas surrounding the marsh were more favorable for Redwing breeding during 1954. In both years approximately 60 breeding females were present at the study site; but only 120 nesting attempts were recorded in 1954, as compared with 160 in 1953. Greater individual success indicated more attempts reached completion, probably resulting in fewer total nestings for 1954.

Habitat destruction was the second major factor producing lowered Redwing nesting success. Fields north of Potrero Road (Figure 3) in Hidden Valley were mowed during mid-May, 1958, removing all vegetation and destroying all active Redwing nests. A small stream at south side of the Sepulveda Basin contained dense marsh and riparian vegetation in 1959. Again, during May at least 250 yards of this vegetation was destroyed by excavation and chemical treatment. Territorial male Redwings appeared to remain at least on the margins of both the field and the stream habitats, but females made no further nesting

attempts at either site.

Timing of the Breeding Cycle

Gonadal Cycle

Redwing males showed a long period of gradual testicular enlargement prior to the breeding season. Female ovarian growth was slow during the same period, with a tremendous increase during six to seven days preceding ovulation (this study; Allen, 1914; Payne, 1965; Wright and Wright, 1944).

The objective was to correlate sexual condition with phases of the reproductive cycle, especially territoriality and the commencement of nesting. Examination of 31 male and 12 female Redwing specimens revealed the following facts.

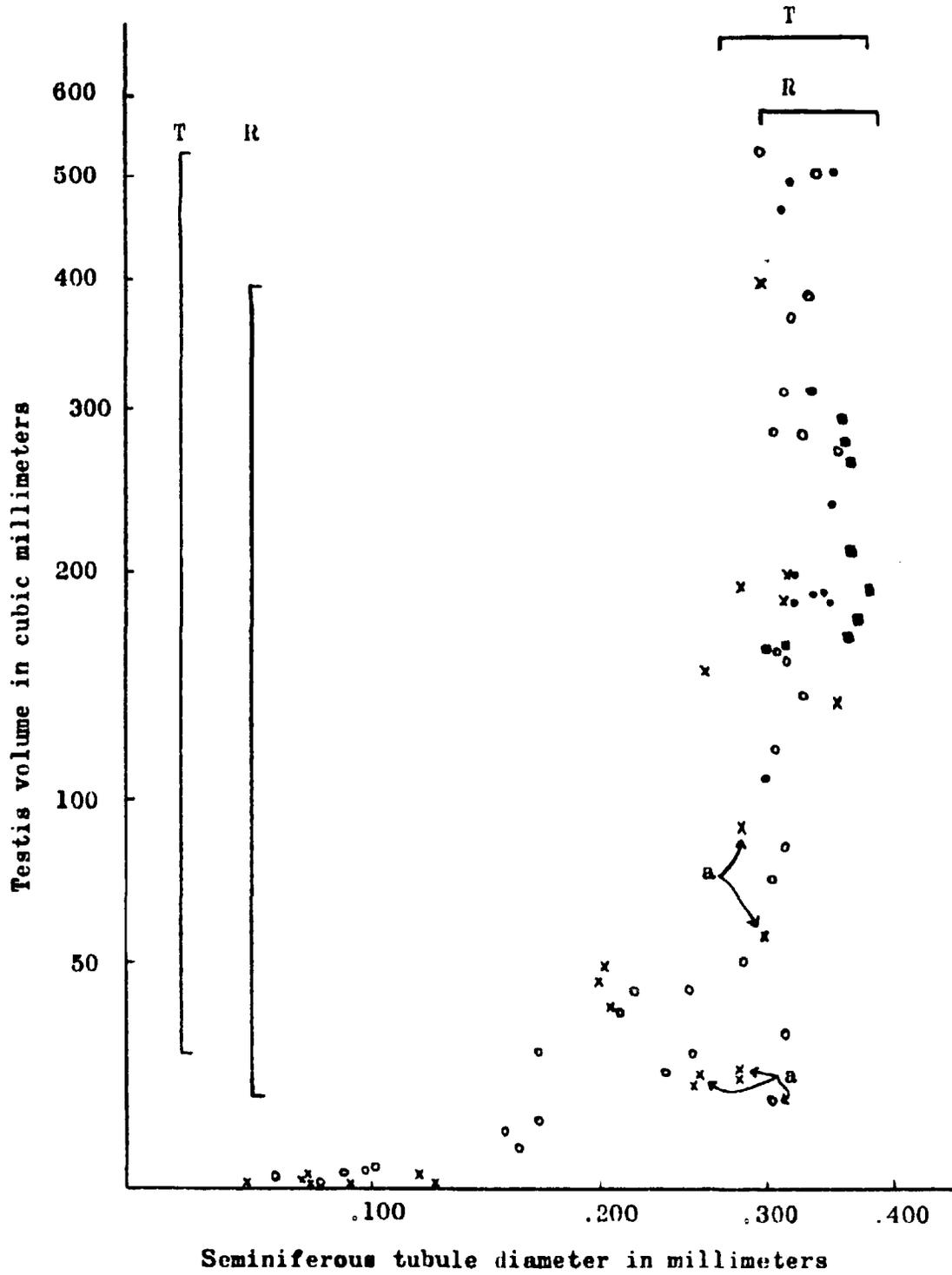
- 1) Male Redwings defended territories long before attaining complete spermatogenesis and interstitial cell development. At the beginning of territorial occupation in late January, testes had barely begun to recrudescence. Males collected at Point Conception, Santa Barbara County, during the third week of February, 1959, were vigorously territorial but showed very early stages of spermatogenesis. In the latter case, interstitial cells were becoming well developed. Redwing breeding at Lake Sherwood typically commenced at the end of March (Table 3). Territorial males collected during the first twelve days of that month were in mature sexual condition, or nearly so (Figure 17).

During that period males collected away from territories often exhibited a less mature sexual condition than known territorial males. Among the latter, any lesser interstitial cell development was not apparent. However, Figure 14 shows that many males attained mature seminiferous tubules of relatively uniform diameter while the testes were still rather small, in part indicating smaller interstitial cell volumes.

2) After mid-March at Lake Sherwood, all adult male testes were in fully developed stage seven of Blanchard (1941). Immature males usually had testes which were smaller in volume, weight, and tubule diameter during the same period (Figure 14), a condition similar to the findings of Wright and Wright (1944).

3) Testicular recrudescence having begun during mid-January, was well advanced by early March. Interstitial cell growth appeared to proceed more rapidly earlier in the season (Jan.-Feb.), with sperm development catching up by early March. This correlates with the work of Vandenberg (1961) which demonstrated that interstitial cell lipids (contributory to cellular androgen production) were most abundant just before and during early territory defense among male Redwings in Pennsylvania. At Lake Sherwood acceleration of seminiferous tubule growth appeared to occur during the last week of February and the first week of March, resulting in full male sexual

Figure 14 shows blackbird testis growth, plotting testis volume against seminiferous tubule diameter. Squares and "x" symbols indicate Redwings (total = 31), with the former representing males collected on breeding territories, and the latter indicating birds collected away from territories. Circles refer to Tricolors (total = 42), of which solid symbols indicate males collected on breeding colonies, and open circles mean birds collected away from such colonies. Collections were made at various study sites, 1953-1961. The symbol "A" refers to immature males of both species. The horizontal and vertical lines on the figure, labeled R (Redwing) and T (Tricolor), indicate the span of volume and diameter over which males were in full reproductive condition. See text for discussion. Circled numbers next to these lines show the number of males in the figure which fell within the span, the smallest vertical and horizontal number represents the maximum individuals in full sexual condition. Compare with Figure 17.



development at least two weeks prior to first observed matings. Since breeding occasionally commenced during the third week of March, as at Lee Lake in 1954, it seemed of adaptive value for males in southern California to attain reproductive maturity by early March in order to take advantage of any potentially favorable conditions such as good weather and receptive females for successful breeding at such an early date. Some males collected at Lee Lake were in even full reproductive condition by March 1. It was clear that gonadal maturation was completed much earlier than at more northerly latitudes such as New York (Allen, 1914), Montana (Wright and Wright, 1944), and even northern California (Payne, 1965). This doubtless contributed to the early territory establishment observed, and conferred a reproductive advantage in itself in view of the earlier development of favorable environmental conditions in southern California, compared with harsher climates of the northern and eastern parts of North America.

Timing of Breeding

There were striking variations observed in the chronology of Redwing breeding, especially in its initiation. Table 2 lists important phases of this cycle according to their temporal sequence. Basically, variations in timing of the cycle related to when prospecting females arrived, and to the duration of the ensuing "pair formation" ritual

described previously.

At Lee Lake in 1954, the sequence proceeded earlier than at any other time recorded in southern California during this study (Table 3). By March 14, copulations were frequent, and half of the 26 newly begun nests had been completed. Although 20 male and at least 26 female Redwings were then active at the breeding site, eggs were laid in only one of these nests before the end of March. Many of the early-completed nests were never used further. No such quantity of abandoned nests was found in any other year.

The single early clutch at Lee Lake in 1954 proved to be infertile. It appeared that females built nests prematurely while still physiologically unprepared for egg-laying, since the latter usually followed nest completion within a week. While the lake proper and adjacent irrigated grassy borders showed no unusual differences in 1954 from other years, the crop cultivation of alfalfa and oats in the area was advanced in growth by mid-March, two to three weeks earlier than any other year observed. Such overtly favorable ecological conditions may have triggered nest-building activities at Lee Lake before the normal sequence of environmental and male behavioral stimulation had produced full ovary development in females. The usual schedule in this study was for laying of successful clutches to begin during the last few days of March, with sub-

sequent phases starting at the intervals listed in Table 3. The only other deviation noted at Lee Lake in 1954 occurred in the mean peak of egg laying, April 8 as compared with April 15 in 1953. This one-week difference might further indicate unusually early good breeding conditions in 1954.

Delay in Redwing breeding appeared related to two types of events. First, Tricolor invasions resulted in disruption and retardation of Redwing nesting on HVM, compared with West Lake Sherwood, in 1959 (Table 3). Second, in the extremely dry year of 1960 (Figure 11) Redwings commenced breeding at least one week late at Lake Sherwood and the Sepulveda Dam area, and delayed at least two weeks at Lee Lake (Table 3). Only at Lake Sherwood did the nesting substrate differ from other years of observation. Males there had maintained territories and undergone pair formation as in previous years, although much of the western end of the lake was completely dry. The situation at Lee Lake was even more unusual since receptive females failed to appear on breeding sites before April 1, at least two weeks later than expected from previous observation. The surrounding landscape was only casually irrigated that year; and the cultivated alfalfa was sparse and stunted. There seems to be a clear correlation of drought-induced, poor environmental conditions with slightly reduced total Redwing populations and delayed onset of nesting during the 1960 season. As Lack (1954)

has suggested for many species, observations indicated Redwings assessed the environment differently in potentially unfavorable years; the as yet undetermined mechanism by which this was accomplished at least involved female behavioral responses. Both Allen (1914) and Orians (1961) have indicated Redwings delayed breeding as much as two weeks until regrowth of winter-burned cattails was sufficient to support nests. Such observations appeared to involve complete vegetation destruction in male territories. Partial burning of WLSM in 1959 described above, produced no delaying effects on the species, which actually began nesting a few days earlier than in 1958 (Table 3), when the marshes had remained completely undisturbed.

Regardless of starting dates for breeding in southern California, no Redwing clutches were begun later than June 15 (1958), nor has the literature recorded such (Bent, 1958). The usual situation is shown in Figure 12, in which the last clutches were completed in late May, 1953. Egg-laying at Lake Sherwood ceased earlier in 1959 than in 1958, the latter year having been repeatedly indicated as a very favorable one. With a rapidly drying marsh, no laying occurred on HVM in 1959 after May 20; and Redwings were finished breeding there by June 3, since the latest-hatched young were lost to predators before fledging.

The abbreviated 1959 breeding season clearly reduced the ability of both sexes to produce offspring success-

fully, compared with the time at their disposal in other seasons. Gonadal evidence was lacking in 1959; but in 1954 at least one male collected was still reproductively competent at the end of May (Figure 17). Moreover, in most years Redwing males continued to behave territorially at least through the third week of June, suggesting continued reproductive condition. Calculating time required during a nesting cycle for a female to fledge young successfully, about 30 days passed between the start of egg-laying and nest departure by fledglings. Thus, from the start of the season, two 30-day periods, mean a female needed until the end of May to rear two broods. The low frequency of nestings in late May (Figure 12) and in June indicates that most Redwings did not produce more than two broods, whether they escaped predation or attempted re-nesting once eggs or young were lost. Both Nero (1956a) and Case and Hewitt (1963) reported a great decrease in re-nestings late in the season; and both suggest a smaller percentage of second broods attempted. Unusually good conditions in 1958 extended egg-laying over a span of 80 or more days at Lake Sherwood, which simply presented more time than usual (Figure 12) for additional nesting attempts. Warm-temperate southern California appeared generally to provide a longer breeding season for Redwings than do the northern and eastern United States with later breeding seasons, indicated by studies of the above-mentioned authors

and others (Mayr, 1941; Thomsen, 1944; Wright and Wright, 1944; Beer and Tibbits, 1950).

The Tricolor

This species is regarded as the most colonial of all North American passerines (Bent, 1958). It has occasionally been recorded in localized, dense breeding populations as large as 200,000 individuals (Neff, 1937). Tricolors have repeatedly been observed to crowd into a restricted part of the nesting habitat, failing to occupy adjacent, putatively suitable vegetation. Such clearly preferential clumping would seem to qualify this species as a truly colonial, compared to dense nesting assemblies which may in part result from limited availability of nesting habitat, such as in some insular seabirds. Tricolor coloniality has been adequately documented (Bent, 1958); and more recently Orians (1961) has elaborated upon organization in such colonies. My object is to augment prior accounts, and particularly to detail events in establishment and maintenance of colonies. Emphasis is placed upon spatial, temporal, and associated behavioral peculiarities which so clearly distinguish Tricolor and Redwing reproductive systems.

Initiation of Breeding

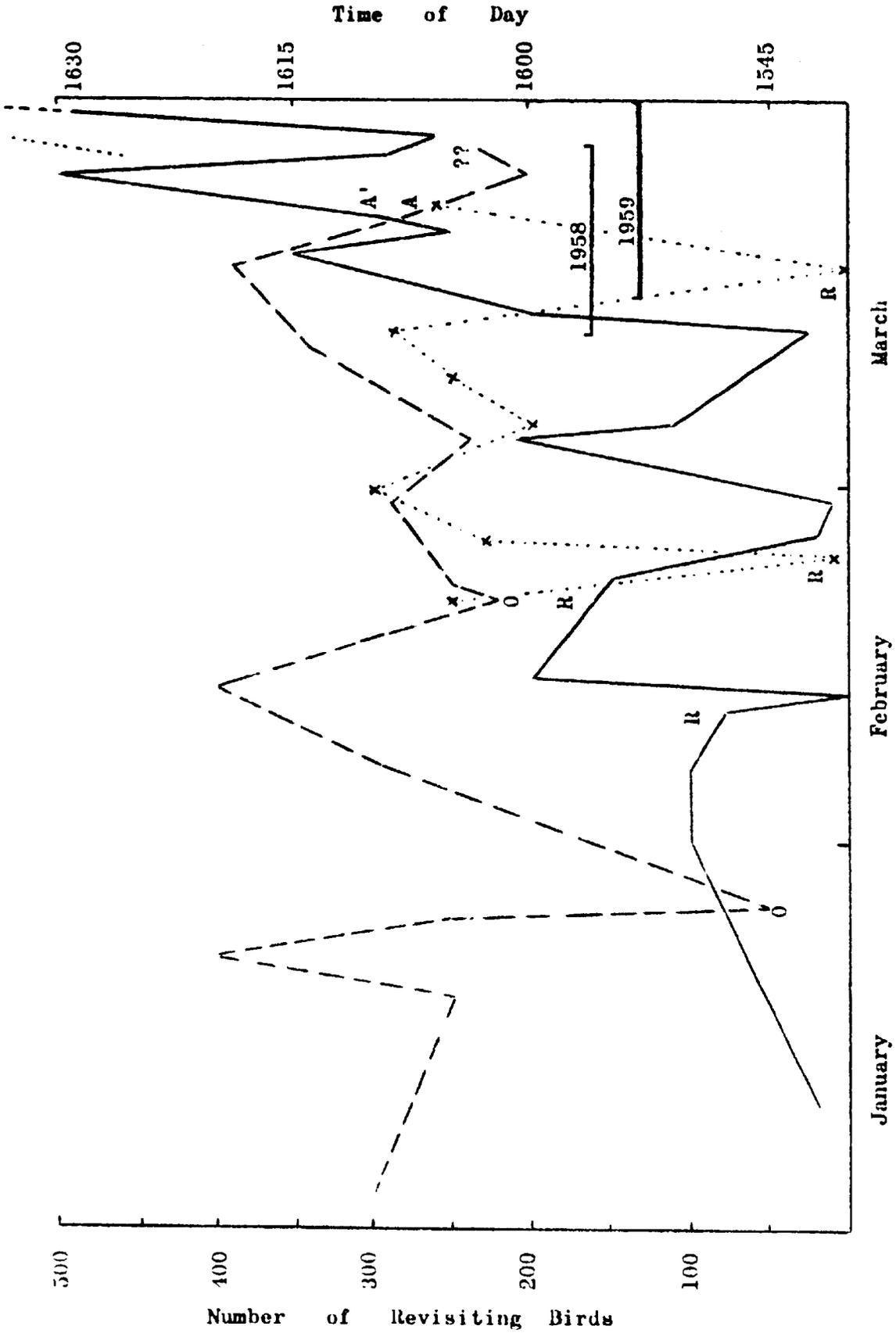
Tricolors did not show the long-term territorial development noted in Redwing; and it was necessary to look elsewhere for behavioral clues to a transition from non-

breeding to breeding condition.

Few significant differences were observed between roosting flocks of the two species. Roosting concentrations of Tricolors at Lake Sherwood tended to pre-empt a particular site for their later breeding; and slight peculiarities in their roosting and associated habits, which became noticeably accentuated in very late winter, were found to forecast reliably impending breeding. Among these, while arousal and morning departure of Tricolor concentrations closely corresponded to other species, their evening arrivals typically began slightly later than the earliest Redwings (Figures 8, 15). Tricolor arrivals seemed to occur in a more concentrated fashion than Redwings, with most of the former reaching roosts before the main body of Redwings. Tricolors also showed slight, fluctuating tendencies to arrive at WLSM roosts earlier in the evening during March, 1959, than they had in previous months (Figure 15) Tricolor pre-roosting activity reflected some aggression; but its population was generally more placid than territorial Redwings and their associates. Sex ratios among Tricolors roosting at Lake Sherwood approximated those recorded in breeding colonies, suggesting little tendency toward sex segregation.

A striking aspect of non-breeding behavior, changes in which accompanied breeding initiation, was observed during mornings when Tricolor groups returned to rest in

Figure 15 summarizes data on roosting arrivals and morning revisitants for the Tricolored Blackbird at West Lake Sherwood Marsh (WLSM) during early 1958 and 1959. The long-dashed upper line plots evening arrival times of the earliest Tricolors. The lower solid and short-dashed lines indicate, respectively, 1959 and 1958 numbers of birds revisiting the roosting marsh during the forenoon. An associated "O" symbol indicates a 1959 date of overcast weather. "R" symbols indicate dates of rain (left two = 1958, right two = 1959). The question marks indicate uncertainty whether birds arrived earlier or later after March 29, 1959. Points "A" and "A'" dates when the Tricolor population first exhibited signs of sexual behavior in 1958 and 1959, respectively (see text). The heavy horizontal lines at the right show the span of colony site prospecting in each year, as indicated.



roosting vegetation, invariably engaging in typical vocal chorusing similar to that of evening flocks. At Lake Sherwood after a complete morning exodus, Tricolor revisitants varied from a few to several hundred birds per flock. Occurrence of such returnees was sporadic; but flock frequency and total revisiting numbers tended to increase notably in March as the breeding season approached (Figure 15). All winter, males rarely comprised less than 75 percent of revisiting flock membership. Similar patterns of changes in roosting flock behavior were exhibited 1958-1960.

There were annual differences observed in distribution of revisiting flocks at Lake Sherwood. During March, 1958 such flock movements were restricted to WLSM and adjacent marshes; while in 1959, they shifted over a wider variety of area, including marshes farther west of the lake (Figure 8). Total numbers of revisitants were also lower in 1959, correlated with a smaller Tricolor roosting population (Table 2) than in 1958.

Colony Site Prospecting

Additional changes were recorded in the pre-breeding behavior of Tricolor revisitants in mid-March. By that time these flocks had become more active in the Lake Sherwood marshes, irregularly shifting positions within the vegetation. Motivation of flock individuals as yet remains undetermined; but such an increase in mobility was

unmistakable. This form of behavior has been designated by Orians (1961) as the prospecting of a potential breeding colony site. My observations showed this change in flocking activities began 12 to 17 days before actual formation of breeding colonies both at Cache Creek and Lake Sherwood (Table 12). Prospecting at the latter site commenced by March 12 and 15 in 1958 and 1959, respectively, and about four weeks later at Cache Creek. For example, on that date in 1958, 300 Tricolors were heard chorusing deep in WLSM at 0930, and during the ensuing two hours sporadically shifted about several spots within that marsh. In addition, numerous small flocks of two to 50 birds shuttled in and out of the marsh during observations. Such daily prospecting movements typically continued until colony establishment. The birds involved consistently moved back and forth between the lake and eastern Hidden Valley. Each shift within WLSM was preceded by a sudden quieting of the chorusing flock, and was followed by a buildup of the chorus. In contrast, during 1959, prospecting flocks began a few days later and continued to shift over a wider area of habitat than 1958, often concentrating in bulrush marsh "G" (Figure 8) west of the lake. During both 1959 and 1960, shuttling flocks also ranged more widely in Hidden Valley. Tricolors repeatedly concentrated prospecting efforts in densest over-water vegetation, which was promoted in 1959 because cattails

Table 12 shows breeding schedules in Tricolor colonies at several study sites, 1956-1960. Parentheses indicate estimated numbers or dates with limited observations. Question marks indicate no observations made. Right-hand "total nests" column indicates all nests built at the site, and approximates the maximum number of females present in one season. As stated in text, the latter equals about twice the male population.

Locality	Initiation	Nest-building	Egg-laying	Incubation	Feeding Young	Total Nests
<u>1956</u>						
Cache Ck.	3rd. wk. Apr.	4/19-(5/5)	4/22 - ?	max. = 5/3	May 5 onward	2000
<u>1957</u>						
HVM Colony A	(April 1)	4/1 - 4/5	4/5 - (4/14)	4/7 - 4/26	4/19 - (5/15)	(75)
Colony B	May 8	5/8 - 5/15	5/10 - 5/17	5/12 - 5/28	5/22 - 6/15	100
<u>1958</u>						
WLSM Col. A	March 28	3/28 - 4/6	4/2 - 4/10	4/4 - 4/22	4/16 - 5/14	1200
Col. B	April 28	4/28 - 5/14	5/1 - (5/16)	5/3 - 5/28	5/14 - 6/13	400
Col. C	5/20; 6/1	5/20 - 6/10	5/22 - 6/13	5/24 - 6/25	6/4 - 7/14	200
Cache Ck.						
Col. A	Apr. 25-26	4/26 - 5/3	4/28 - 5/5	4/30 - 5/16	5/11 - 6/10	450
Col. B	(June 1)	(6/1 - 6/9)	6/3 - 6/12	6/4 - 6/23	6/15 - 7/12	50
<u>1959</u>						
WLSM	April 1	4/6 - 6/1	4/10 - 6/4	4/12 - 6/14	4/24 - 6/29	1200
HVM	April 1	4/1 - 4/12	4/2 - 4/15	4/4 - 4/26	4/15 - 5/5	65
Marsh "G"	March 31	4/4 - (4/20)	4/7 - (4/21)	4/9 - 5/2	4/20 - (5/20)	200
S. F. Res.	March 31	?	?	?	?	(600)
Cache Ck.	(April 25)	(4/26)- 5/3	(4/27) - 5/5	4/29 - 5/17	5/9 - 6/6	285
Col. B	(May 12)	(5/12 - 5/18)	5/14 - 5/21	5/15 - 6/2	5/26 - 6/23	120
<u>1960</u>						
S. F. Res.	Mar. 28-29	(3/31) - 4/10	4/3 - 4/13	4/6 - 4/25	4/16 - 5/15	300
Blue Moon R.	(Mar. 26-28)	(3/28 - 4/4)	3/31 - 4/6	4/2 - 4/18	4/13 - (5/15)	750
Cache Ck.	April 18	4/18 - 4/28	4/21 - 5/1	4/24 - 5/12	5/4 - 5/31	200

and bulrushes over dry land had been burned in mid-February. Breeding colonies were always established earliest (Table 12) in most intensively prospected vegetation.

Tricolors which nested in habitat where they did not roost during winter first appeared there at the beginning of the prospecting period, averaging two weeks before colony establishment. Such behavior was evident in the dry fields at Blue Moon Ranch, and in the riparian site at Cache Creek. In both localities the species appeared to roost in marshes a half-mile or more distant from the ultimate breeding site which was prospected during the day.

Colony Establishment

This phase of the cycle abruptly succeeded prospecting, and began on the first date when Tricolor flocks remained at a nesting site part or all of that day. Birds forming a colony simultaneously showed a full range of reproductive behavior from territoriality through nest construction. Although such activities literally "burst forth" within the population on a specific date, partial and irregular manifestations of them were observed during the prospecting period. Courtship displays by males on WLSM had first been noted March 22, 1958, between 0800 and 1015 hours, with initial colony establishment taking place March 28 (Table 12). On the same date in 1959 such incipient courtship was observed in the evening among pre-

roosting Tricolors. At the same time also a few females were first observed carrying slender strands of nesting material, which they discarded upon alighting at Lake Sherwood roosts. Following a longer prospecting period in the latter year, Tricolors formed colonies at several marshes on and near the lake, March 31 through April 2 (Table 12). Exhibitions of partial breeding behavior increased in frequency and intensity during the five to nine days between its first signs and colony formation. Incipient territorial advertising displays among males also increased during such flock behavioral changes late in the prospecting period. Females only started to appear in substantial numbers two or three days prior to colony establishment at Lake Sherwood.

As Table 12 indicates, highly synchronous colonies ranging between 75 and 3,000 Tricolors were observed. This means relatively large numbers of birds began reproducing at the same time, and maintained such simultaneity throughout a nesting cycle. While typically much smaller than the massive colonies of 50,000 to 200,000 birds reported from extensive agricultural areas in the Central Valley by Neff (1937) and Orians (1961), synchronous colony establishments which I have observed conformed to patterns reported by these authors. Colonies showed three additional modes of formation besides a fully synchronous one. Some continued to expand around their margins with varying

numbers of newly established individuals for several weeks, as at WLSM, 1959 (Table 12). Others increased peripherally by one or more discrete, synchronous sub-colony additions later in the breeding season, such as WLSM in 1958 (groups "B" and "C", Table 12). Finally, in the tower bulrushes of WLSM during 1959, there was clear evidence that newly arrived Tricolors replaced birds which had attempted or completed one nesting cycle. Replacements simply appeared to settle in evacuated spaces among remaining Tricolors once the previous occupants departed. New arrivals never engaged in aggressive contests to establish themselves. All of these efforts clearly constituted colony establishment deviating somewhat from the usual initial synchronization of breeding in this species. One further population trend, similar to that reported by Orians (1961), was observed in Tricolor colony establishment at Lake Sherwood and Cache Creek. At these sites during 1958-1960, total roosting and prospecting numbers were always larger than those initially establishing colonies. This is seen by comparing Tables 2, 14 and 17. For example, during a very favorable 1958 at Lake Sherwood, 3,000 or more Tricolors were roosting in marshes during late March; but only about 1,800 birds actually formed the initial colony establishment, and an estimated total of 2,500 adults attempted breeding during the whole season. Thus, it appeared that a substantial percentage of potentially breeding Tricolors

deserted some nesting localities without establishing themselves. The ultimate in such a population adjustment was the complete desertion of Lake Sherwood by 1,500 Tricolors following abortive colony establishment attempts during late March (Table 14).

Breeding Habitat

The apparent, intensive focus by Tricolors on selection of particular vegetation for breeding sites leads me to review this phenomenon before proceeding to other aspects of the cycle. Like Redwings, Tricolors typically inhabited marshes. Seventy-five percent of Neff's (1937) colonies were in cattails and bulrushes. Selection of non-marsh habitat by the species has been amply documented (this study; Dawson, 1923; Bent, 1958; Orians, 1961; Richardson, 1961); and such habits require further examination. Still, marsh habitats appeared to furnish conspicuously dense and well protected substrate for successful breeding. Table 13 indicates all observed sites but two were located in marsh or riparian situations.

Basically, marshes provided limited area, the use of which was further restricted by Tricolor preference of only certain portions of selected locations. At Lake Sherwood, bulrushes were preferred, unless prior occupation or destruction had rendered them unavailable. In these instances, cattails were chosen, but never dry-land habitat. Along the San Diego River in 1962, Tricolors

Table 13 summarizes observational and literature data on Tricolor breeding habitat through 1962 in southern California. The second column from the left means the number of new discoveries each year. Numbers in the other columns indicate number of breeding colonies known each year of the study listed. Question mark means an uncertain number; dashed lines mean no observations of that habitat in a given year; parentheses mean breeding in a particular habitat was presumed, but not actually observed. Annual totals of observed colonies are included in the right-hand column.

Year	New discov.	Riparian- willow	Cattails stream	Cattails marsh	Bul-rushes	Nettles	Open fields	Totals observed
1956	1	1	1	---	---	---	---	2
1957	2	?	---	(1)	1	---	---	1(1)
1958	1	1	1	(1)	1	1	---	4
1959	3	1	1	(1) 1	3	1	---	7(1)
1960	5	1	---	1	4	1	1	8
1961	3	0	0	1	2	0	0	3
1962	6	0	0	4	2	1	0	7
Published re-ports; pers. communications								
		1	6	16	10	1	3	

bred in extensive cattails, avoiding nearby deep-water bulrushes. Choice of nettles at San Fernando seemed favorable even in 1960, when the habitat was dry, because of the potential protection afforded by the vegetation. Even that site was deserted during 1961.

A search for reasons in choice of some habitat and rejection of others nearby, revealed the following. In general avoided marshes showed a long, narrow configuration of the kind found along drainage ditches or confined to pond margins in narrow bands. Marshes selected by the birds showed reasonably broad, circular or irregularly polygonal (Figure 27) shapes. In cases where two marsh types were of similar extent, as on WLSM, again better protected habitat (bulrushes) was preferred over cattails. In no situations was initially dry marsh habitat (excluding nettles) selected, regardless of aerial configuration. In the one observed dry-field colony, that vegetation was chosen in lieu of narrow stands of bulrushes along drainage ditches less than one mile distant. The field in question was extensive in area, and contained numerous stands of mustard plants, providing greater vegetation density and support than most other fields observed. An exception to the broad configuration habitat correlation occurred at Cache Creek, whose riparian habitat was long and narrow. Several factors were apparent. From 1958-1960, small Tricolor colonies (Table 14) were confined to

well protected, tall, mature willows in the upper-stream part of the study site (Figure 2). In 1956, when about 3000 synchronously breeding Tricolors were present, at least 300 yards of habitat was utilized, including dense stands of young willow saplings and cattails. The 40-foot width of the creek vegetation, or its availability as the only suitable breeding site in marginal xeric conditions, may have influenced Tricolor choice.

As in any other avian species, inspection of Figures 2 to 4, indicates reasonable proximity of breeding sites to a food supply adequate to support the population. Where suitable nesting sites ceased to exist, or apparent food inadequacy was suspected, Tricolors consistently forsook the locations (Table 14). These relationships are developed in appropriate sections below.

Territoriality

Male Tricolors were overtly territorial during certain phases of the reproductive period, expelling intruding males of their own species (as well as occasional Redwings) from territories which averaged in this study about 36 sq. ft. (Table 15). The main differences between Redwing and Tricolor territoriality involved duration and mode of territory development, size of territory, and length of time and manner of defense. As indicated in the outline of breeding initiation, males showed complete territory occupancy and defense on the particular day that a colony

Table 14 (upper) shows Tricolor breeding population size maxima at six study sites, 1956-1962. Presence of a dashed line means no observations made; a question mark means birds were not counted during observations; an asterisk means a cursory estimate was made; superscript "a" means a cumulative total of five separate populations along eight miles of river bed; an "x" means no counts or estimates made while observing in the general area.

Table 15 (lower) shows ranges and means of male Tricolor territory sizes at four study sites, 1959-1960. Sizes are measured in square feet, except Cache Creek, 1960, which was estimated in cubic feet. In duration column at right, superscripts mean: a) Tricolors had invaded Redwing marsh; b) 3500 sq. ft. area of WLSM called "tower bulrushes" (TBR); c) "Tower bulrushes" (see text) marked males; d) late in breeding season --- during care-of-young period. Compare Figure 16 for HVM, 1959.

	1956	1957	1958	1959	1960	1961	1962
Cache Creek	3000	?	700	600	300	0	0
WLSM	--	X	2500	2000	0	0	(1000*)
HVM	--	200	0	150-2	0	0	0
San Fern. Res.	--	--	(2000*)	(1500*)	600	0	500*
Blue Moon R.	--	--	--	--	1000	0	0
S. D. River	--	--	--	--	--	--	2500 ^a

Location/year	Number males	Range	Mean	Standard Deviation	Duration
HVM 1959	18 (unbanded)	23-41 sq. ft.	32.4	4.32	4/1-4/7 ^a
WLSM 1959	100 (Unbanded)	--	35	--	4/7-4/30 ^b
" "	3 (banded)	30-42 sq. ft.	36	4.9	5/14-6/10 ^c
Cache Ck. 1960	7 (unbanded)	300-400 cu. ft.	--	--	5/22-6/17 ^d
S.F. Res. 1960	30 (unbanded)	--	ca. 36	--	5/18-5/20
" "	3 (banded)	28-49 sq. ft.	39.7	8.7	" "

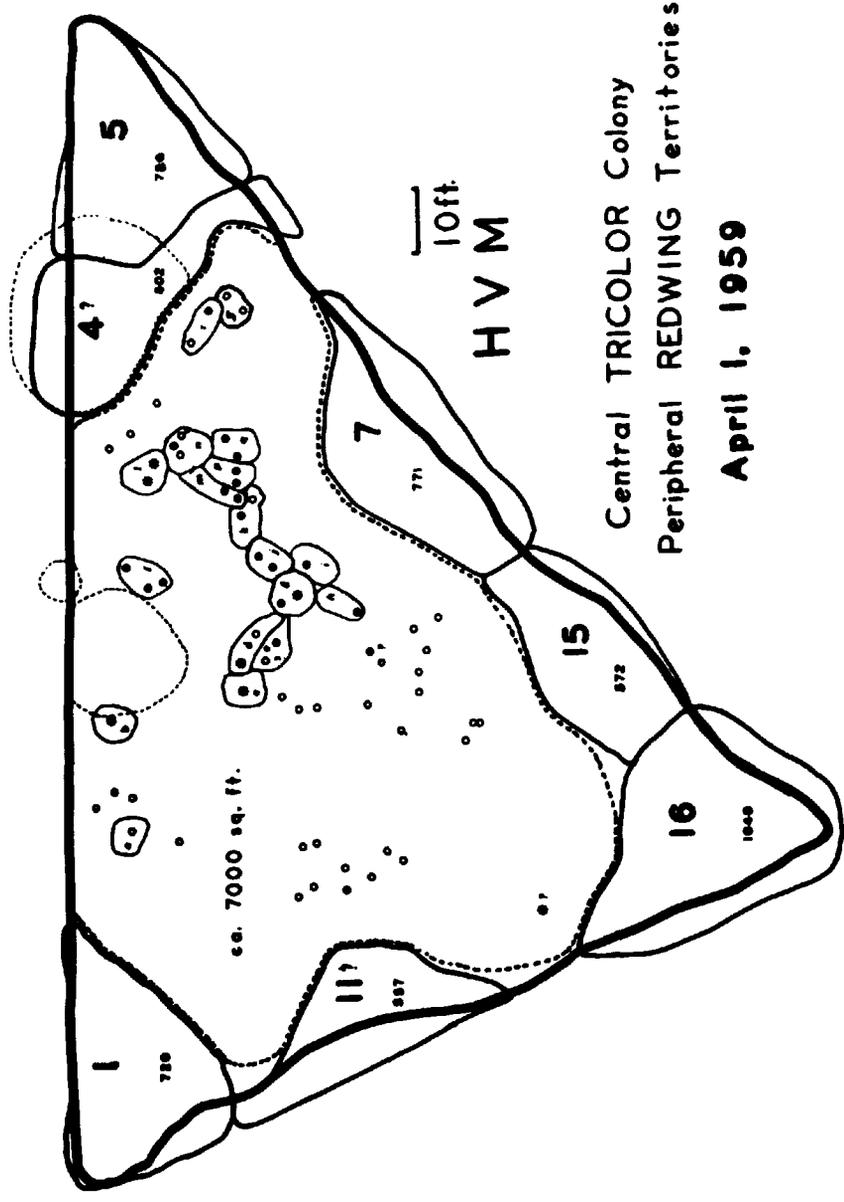
became established, before which, territoriality was sporadic, and incompletely manifested. It was observed mainly during pre-roosting activities, and shifted location as the flock moved about during colony site prospecting, which seemed to afford very little opportunity for stationary hostile interactions. The low intensity of territoriality before breeding was also suggested by the gradual development of advertising and threat displays. As such prospecting rituals continued, males commenced to accompany song with spread display (see below), occasionally pecking and growling at adjacent males. This coincided with intermittent courtship invitation displays toward females. Birds spent much time two or three feet below the top of marsh vegetation in such prospecting flocks. On the date of definitive colony establishment, territorial males clearly remained in a circumscribed area, on a platform of broken or bent marsh vegetation, or other suitable vegetation in the habitat. A difference was then seen in the degree of defense of portions of a territory. In the tops of particular vegetation, a male was quite lax in attacking transient intruders unless they lingered several minutes. Immature males were most often guilty of prolonged trespass, and were vigorously attacked by resident adult males. The top of the vegetation was frequented by passing males still apparently prospecting territories on the colony site. Deeper in the vegetation attack upon in-

truding males was immediate. It was in the deeper vegetation that intensive sexual displays, mating, and nest-building also took place. Initial defenses of a territory occurred only for the four to 10 days required to secure a mate or mates and for eggs to be laid. Subsequently the male deserted during the day until advent of hatching.

The fact that Tricolor males defended very small territories logically relates to their capacity to breed colonially in a restricted area. Earlier studies have indicated that males occupied territories measuring about six feet square (Lack and Emlen, 1939; Orians, 1961). An advantage in study of relatively small colonies in my experience was that it enabled me to observe territories under less confusing conditions than those admittedly existing in larger colonies (Lack and Emlen, 1939; Neff, 1937). A problem in measurement of such irregularly-shaped small territories was that misjudgement by a few inches or a foot could result in an areal error of as much as 20 to 40 percent.

Territories were measured in the HVM colony of April, 1959, utilizing the recurrence of an unmarked male on a specific spot, and his reactions to male and female stuffed dummies. Eighteen territories were so estimated (Figure 16; Table 15), ranging in area from 23 to 41 sq. ft., and averaging 32.4 sq. ft. From the WLSM tower, observations during April 15 - 20, 1959, indicated ca. 100 males terri-

Figure 16 shows Hidden Valley Marsh in early April, 1959, after an invasion by Tricolors. The seven peripheral territories are those of Redwings, with the large numbers corresponding to territories of early March. The small numbers indicate Redwing territory area in square feet on April 1. The central area, bordered by the dashed line, is that dominated by invading Tricolors. Within this area, are outlined eighteen small territories of male Tricolors (lettered a-s). The open circles indicate locations of incomplete Tricolor nests. The closed circles mark completed Tricolor nests, with the "stars" indicating nests in which eggs were laid. The question marks indicate territory or nest of uncertain ownership.



Central TRICOLOR Colony
Peripheral REDWING Territories
April 1, 1959

torial on a small bulrush clump, with an average territory of 35 sq. ft. The HVM situation was unstable, as the birds nearly all deserted by the end of April; and those present never crowded into all the approximately 7000 sq. ft. area of Tricolor activity (Figure 16). Doubtless more than 18 males had attempted colony establishment (between 80 and 100 were there April 7); but more could not be determined as constantly present. From April 10, fewer than 18 males remained, and only four territories, with nests, continued active after April 17. Dwindling species numbers failed to result in expansion of Tricolor territory size (Figure 16), although much evacuated area was not effectively occupied immediately by Redwings (see Figure 26).

The WLSM tower-bulrush situation seemed one in which all the space was used (ca. 3500 sq. ft.) during most of April and May, 1959. Between May 14 and June 7, the activities of four color-banded male Tricolors on the tower bulrush were followed closely. This was mainly during the period of hatching of young, when males re-assumed territoriality (see below). One marked male disappeared from the marsh soon after released, which correlated with the apparent tendency of Tricolors, at least males, to desert a specific nesting site once a brood had been reared. Deserting birds, having attempted or completed a nesting cycle, appeared to be replaced by other territorial males (undoubtedly some were new arrivals),

which proceeded to breed soon after the former left. A total of 140 territorial males was estimated to have occupied the tower bulrush between 7 April and 7 June, 1959.

Territory size in colonies other than Lake Sherwood fell within the range of those territories measured (Table 15). Cache Creek males defended areas within tall willows from just below the top canopy down to a point just below the nests within the territory in 1960. These volumes appeared to range between 300-400 cubic feet. Total riparian volume (stream-bed to tree tops) was estimated at 200,000 cu. ft. in which there were about 100 territorial males. Measurements of the territories of three marked males at San Fernando Reservoir, also a small colony, between May 18 - 20, 1960, ranged from 28 to 49 sq. ft. These were irregularly polygonal, and scattered over an extensive nettle growth. Long-term observations suggested most Tricolor territories were between 30 - 40 sq. ft. Even the largest Tricolor territory measured was less than one-tenth as large as the smallest functional Redwing territory; and Tricolors averaged only one one-hundredth as large as most Redwing territories. Size variation among Tricolors ranged to slightly over 100% (23 to 49 sq. ft.), compared with more than 2000% (500 to 11,000 sq. ft.) in Redwings.

Pair Formation and Sex Ratios

The conspicuous paucity of females in early prospec-

ting flocks seemed to preclude pair-formation activities during that period on potential nesting marshes. Observation of flocks foraging in fields west of Lake Sherwood provided no overt indications of pair formation. The only hints of impending reproductive behavior have been described above during Tricolor pre-roosting activities on Lake Sherwood. Such sporadic sexual displays, including at least occasional abortive or symbolic carrying of nest materials by females, suggested that they were selecting mates or preparing to do so at the latest mid-March at Lake Sherwood. Whatever preparatory interactions occurred between males and females previously, there ensued a firm male territorial retention, and the positive attraction to, and immediate orientation within, the system by females on the date of colony establishment. Females visited territorial males who persisted in wing-arching, nest invitation displays and song (see below) directed toward females. Mate selection clearly occurred no later than the first few days of colony formation. Females seemed immediately to select a particular nest site, repeatedly returning to it, accompanied by vigorous posturing attentiveness of the males. A male appeared to invite every female entering his territory initially, evicting only other males. Males were not observed to mediate entry of additional females into their territories, as described for Redwings. At least in synchronous colonies,

all females had established themselves at nest sites within 48 hours after colony formation began. Contemporaneous nests were never observed closer than 18 inches from one another.

Comparison of Tables 12, 14 and 16 indicates, on a total population basis, that mean sex ratios ranged between two and three females per male. There was a further tendency for such ratios to be higher in 1958 than other years at Cache Creek and Lake Sherwood, under apparently highly favorable environmental conditions.

In certain observational situations, more precise measurements of ratios were obtained. It was previously estimated that a total of 140 Tricolor males occupied the WLSM tower bulrushes during the 1959 season. Within that vegetation 298 completed and utilized nests were recorded, furnishing an overall seasonal average of 2.13 nests per male. During the censusing period used in Table 15, approximately 100 males and a maximum of 185 females were estimated present on that marsh. In addition, six banded females there in late May, 1959, were observed attending the only active nests in the territories of their respective unbanded mates --- i.e., one female per male. The three banded males recorded in the same tower bulrushes (Table 15) respectively possessed one, two, and two unbanded mates. Finally, in the abortive Tricolor colony on HVM in April, 1959, among 15 territorial males, whose

mates had completed nests (Figure 16), the potential sex ratio was one and one-half females per male. This was probably lower than would be expected in a successful colony. In any event, while both species are polygynous, estimated and counted Tricolor sex ratios proved consistently lower than those of Redwings (Table 4; Figure 26) under similar conditions.

Nests and Nest-building

Nests were constructed exclusively by Tricolor females, as in the Redwing. A Tricolor female required at most three days to finish a utilized nest, a feat occasionally equalled by a Redwing. Further, Tricolors usually laid eggs in nests within two days after completion. This means a minimum of about three days was possible between colony establishment and laying of the first egg, which was a further reflection of breeding synchronization in this species.

Salient features of observed nest construction involved collection of the most readily available nest materials, and provision of the three component structural layers previously listed for Redwings. Exceptions to this rule were many nests at Cache Creek and Blue Moon Ranch in 1960, and late season nests in south-WLSM, 1959, whose bases and inner linings were often so thinly woven that small holes were clearly visible in the bottom of the nest. In spite of this, eggs were successfully incubated in most

such flimsy nests.

A peculiarity of Tricolor nest-building was the frequent use of green plant material in nests. This was most widespread at Cache Creek in 1958. During that unusually wet year, herbaceous growth in the vicinity was luxuriant long before Tricolors began nesting. A small wild mustard plant (Descurainia sophia) grew abundantly near the colony each year, and many females incorporated large amounts of this plant in nest bases. No obvious adaptive significance could be assigned to such usage which simply correlated with availability, and readiness of the birds to utilize these materials.

Tricolors also chose the sturdiest vegetation for nest attachments, such as the mustard plants previously described at Blue Moon Ranch. This was particularly true at Cache Creek whose willow branches, used to attach nests, were not only sturdy, but also enduring, and limited in number of suitable attachment sites. Often females simply rebuilt nests there by revamping the eroded mud-cup portion and adding a grass lining.

Clutch Size and Incubation

Tricolor clutches ranged from two to five eggs. This represented one reproductive phase not amenable to abbreviation in breeding synchronization; since Tricolor females appeared to require twenty-four hours to manufacture each egg (see also, Payne, 1965). However, mean clutch sizes

of Tricolors in southern California tended to be smaller than those of Redwings. With few exceptions, three-egg clutches predominated among Tricolors (Table 16). This represented at least a potential means of shortening the laying period (as well as an adjustment to resources) in a colonial species.

The two lowest means recorded were obtained in unusual circumstances. The average of 2.67 at HVM in 1959 included all six Tricolor nests receiving eggs there, with most of the colony having evacuated even before that laying was completed. At the 1960 synchronous Blue Moon colony, where the mean clutch was 2.97 eggs, the count was made near the end of incubation when some hatching had already begun, so that incubation egg losses had probably already operated in reducing clutch sizes. Other colonies were censused earlier in the incubation periods, or were visited regularly during the span of egg-laying.

Colonies whose members were not wholly synchronous in nesting, either with periodic-subcolonial additions, or season-long egg-laying (Table 12), usually did not show significant differences in clutch size at different times during a breeding season, in contrast to most Redwings. The situation at Cache Creek in 1958 was an exception. During May, nearly all of the 50-clutch sample contained four eggs, with a mean of 3.88, which was the highest obtained in this study. Nearly all nests sampled from a

Table 16 shows ranges and means of Tricolor clutch size at various study sites, 1956-62. Asterisk signifies combined May and June, 1958, counts whose respective means were 3.88 (N=50) and 3.08 (N=25). Superscript "a" means completed utilized nests in one season. Superscript "b" five populations combined, with sample counts as listed.

Total ^a Nests	Locality	Year	Clutch Sizes					Mean
			2	3	4	5		
2000	Cache Creek	1956	9	79	26	0	3.06	
450	"	1958*	4	24	46	1	3.58	
400	"	1959	5	48	15	0	3.19	
200	"	1960	2	27	4	0	3.06	
150	HVM	1957	0	5	4	0	3.44	
20	"	1959	2	4	0	0	2.67	
1800	WLSM	1958	3	76	15	0	3.13	
1200	"	1959	4	58	9	0	3.07	
300	S.F. Res.	1960	2	38	13	1	3.24	
700	Blue Moon	1960	12	74	9	0	2.97	
1300 ^b	S.D. River	1962	2	243	47	0	3.15	
	Totals		45	666	192	2	3.17	

second, smaller population of Tricolors (Table 12), upstream from the May colony, contained three-egg clutches in June, producing a mean of 3.08 (Table 16). Such a remarkable divergence would be completely obscured by simply combining samples for the whole population in 1958. Whether Tricolors adjusted clutch size as a response to changed ecological conditions, as documented in some song birds and raptors (Lack, 1954), was not conclusively demonstrated, although initial population-size adjustment has already been proposed in a previous section. Nevertheless, seasonal change at Cache Creek involved a transition from luxuriant, moist conditions in April and May to a substantially dessicated adjacent landscape by early June.

Only the female sat on eggs in this species, as in the Redwing. Incubation, beginning with the laying of the final egg in a clutch, lasted eleven to twelve days as had been previously reported (Emlen, 1941). More precise data on the proportion of 11 and 12-day periods were not obtained.

In breeding colonies with highly synchronous timing, such as the 1956 Cache Creek and 1958 WLSM colonies, the whole population on the nesting site gradually became quieter, nearly silent, toward the end of the laying period. This was primarily due to the diurnal departure of nearly all males from the colony during that time, and

cessation of male territoriality. Approaching a seemingly empty marsh during the middle of incubation, I saw the quiet shuttling of incubating females as they flew to and from nearby fields in which they foraged. This situation prevailed from April 9 - 15 at the WLSM colony in 1958, where about 1200 nests were begun from March 28 to April 3 (Table 12).

During the height of incubation, males which had been vigorously territorial only a few days previously, ranged widely in feeding flocks over parts of Hidden Valley, or several miles farther west and northwest. Males tended to frequent the above-mentioned nearby foraging sites of females only during the evenings when they returned to roost. During that period many males returned to WLSM to roost, generally behaving like the members of winter roosting flocks. Some males apparently entered their own territories, deduced in part from placid acceptance of this return by incubating females present; but most of them roosted elsewhere in the same marsh (Lack and Emlen, 1939), much of which was not being exploited by Tricolors for nest sites in 1958.

Motivation of activities by roosting immature and adult males during this quiescent period was obscure; but the birds were generally subdued, chorusing in pre-roosting groups, and exhibited few sexual or aggressive displays. In general, their behavior indicated greatly reduced terri-

toriality. Incubating females seemed outwardly little concerned by adult male Tricolors, even in non-synchronous colonies where daily male presence lasted many weeks. Only at HVM in 1957 did any Tricolor females exhibit distress over presence of males. At that time, in the midst of a turbulent interspecifically competitive situation (see below), immature male Tricolors and a few Redwings repeatedly wandered through the small Tricolor colony (Table 12) evoking strident screeches and frequent attacks from incubating Tricolor females. Otherwise, under normal undisturbed conditions, Tricolor females postured in an exaggerated wing-spread bowing display (Figure 24) at the nest when their mates re-entered territories during the incubation period; and they nearly always uttered a special, subdued chattering call ("Nest-site Screech"), when leaving or returning to the nest.

Foraging and Care of Young

A day or two after young began hatching, males reappeared on their territories; and they had assumed an active role in providing nestling food by the time the latter had reached an age of three days. How males knew hatching occurred was not clear; but their evening roosting returns presumably provided ample opportunity to monitor the situation. Females received much more help from mates than did Redwing females. For example, male Tricolors regularly delivered food to 75 percent of nests observed

at Cache Creek and San Fernando Reservoirs in 1960 (Table 17).

Since the male assumed a dual role during this period, reasserting his territoriality, several questions arose about his performance. These involve males' foraging rates, specific relations to female contributions, and the number of nests attended simultaneously by a polygynous male.

As in Redwings, the daily and day-to-day frequency of foraging trips was quite variable for both sexes. Gross estimates, based on counts of feeding flock shuttles at sites included in Tables 17 and 18, showed that the ratio of female trips averaged five to one over males' at the height of feeding young. Since females outnumbered males by approximately two to one in most breeding colonies, such observations suggested that foraging females made twice or thrice the number of trips undertaken by males. Specifically, nest observations indicated two to four female visits for every one by a male.

Average intervals between trips by females carrying food (Table 17) ranged from 14 minutes at Lake Sherwood to 19 minutes at Cache Creek. During the same periods male trips averaged from 27 to 40 minutes each. Observations of nests which included visits by both sexes suggested that an overall approximate mean of slightly less than four trips per hour by females was augmented to

Table 17 shows adult male and female Tricolor food deliveries to nestlings on selected dates at four study sites, 1958-1960. Included respectively in the third column from the left are: Number of nests, age of nestlings, and number of nestlings (in parentheses). See text for discussion.

Locality Year-Date	Parent Sex	Nest and No. Young (age)	No. Trips	Mean Trip Interval mins.	Range of trip Intervals mins.
HVM, 1958					
5/30	Female	1 nest; 8 day (2)	7	14.1	(5-22)
	Male	"	2	45	--
WLSN, 1959					
5/15	Females	2 nests; 1 day (3)	18	14.5	(4-37)
5/17	Female	1 nest; 3 day (2)	14	15.25	(6-30)
	Male	"	5	35	(15-65)
5/19	Females	3 nests; 5 day (2,2,3)	35	14.2	(9-26)
	Males	"	15	32.3	(10-107)
5/26	Females	4 nests; 4 day (2)	11	17.4	(5-29.5)
	Males	"	7	27.5	(13-70)
Cache Creek, 1960					
5/30-6/7 - 6 nests					
	Females	2 nests; 4 day (2)	13	19.25	(6-52)
	Females	3 nests; 6 day (2)	15	18.75	(5-37.5)
	Males	"	7	40	(17-95)
San Fer. Res., 1960					
5/20; 22	Females	11 nests; 3-4 day (3)	37	16.15	(8-26.5)
	Males	8 nests; 3-4 day (3)	14	34.6	(10-89)

nearly six trips (or more) per hour with male contributions. As recorded for Redwings in this study, and many other passerines (Kendeigh, 1952), nest visits increased slightly with the age of the young. Although broad foraging trends attributable to ecological conditions or distances to sites were not substantiated, fewest feeding trips per hour, least male help, and possibly the longest average travel distances were observed under very dry conditions in the small Cache Creek colony during June, 1960 (Table 17). Three additional facets of male feeding behavior were also noted. First, males were often observed returning from foraging trips with only one or two insects in their beaks. Although no quantitative comparisons were made on food gathering efficiency between the two sexes, my impression was that females consistently averaged more food items per trip. Second, males tended to behave in a nervous manner on their territories, seemed more reluctant to deliver food in the presence of an unconcealed observer, and were even occasionally observed to swallow food brought back to the colony. Females never did the latter. Third, data on simultaneous male provision of food at two nests in his territory were inconclusive. Two suggestive phenomena were noted. A single marked male at San Fernando Reservoir in 1960 (Table 15) had two nests with young in his territory during the observation period, and seemed to

divide his attention between the two nests, concentrating efforts on the one with older nestlings in it, which presumably he had begun to feed first. Not more than 25 percent of observed nests were attended solely by females. Most males had more than one mate; and it seemed reasonable that if most individual males delivered food only to one nest in each territory, then exclusively female attendance would have been higher than 25 percent. Comparative feeding rates between assisted and unassisted females were not obtained.

Tricolor foraging exploitation was striking in this study, as much for the large numbers of birds involved in shuttling flocks between feeding and breeding sites, as for the average and maximum distances travelled. Capacity for this species to exploit food as far as four miles from breeding colonies has been documented previously (Grinnell and Miller, 1944; Orians, 1961). Salient features of foraging sites and distances from breeding colonies in this study are summarized in Table 18, which may be compared to Figures 2-4. Broadly, they ranged from 200 yards to three miles distant from nesting sites, although most intensive feeding usually took place within a mile of observed colonies. Tricolors only incidentally foraged within marsh habitats, although some feeding sites were moist areas (Table 18). For example, birds intermittently hawked insects overhead during prospecting

Table 18 describes various foraging sites at four Tricolor breeding localities, and ranges of distances traveled to them, 1956-1960. Compare with diagrams in Figures 2, 3 and 4.

	Site	Distance
Cache Creek		
1956	Dry pasture; wet stream outflow, southwest.	200 to 600 yards
1958	Wet stream outflow, SW.	same
"	Sand Canyon dry fields and cultivation, WNW.	three miles
1959	Same two areas as 1958	same distances
1960	Same two areas as 1958	same distances
"	Wet stream outflow, WSW	one mile
WLSM		
1958	Wet and dry pasture, WSW	200 to 500 yards
"	Grain fields, wet and dry pastures, NW.	440 yards to one mile
1959	Grain fields, pastures, NW	440 yards to 1.5 miles
Blue Moon R.		
1960	Grain fields, wet live-stock pastures, E., and NE.	Range 200 to 1300 yards
San Fern. Res.		
1960	Grassland, lake-edge, riparian, NW	440 yards to one mile
"	Dry fields, abandoned pastures, E., south.	200 to 880 yards

and colony establishment periods at Lake Sherwood. The only instance in which birds foraged actively within nesting vegetation was noted at Blue Moon Ranch where limited feeding occurred in the cultivated barley fields.

Specific food of Tricolors has been little studied. In the following accounts I have attempted to assay food seasonally and spatially. This was done most intensively at Cache Creek prior to breeding initiation and during its early phases. Figure 13 above indicates a diversity of foods found in Tricolors, and suggests that they are no more food specialists than the generalized Redwing. Generally, fall and winter flocks, exemplified by individuals roosting at Blue Moon Ranch in mid-October 1960; were almost exclusively granivorous. Even specimens collected at cattle feed yards in the southern San Joaquin Valley during mid-April 1960 often were feeding mainly on cracked grain incorporated in high protein livestock food. As with Redwings, Tricolors had usually switched to a predominantly insect diet by the onset of breeding or before (Figure 13); and food deliveries to nestlings averaged around 90 percent insects (Figure 13). While not limited to a special food source, Tricolors did often rely heavily on lepidopterous (Noctuidae) larvae, dipterous larvae and to some extent on locusts (Orthoptera), especially as food items delivered to nestlings. Aphids and beetles were found abundant in crops and stomachs of

specimens collected from prospecting flocks at Cache Creek during April, 1958-1960.

Several cases of concentrated collection of certain food types were recorded. In May, 1956, at Cache Creek nearly the whole Tricolor colony foraged widely in dry livestock pastures (Table 18) from which they obtained abundant noctuid and dipteran larvae. In subsequent years, the dwindling colonies there (Table 14) had forsaken such a dry area (Figure 2; Table 18).

During June, 1960, at their farthest distant feeding location (Table 18), colony members obtained large numbers of small Valley locusts (Dedaleonotus enigma). Tricolors in one small colony along the San Diego River during April, 1962, were observed to exploit localized, dense concentrations of a larval noctuid moth (Peridroma margaritosa). In all study sites the apparent trend was for adult insects to increase in the birds diet during the season, especially the aforementioned orthopterans (locusts), and odonatans (damselflies).

Reproductive Success

As in the Redwing, major factors affecting Tricolor nesting success were divisible into parental care-giving capacity, predation, and adverse environmental effects. Success of breeding colonies is summarized in Table 19, following the same format as Table 9 for Redwings. The ensuing discussion emphasizes comparisons of populational

Table 19 shows Tricolor nesting success at several study sites for specified parts of the breeding season, 1956-1962. The column listing total nests indicates actual or estimated number of nests in which eggs were laid at each site; and the asterisk next to total nests at San Diego indicates this secondary colony reformed after marsh was burned. Column "A" indicates number of successful nests over number of observed nests at each site. Column "B" indicates number of fledglings reared per successful nest. Column "C" indicates number of young fledged per nest in all nests observed. Column "D" indicates percent total success for all nests observed. Column "E" indicates percent actual fledging in those successful nests producing young at each site. For 1959, Westend-Lake Sherwood is subdivided into several specified portions (see text for discussion of their success).

Locale	Year	Month	Total Nests	A	B	C	D	E
Cache Creek	1956	5/11-30	2000	9/12	3.0	2.25	69.2	100
	1959	5/15- 6/22	400	11/13	2.0	1.69	53.7	64.4
	1960	5/20- 6/15	200	14/17	1.93	1.58	54	64.3
HVM	1957	May	125	No counts; but dozens of fledglings observed.				
	1959	4/15- 5/2	6	1/6	1.0	0.17	16.7	33.3
WLS area (wet)	1958	5/15- 6/28	1800	23/29	2.43	1.59	62.2	77.8
	1959		(1200)					
a) Isol. bulrush clumps (dry)		4/15- 5/26	150	5/15	2.60	0.87	29.5	81.2
b) Tower bulrushes (wet)		5/7- 6/18	298	18/26	2.11	1.46	48.1	66.7
c) So. WLSM cattails (dry)		5/30- 6/18	65	5/20	2.2	0.4	18.6	76.6
d) Marsh "G" (wet)		4/18- 5/14	150	8/13	2.13	1.31	43.6	70.8
S. F. Res. (dry)	1960	5/1-27	300	31/40	1.84	1.43	44	57
San Diego River (wet)	1962	4/30- 5/20	*200	56/75	1.61	1.20	38.2	51.4

and individual nesting success.

In palustrine habitat, there was a clear correlation of breeding success or failure with wet or dry marsh conditions. During the favorable year, 1958 (34 inches rainfall), both qualitative impressions and actual counts of nesting success at Lake Sherwood showed a high percentage of success. In other years, those marshes situated over water consistently produced more successful fledgling Tricolors than did dry or dessicating marshes (Table 19). As previously discussed, dry marshes were marginal, usually non-preferred habitat for Tricolor breeding colonies. However, in 1959, exceptionally crowded conditions, caused by partial habitat destruction through burning, apparently necessitated some Tricolor nesting (rather than desertion) in isolated, drying bulrush clumps at WLSM. Such nestings, along with later-breeding sub-colonies (Table 12) in dry cattails near the south edge of WLSM, suffered great losses (Table 19), both during incubation and when nestlings reached the age of three to four days, at which time their begging calls had become noticeably louder.

The same array of terrestrial predators outlined for Redwings has been invoked as potential instruments of such nest destruction. Three observations of gopher snake (Pituophis melanoleucus) egg predation in Tricolor nests on WLSM provided additional documentation. Furthermore, captures of adult Tricolors on the

tower bulrushes by one or more Cooper hawks (Accipiter cooperi) during May-June, 1959, were occasionally observed. The comparatively greater success in over-water marshes during all years doubtless seemed clearly the result of lower terrestrial, and perhaps aerial, predation. Table 19 excludes early-season observations of WLSM in 1958, when at least some nests and eggs were destroyed by drenching heavy rains at the end of March; but subsequently, numerous fledglings were encountered throughout the marsh, reflecting high fledging rates among surviving nests. Neff (1937) reported greatly increased Tricolor egg and nestling losses to putative terrestrial predators in drying, or suddenly drained marshes during all years of study. The Cache Creek situation, 1956-1960, at best featuring an exposed, semi-marsh and riparian situation, failed to show low levels of total nesting success during all years of study. However, that rather remote habitat, on the desert edge, may well have lacked predator populations sufficient to exert much pressure on the Tricolors. Likewise, the relatively dry, semi-marsh habitat at San Fernando Reservoir in 1960 did not suffer great predator pressure (Table 19), although much wetter and less accessible in preceding years. The dense nettle vegetation, a deterrent to un-gloved nest observers, whatever the potential predator population, may have discouraged efforts by the latter. A single instance of nest loss at that

site tended to support Neff's (1937) hypothesis of lethal high ambient temperature effects on nestlings. Within twenty minutes after removal of shading leaves in an attempt to improve my view of a particular nest, the nestling contained therein died from sun exposure during mid-afternoon, 22 May, 1960.

Completely dry-land breeding by Tricolors in this study was closely observed only at Blue Moon Ranch. No aerial or terrestrial predators were ever seen; and the qualitative impressions of numerous fledglings by 26 April, 1960, strongly suggested substantial breeding success and lack of devastating predator effects in a completely accessible habitat. Numerous other successful terrestrial Tricolor breeding efforts have been reported (Neff, 1937; Bent, 1958). The following conclusions seem reasonable. Consistent Tricolor nomadism renders low the predictability of the species' presence at all breeding sites. Dry fields, as exemplified by Blue Moon Ranch (Table 14), appear less permanent fixtures, both of more widespread and ephemeral occurrence, than marsh habitats. While Tricolor colony sizes and densities were high in comparison to Redwing populations, their actual and potential synchronous scheduling enabled the former to exploit terrestrial and other habitats for a complete nesting cycle within a span of five weeks, one-third of which time was potentially characterized by virtual silence

during incubation. Such combinations of factors could clearly reduce the availability and conspicuousness of Tricolors to predators.

Revealing comparisons of individual success in Tricolor colonies were possible (Table 19). These showed a general trend for fewer successful fledglings per nest in potentially less favorable dry years at Cache Creek, Lake Sherwood, and probably at San Fernando Reservoir. Although the evidence is indirect, the data seem to point potentially to starvation of more nestlings in unfavorable years. In the moderately dry year of 1959 (Figure 11), those nests actually producing fledglings showed equally high fledging success in both dry marshes and wet marshes, with a suggestion of greater success earlier in the season than among later nesters in all marshes. In this connection, the low individual nest success at the San Diego River colony and an apparently favorable wet year, 1962, furnished a special example. In early April, Tricolor desertion had been forced by burning much of the occupied marsh. Subsequent colony re-establishment there represented a smaller, late-season population (see below). In the absence of nesting success data earlier in the season, such late nesting birds in a marsh otherwise well protected by flooding, and with foraging conditions described above, showed unexpectedly low success per nest (Table 19).

Mass desertions of Tricolor nests and eggs have been described by others (Neff, 1937; Lack and Emlen, 1939; Orians and Collier, 1963). With one exception, desertions in my study occurred prior to full exhibition of either of these breeding phases. In 1959, at HVM, Tricolors successively deserted 45 incomplete nests, 14 complete nests, and two nests with eggs. Remaining losses by Tricolors there represented all eggs and young, except for a single fledgling reared (Table 19). Such colony abandonment, as a nesting failure, was associated with three phenomena. The first was regrowth of bulrushes in another marsh, and potential improvement of availability of preferable nest sites elsewhere. Second was the deterioration of HVM by gradual drying, discussed previously in reduced Redwing breeding success. Third was behavioral interference by Redwings, discussed below under competition. All of these, individually or collectively, clearly could have devastating effects on Tricolors attempting to breed under those conditions. Basically, nesting success depended upon combinations of resource availability. A habitat, adequately protected, or undetected was basic. Once the species began breeding, presumably based upon its assessment of manifold resource suitability, it clearly depended upon food adequacy for the young, in concert with continued habitat protection and lack of interference by Redwings.

Timing of the Cycle

Timing of Breeding

Earliest commencement of Tricolor breeding in seasons during this study consistently occurred soon after the vernal equinox. Typically, in lowland southern California, colonies were established during the last six days of March, with initial egg-laying periods lasting from April 1 to 15 (Table 12), regardless of population size or subsequent increases in numbers of breeding birds. With breeding colony expansions later in a season, egg dates extended at least through June 13 in 1958, terminating somewhat earlier in other years --- all of which produced less rainfall than 1958. Timing of events seemed to begin earlier during ecologically favorable years, in undisturbed habitats. Correspondingly, extension of the season was longest, with greater numbers of synchronous population increments during wet 1958 at Lake Sherwood (Table 12), and probably at Cache Creek.

Delays in breeding initiation were also observed, the most striking being associated with habitat disturbances or apparent suitability. In 1959, when burning limited initially favorable nesting vegetation on WLSM and overflow of nesting Tricolors occurred to other areas, colonies were not only established slightly later than other years, but egg-laying, especially in unburned marsh remnants, began nearly a week later than the preceding year. As

more marsh reached apparent suitability for nesting in 1959, an almost steady increase of new breeding members prevailed at WLSM. Indirectly, Tricolor desertion of HVM in 1959, and Lake Sherwood in 1960 and 1961, represented observed delays in timing of breeding initiation. This assumes the actuality of the previously suggested movement by the birds elsewhere to breed. Documentation of such potential was furnished by interruption of the normal cycle, mentioned above, causing a nesting delay at one San Diego River marsh during April 1962. A 1000-bird colony began on March 26, with the marsh being burned by vandals on April 6. Nearly all eggs and nests were destroyed; whereupon Tricolors abandoned the site for nearly three weeks. During that period, shifting flocks totaling about 500 Tricolors were observed in the vicinity of a second, marsh-nesting colony three miles downstream. Such nomadic flocks moved about the local hillsides and nearby golf course, showing no definite signs of breeding at the second colony. By the last week of April, a second colony of about 300 Tricolors had become re-established mainly in unburned parts of the former breeding site upstream, where they continued a successful breeding effort through May. Coincidental with formation of the latter colony at the burned site was the disappearance of shifting Tricolors flocks near the downstream colony. Although all observed birds were unmarked, this remarkable

sequence of events strongly suggested that the shifting birds had been those driven from the burned marsh, and the re-established colony represented many of those individuals. It seems quite reasonable that all late season breeding establishments, individual and colonial, could be explained by naturally or artificially produced unfavorable or unsuitable conditions such as those outlined.

Bent (1958) lists egg dates for this species from April 1 to June 17 in all parts of its range; and in central California, Orians (1961) and Payne (1965) recorded colonies started from early April through the end of May, 1958-1964. Near the northern limits of its range Richardson (1961 and 1964) has recorded Tricolor colonies starting as late as the end of May. The latest establishment observed in this study was that of a small sub-colony of about 75 Tricolors on June 1, 1958, in the southwest corner of Lake Sherwood (Figure 8; Table 12). This resulted in presence of eggs there until June 25, about a week later than previously reported (Bent, 1958).

Climatically, even the earliest Tricolors usually began nesting under the relatively mild conditions of early spring, when most freezing weather had passed, and toward the end of the rainy season. Under normal conditions, starting dates I recorded at lowland areas between San Diego and 250 miles northward in the San Joaquin Valley occurred during the first week of April. The up-

land study site at Cache Creek, approximately the same latitude as Blue Moon Ranch in the Valley lowlands (Figure 1), exhibited unfavorable climate as late as April 23, 1960, when snow flurries, heavy winds and bitterly cold weather were recorded. In both large and small colonies at that site no eggs were ever laid earlier than April 22, three weeks later than the lower elevations. These dates compared favorably with the mean starting dates of colonies reported by Orians, 1961 in low-foothill areas of central California, 300 miles farther north. Thus, altitudinal, and to some extent latitudinal seasonal conditions appeared to affect timing of Tricolor reproductive efforts.

Gonadal Cycle

Broad temporal differences in commencement of breeding among Tricolor colonies focuses attention on their gonadal cycle. For a complete histological and physiological treatment of the subject, the recent work of Payne (1965) may be consulted. In this study, discussion will be largely confined to the information on reproductive timing in southern California provided by collected specimens represented in Figures 14 and 17.

Tricolors were not collected earlier than March 10 prior to the breeding season, excepting the sexually quiescent males in mid-October. Thus, no very small testis volumes were obtained. Although some immature

Figure 17 shows testicular development in the two species, as growth stage plotted against time of year for 81 specimens. Tricolors are designated by the appropriate closed circles listed in the upper left portion of the figure. Similarly, years and open-circle symbols represent Redwings. Numbers next to symbols in the figure indicate the number of males in that condition on the specific date. The lower case "m" in spermatogenic stages indicates a condition halfway between two stages (Blanchard, 1941).

gonads were found, seminiferous tubule diameters fell within the usual range for reproductively mature males (Figure 14). Most Tricolor males were found to be in a mature spermatogenic condition (Figure 17). However, there was a distinct shift in this condition during March, even among males collected away from potential breeding sites. Specimens from cattle feedyards at Shafter in the San Joaquin Valley, March 10, 1960, exhibited testicular development mostly in early to middle spermatogenic stages; but all birds taken there at the end of March were in late stages, and 60 percent were fully mature (Figure 17). Likewise, most lowland males, collected during mid-March on potential breeding sites had mature gonads, as did all those taken during April and May. Table 17 reflects a lag in gonadal development by Tricolors during early March, compared to Redwings. This is apparently followed by a very rapid maturation in three weeks or less, a condition also suggested by Payne (1965).

All males from Cache Creek showed mature testis condition from March 17 (earliest collection date, and before site prospecting) onward, similar to the Valley lowlands. This clearly indicates that factors other than male sexual maturation retarded breeding in such upland areas.

Few birds were taken at Lake Sherwood, in order to

disturb the population minimally. The only males examined, a week before colony establishment in 1959, were in full reproductive condition.

Gross examination of ovaries performed at Cache Creek showed that Tricolor females retained relatively small ova until about a week before first laying in a colony, a fact also reported in detail by Payne (1965). This paralleled the condition in Redwing females. Such abrupt initiation of accelerated ovarian development approximately coincided with the time at which large numbers of females joined prospecting or establishing colonies, thenceforth experiencing increased male behavioral influence.

Since Payne (1965) has demonstrated a usual songbird photoperiodic response (Farner, 1967) for male Tricolors, it seems likely that most of them achieve sexual maturity early in the season; and both stationary and wandering flocks are inhibited from breeding until appropriate social and environmental conditions are encountered. Since female presence and acceptance of the situation are clearly necessary to begin a colony and to complete ovarian development, that sex may well determine by her behavior whether a prospecting flock (initially made up of singing males) remains at, or deserts a site. Thus, the female's assessment of conditions could be as vital in timing Tricolor breeding as it was suggested to be for Redwings.

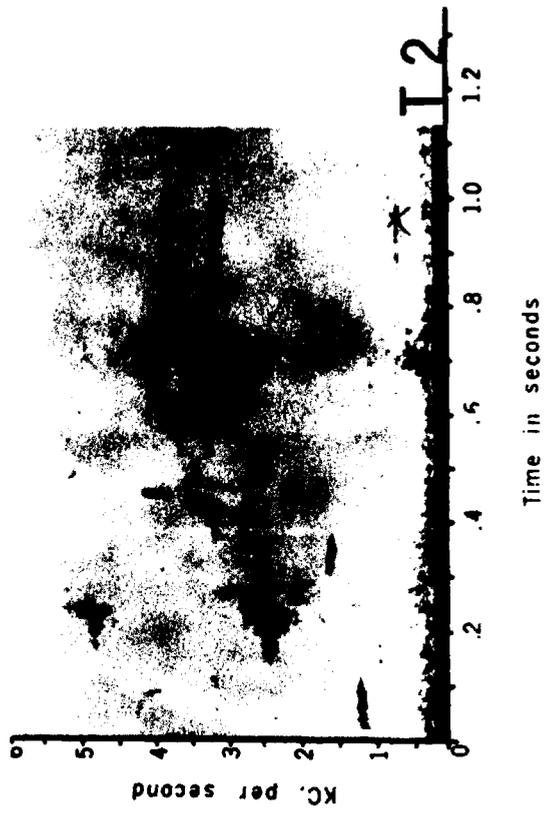
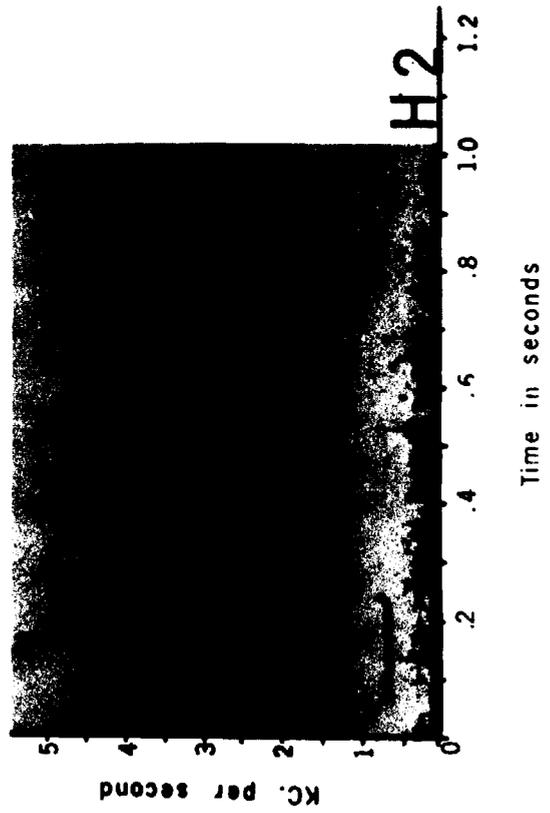
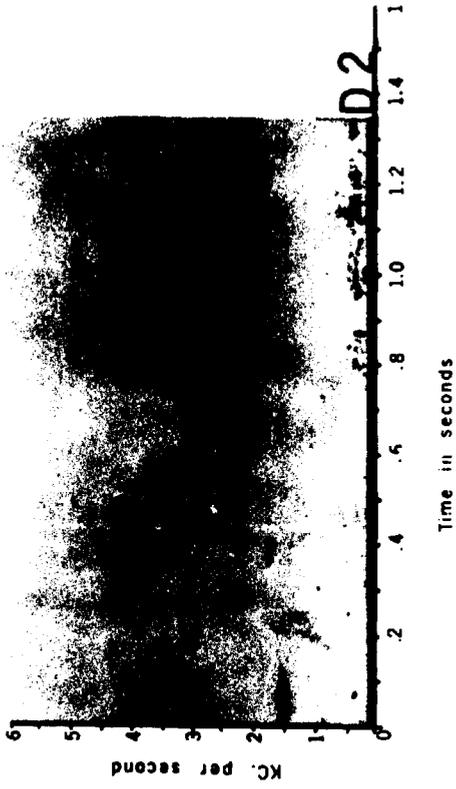
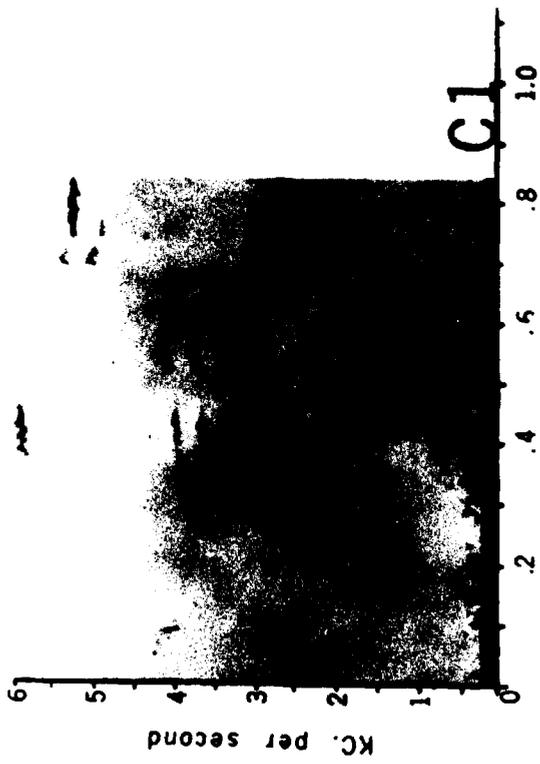
VI. VOCALIZATIONS AND DISPLAYS

The succeeding presentation consists of descriptions and analyses of various prominent sounds and postures observed in the two species during this study. Since emphasis has been placed upon the reproductive cycle and its significant vocal and postural communications within and between the sexes, this account is regarded as an incomplete compilation of Tricolor and Redwing repertoires and their variations. Further coverage of the subject may be found in Orians and Christman (1968, in press). Significance here means the observed, apparently meaningful, communicatory contexts in which vocalizations and displays were used among the birds themselves. This section forms the basis for discussion of field experiments in a subsequent section covering "Experimental Analysis of Behavior".

Redwing Vocalizations

Male Song --- Song is generally considered a complicated and elaborate vocalization of passerine species, as distinct from simpler and shorter call notes (Armstrong, 1963). It is the traditional sound by which Redwings are recognized in the field. Redwing song shows considerable geographic variation (Figure 18), as well documented by Dawson (1921) for Redwings in various parts of California. Males sing throughout the year. Individually, it is most

Figure 18 contains sonagrams illustrating the geographic variation characteristic of Redwing male songs. In each sonagram, sound frequency in kilocycles per second is plotted on the vertical axis, and time marked in tenths of seconds, up to 1.8 seconds, is plotted on the horizontal axis. Sonagrams are coded as follows: C-1 is the song of a male Redwing at East Park Reservoir, Colusa County, California (see Orians, 1961); D-2 is a song from Dane County, Wisconsin; H-2 is a song from HVM, Ventura County, California (this study); T-2 is a song from the "Silverado Trail", Napa County, California (see text for explanation). These sonagrams were made with a narrow band filter, emphasizing sound frequency. Compare with Table 42.



distinctive among territorial males during breeding, when they sing from one or more prominent sites or song perches within territories. Song advertises the singer to competing males, and to both mated and unmated females as an integral part of courtship. The latter has been presumed to be a component of the male behavioral role in completing female breeding development (Nero, 1956a). In this study no attempt was made to determine any distinctions between types of song used in courtship and aggressive behavior. At least during territory establishment and breeding, males generally accompanied song with spread display (see below).

In Los Angeles and Ventura counties song length ranged between 0.4 and 1.3 seconds. Phonetically it resembled "KER-A-LEE-OO", a rather liquid, melodic rendition which differed markedly from most other California Redwings, and from eastern populations of the species most of which exhibit an attenuated, segmented terminal trill in songs (Figure 18, D-2). Such differences clearly reflect geographic isolation among populations of the widespread Redwing species, similar to that recorded in other passerines (Lanyon and Fish, 1958). Variation notwithstanding, all songs of Redwing males contained a short segment of one to three introductory notes, a major central segment with multiharmonics and broad frequency range (rarely segmented), and a terminal liquid or trilled seg-

ment. Such diversity of component frequencies, their changes, and the apparent strength of sound energy in more than the dominant frequency, clearly reflected the large potential of discrete information contained in an individual male's song.

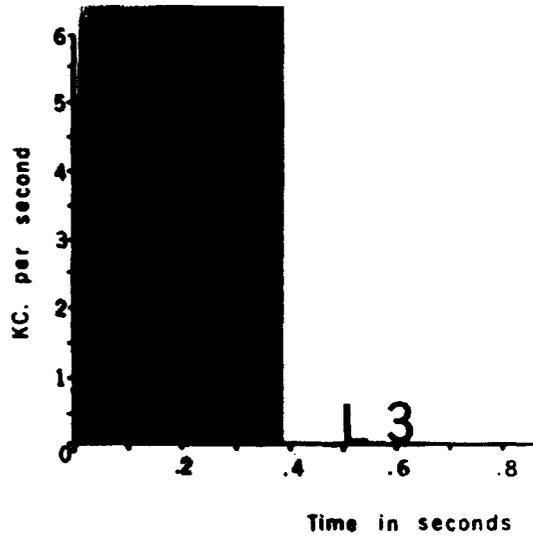
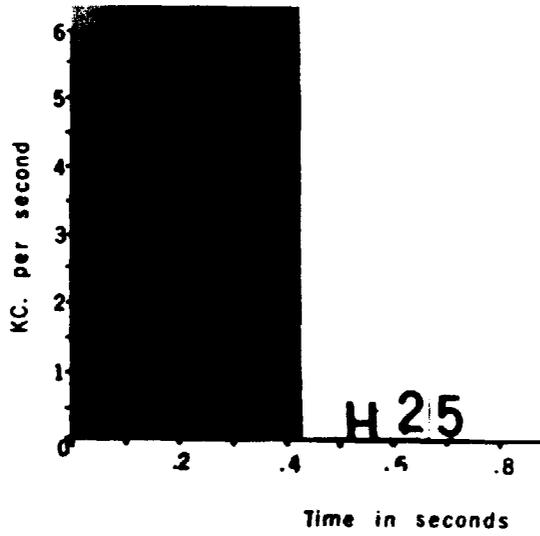
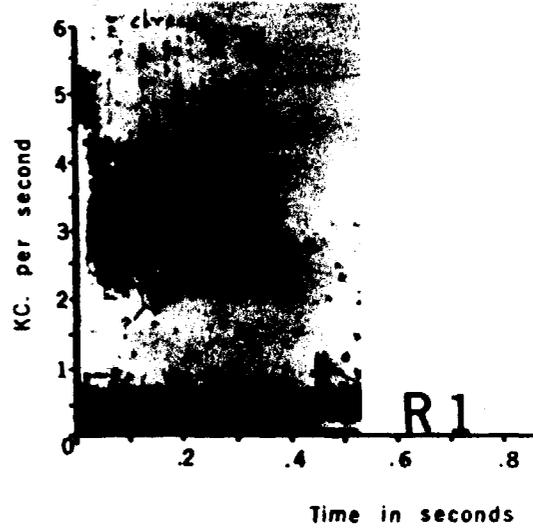
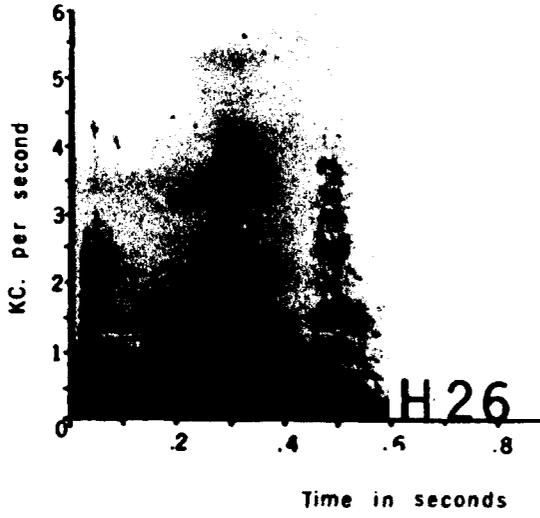
Female Song --- This vocalization was first clearly distinguished by Nero (1956a), who describes it as directed toward other females in aggressive sub-territorial behavior. It was accompanied by female spread display (see below). In my experience, it was rarely uttered under any circumstances. Nesting females failed to emit the song in the presence of a nearby stuffed male or female dummy. Female song, more harsh, strident and less melodic than the male may be phonetically rendered as "CHUCK-CHUCKA-SCREE-SCREE-SCREE". It consists of one or two abrupt, sharp and low-pitched introductory notes, followed by several segmented, shrill bursts of screeches with wide frequency range. I failed to detect any dialectic differences in female song. The vocalization resembles nest site screech (Figure 20; see text), but it is longer and more complex. No sonagrams of this specific song were obtained.

Song-flight Announcement --- This vocalization was given by a territorial male just before or during departure from, or upon his return to, the territory (Beer and Tibbits, 1950; Nero, 1956a). It was also heard to

accompany a male's flight over his territory upon the eviction of an intruding male Redwing. It was clearly used in territorial maintenance and seemed to advertise specific movements of the territorial male. It was not heard during the non-breeding season. Phonetically, it resembles "CHOCK-CHREEE-CHREEE-CHREEE", with some shorter variations. The announcement is composed of one to three low-pitched, sharp introductory notes, followed by one or more shrill, ringing terminal phrases which are usually segmented. Such a rendition might be repeated several times by a male.

Species Contact Call --- This consists of a soft, broad-fronted, single short note, with a mean dominant frequency of 2500 cycles per second (Figure 19). Phonetically the sound resembles "TEEK" or "PEEK". It was uttered by both sexes at all times of the year. Both perched and flying individuals in Redwing flocks were heard to give the call. Resting flocks at midday often vocalized in this manner upon being flushed from vegetation. It is the call typically heard from Redwing flocks flying overhead, by which this species was readily distinguished from other blackbirds by audition alone. The contact call seemed likely to function as species recognition signals and as a device which maintains flock continuity, as suggested by Collias (1960) in a variety of avian species.

Figure 19 illustrates several Redwing and Tricolor call notes. H-25 and L-3 are, respectively Redwing low intensity and high intensity terrestrial alarm notes. H-26 shows Redwing contact note on the left, and Tricolor contact note on the right. R-1 represents one rendition of a Redwing aerial alarm call.



Low Intensity Alarm Call --- This call is also a single, partly harmonic syllable, with a metallic ring to it (Figure 19). It is rendered phonetically as "TINK" or "FLINK". It is a louder, sharper sound than the contact call. Spectrographically, it forms a steep-fronted note, between 2500 and 3800 c.p.s., attenuating in length to 0.3 seconds, with a level, mean dominant frequency of 3200 cycles per second. The sound was uttered by both sexes, and appeared to be elicited upon the distant approach of a potential ground predator, such as the human observer. The call frequently followed initial response of species contact calls in a Redwing flock, or among territorial males abruptly replaced song, whenever I approached the birds. Such characteristics seemed to qualify it as a low level alarm or warning note, whose form changed upon closer predator approach (see below).

High Intensity Alarm Whistle --- This is a sharp, high-pitched sound uttered exclusively by males. Phonetically, it was a ringing, disyllabic, attenuated "CHEE-ER", "CHU-LEE" or "TS-EEE" (Figure 19). It ran from 5500 to 4500 cps. on the faint first syllable and gradually descending on the second from 4000 to 3500 cycles, each in 0.3 seconds. The second syllable lacked harmonics, and no significance has been determined for the phonetic variations mentioned. Its utterance was clearly associated with the close approach of a potential

ground predator, such as myself; and it usually succeeded the previously described low intensity alarm call. The high level of alarm or warning was assessed as a correlation with proximity of potential danger. Its greatest intensity, and rate of delivery seemed to emanate from males who dived at me in attacks as I passed through their territories. Similar alarm notes were described by Collias (1960) for eastern populations of Redwing males.

Aerial Alarm Call --- This is a shrill, disyllabic, high-pitched vocalization. Phonetically, it sounds like "CH-REENG". Spectrographically, it is a compactly segmented sound about 0.4 seconds long, with several high harmonics, whose dominant frequency mean lies at 3000 cycles per second (Figure 19). It appeared to function as a warning call associated with aerial predators. The call was heard several times in the presence of such large, slow flying raptors as Marsh Hawks (Circus hudsonicus) and Red-tailed Hawks (Buteo jamaicensis), and as Redwing males rose to attack such potential predators. In contrast, smaller, more rapid flyers such as Cooper Hawks generally met with silence by Redwings, and never with the aerial alarm note.

Threat and Alarm Hiss --- This was an attenuated, low buzzing or hissing sound, at least part of which seemed to be unvoiced or non-vocal. Phonetically, it is represented as "CHAAA AH" which may exhibit a wavering loudness

that diminishes at the end of the call. Spectrograms were not obtained; but the sound was clearly low frequency, possibly containing compact segmentation and harmonics. It was emitted by territorial males when threatening at close range, or attacking predators perched on or near the ground. It was directed toward humans on occasion, especially in the vicinity of a nest; but it was usually heard in the presence of such animals as domestic cats, dogs, and squirrels, likely predators listed above in the section covering reproductive success. In one instance at Lee Lake, 1953, the call was directed toward a quietly perched American Bittern (Botaurus lentiginosus). It was infrequently uttered as an apparently low intensity threat by Redwing females in driving other avian species away from nests.

Female High Intensity Distress Call --- This is a loud, strident vocalization which was uttered by females under stress during hostile encounters with intruding males, either Redwing or Tricolor, near a nest. Phonetically it can be described as an undulating, trisyllabic, compactly segmented "CHU-AYAAH", rising on the middle syllable and falling on the last. A similar note was heard from captured females and fledglings held in the hand. Such apparent distress signals quickly attracted many members of a breeding population to the site in an apparent mobbing reaction, during which some excited fe-

males called in this manner. Altmann (1956) found a similar reaction among female Redwings mobbing stuffed raptor specimens.

Male Recognition Call --- This call was a sharp, abrupt, low-pitched and disyllabic note. It is rendered phonetically as "KEK-KEK" or "KUK-KUK". The call was heard from territorial males when females entered their territories, and appeared to precede sexual chasing (see below). At least to the observer, the utterance signified male recognition of the female's presence or initial arrival.

Sexual Chase Call --- This call resembled an abbreviated version of the threat and alarm hiss, and phonetically is rendered as "CHRAAH". It is harsher and more subdued, repeated three or four times rapidly. Only males chasing females uttered this note; and it was only heard intermittently during the brief period of pair formation, characterized by frequent sexual chases. As indicated by Nero (1956a), such chases are ambivalent, exhibiting positive sexual and negative hostile qualities; and it seemed clear that the accompanying vocalization reflected a potential of both attraction (and stimulation) and repulsion of the female, as well as ambivalence in male motivation.

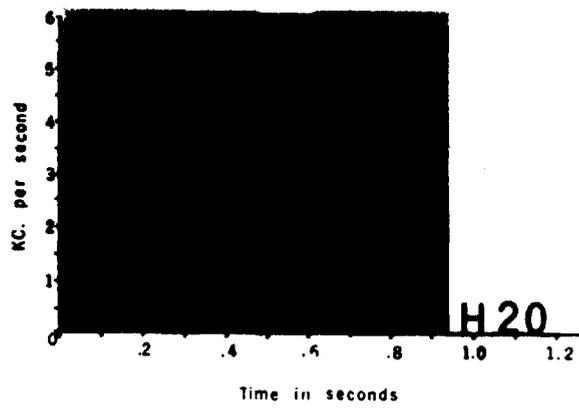
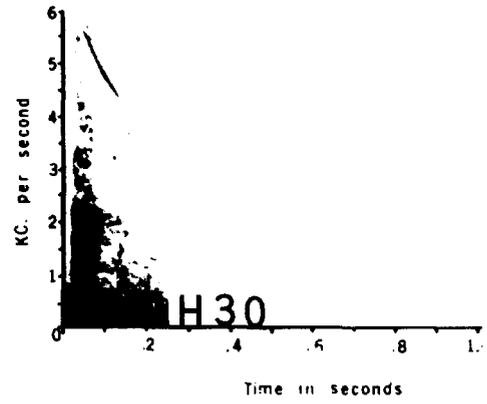
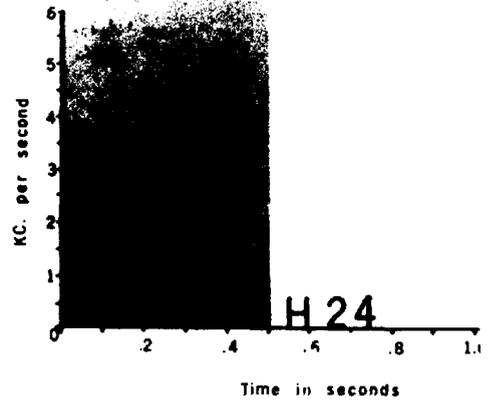
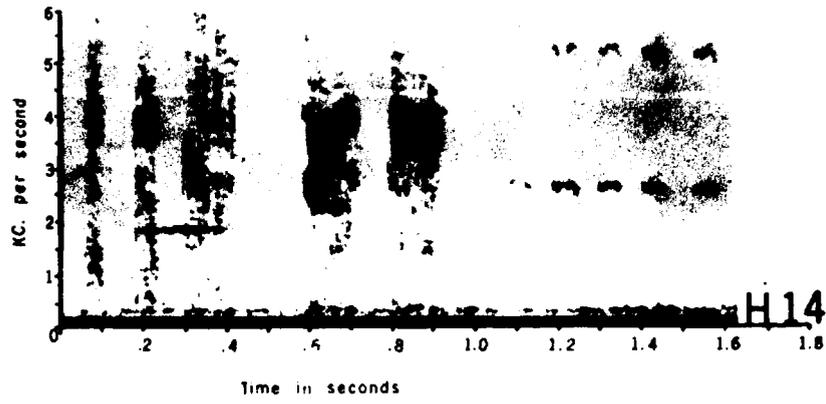
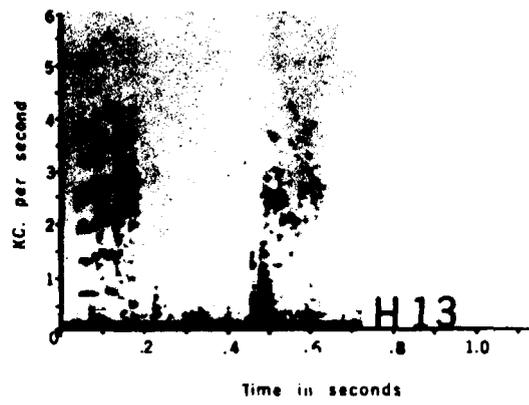
Nest Invitation Call --- This vocalization is a low, hissing or buzzing, trisyllabic sound. It is phonetically

represented as "HISSAYAAH". Occasionally it seemed to be disyllabic, but was always more attenuated than the threat or sexual-chase calls described above. However, Nero (1956a), equates this nest invitation call with the latter vocalizations. The call was commonly uttered by a male during the nest-site selection period, when he and his mate wandered through the territory in an apparent search which consummated in the choice of an appropriate nest site (see below; Nero, 1956a).

Male Precoital Call --- This call consists of a thin or weak, high-pitched series of notes rapidly repeated. The phonetic rendition is "TI-TI-TI-TI", resembling the terminal portion of the corresponding female call (Figure 20). It differs from the latter in that each syllable seems less loud, of higher frequency, and shorter in length. Males were heard to utter this call just before mounting a female in copulation, as well as right after completion of the act. Stuffed female dummies often elicited this call, after initial male reactions including spread display (see below). In such contexts, it clearly reflected a high level of sexual excitement in males.

Nest Site Screech --- This call is a shrill, broad-frequencied screech of several repeated syllables, each containing four to eight compact segments (Figure 20). Phonetically it sounded like "SCREE-SCREE-SCREE-SCREE".

Figure 20 illustrates sonagrams of several Redwing and Tricolor calls. Time and frequency scales are explained in Figure 18. Sonagram H-14 is female Redwing nest site screech, followed by female precoitional calls. H-20 is Tricolor female nest site screech. H-13 shows Tricolor male flight song. H-24 shows Tricolor male threat growl. H-30 shows low intensity Tricolor alarm call.



It was uttered by the female in the vicinity of her nest, during building, incubation and care of young. During the latter phase of breeding, the call was most frequent as females shuttled to and from nests; and nearly always it was given upon the approach of the mate, or while he was nearby. In such cases, wing flipping display (see below; Nero, 1956a) accompanied the call. The function was potentially an announcement of the female's movements. Further, it seemed associated with potentially submissive behavior by the female, advantageous in forestalling mistaken and disruptive attack or interference by her territorial mate. Although simpler and shorter, this screech resembles female song, incorporating some of the apparently intimidative or repelling qualities of song.

Female Precoititional Call --- As previously indicated, this call resembled that of the male. It consisted of a high-pitched, rapid series of monosyllabic components, phonetically resembling "TEE-TEE-TEE-TEE". Sonograms show it as a di-harmonic note at 2200 and 4800 cycles per second (Figure 20). The call was uttered typically by estrous females on the territory of the mate prior to copulation. Observation indicated that it signaled female readiness to copulate, accompanying precoititional posturing (Figure 21), and directing male attention to the displaying female. Often it was heard to follow the nest site screech call (Figure 20) during courtship

period.

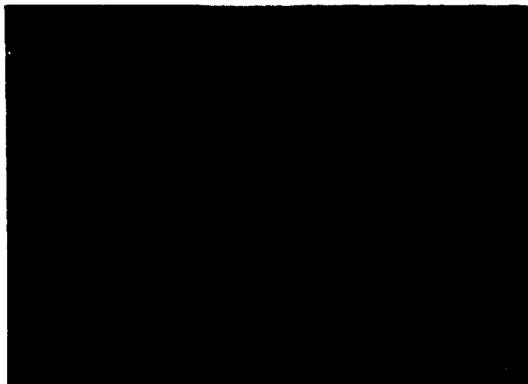
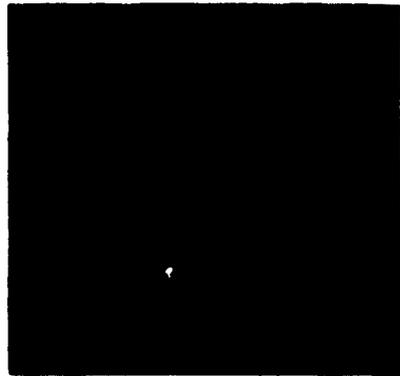
Redwing Displays

Spread Display --- This male display generally accompanied song. Territorial males performed it most frequently and to its fullest extent. Incomplete manifestations of the display were occasional among non-breeding males. The reproductively significant contexts with which it was associated in territoriality and sexuality involved repelling males and audiovisual attraction of females.

The essential configurational features of this display are: 1) thrust or lift forward of the head; 2) opening of beak, when song accompanies it; 3) lateral and slightly ventral spreading of wings, resulting in an arching or cupping of them along the sides of the body; 4) erection of the red lesser wing coverts; 5) lowering and fan-like spread of rectrices. Fullest intensity or manifestation of the display involved maximum use of each described component (1-5). Figure 21 illustrates three views of complete spread display.

To an observer the total effect of this display caused the bird to appear larger by erection and spread of plumage, and to render most conspicuous the exposed and elevated red epaulets. A minimal display performance consisted of exposure and partial elevation of epaulets, with a taut or tense forward thrust of the head. In this

Figure 21 is a composite showing photographs of Redwing displays. The two upper photos illustrate male spread display at HVM. The center photo shows male precoital display at Lee Lake. The lower picture shows bill-tilting display by a Redwing male toward a male Tricolor on HVM, April, 1959.



connection, three apparent levels of display intensity may be described, and correlated with those published by previous workers. The aforementioned minimal level seemed to correspond to "at rest" posture of Beer and Tibbits, (1950) and "exposed epaulets" of Nero (1956a). An intermediate level of display, adding to the minimal one, included partial wing spread and epaulet erection, and appeared identical to Nero's "crouch" posture and Beer and Tibbits "directional display". As previously described, maximal performance, including open beak and song, corresponded to Nero's "song spread" display and Beer and Tibbits "song display". During the breeding season, song only accompanied full spread display. Whether regarded as distinct displays or gradations of the same one, the postures described were tentatively considered to represent different motivational states. Such psychological extrapolation is partly based upon the apparent strengths of external stimuli in the form of other males and females, the least conspicuous or the farthest distant individuals seeming to elicit least vigorous display. In addition, maximal display always involved the instantaneous transition from a quiet perching posture, through intermediate levels, to full manifestation of the behavior.

Song Flight --- This is an aerial display performed by males leaving or returning to territory. It consisted of a slow, coasting flight with maximal display of the

broad wings and elevated epaulets. Song-flight announcement (see text above) always accompanied the display as a male left his territory, and was often uttered when he coasted back to a song perch in the territory. In addition, such a return flight was frequently terminated by a typical song just as the male alighted. Song flight was clearly an advertisement display, and was performed exclusively by successfully territorial male Redwings. The display was equivalent to posturing described in Nero's "flight-song", and to that of Beer and Tibbits "victory flight" or "song flight".

Bill-tilting --- In this display, male and female Redwings appressed the plumage, stretched the neck and body vertically, pointed or tilted the beak straight up, and usually faced the bird toward which the display was directed. Invariably males directed it toward other males, and females toward other females. The display lacked any accompanying vocalization. It was most often performed mutually by two males at their contiguous territorial borders, or by two females at the edges of their subterritories. The posture either preceded or followed actual combat in several instances. It was clearly an aggressive display, functioning in threat or intimidation directed toward other male or female Redwings and toward Tricolors (Figure 21).

Female Spread Display --- This was similar to the

spread display described in male Redwings, although females never extended their wings as much as did males. The display was exhibited solely in actual defense of a female sub-territory against other females. It was nearly always accompanied by female song (see text above). Agonistic situations generally seemed to elicit such display, and the latter failed to appear in sexual interactions. This display corresponded to the postural aspects of Nero's (1956a) "female song-spread".

Sexual Chase --- This consisted of an aerial display performed by breeding males, in which one male vigorously pursued a female which entered his territory. As explained above, this behavior signaled the initial observed stage of pair formation. Participation by the female simply involved erratic flight and avoidance of the male, usually within his territorial confines. Once paired, the female failed to evoke such responses from her mate. Duration of a chase varied from a brief dive after the female to prolonged erratic pursuit. Only rarely did a male actually strike the female. Occasional group sexual chases were observed, also reported by Nero, (1956a), which involved several adjacent territorial males and even some peripheral non-breeding males. The latter behavior appeared to stem from chasing which extended far outside the territory of the male who initiated it, thus affording opportunity and stimulus to other males.

Nest Invitation Display --- This display involved ritualized posturing in which a male raised his wings dorsolaterally to a point about 45° above horizontal, simultaneously uttering the aforementioned nest invitation call. The male also puffed his feathers and bowed his head slightly toward his mate during the wing-arching. On two occasions, such display was also directed toward female stuffed dummies. It was apparently always manifested subsequent to the initial stage of intense sexual chasing, within one to four days after the female had arrived on a territory. During such activity the female seemed to follow the male about intently watching him as he displayed on one or more sites within the territory, or strictly inside her subterritory when she was the second or later-acquired mate. Usually the female completed a nest on or near one of these display sites; and the inferred functions of such display and vocalization were to invite or entice the female to begin nest-building at some suitable point within the territory, and probably to enhance her sexual maturation.

Symbolic Nest-building --- This term was applied by Nero (1956a) to behavior of male Redwings which often pulled or detached pieces of potential nest material from vegetation visited during nest invitation display. Although the two displays were closely associated, symbolic nest-building was never performed simultaneously with

nest invitation. As also suggested by Nero, the latter may have served as an added stimulus to the female to nest-build.

Male Precoititional Display --- This was a vigorous courtship activity performed by the male which assumed a posture similar to that of spread display. It was always directed toward a female or a stuffed female dummy (Figure 21). The display involved full lateral extension of the wings, erection of body contour feathers, maximal elevation of epaulets, and spread-lowering of the tail. The bird's neck was not stretched, and the head and bill pointed downward. In addition to approach to the female culminating in copulation, maximum display intensity included rapid, slight quivering of wing tips and epaulets. Movement toward a female culminated in a sudden forward rush, mounting and attempted copulation. The precoititional call was frequently associated with this display. This behavior generally appeared later in courtship than the symbolic nest-site activities described above.

Female Precoititional Display --- This display was performed by an estrous female, usually in the male's presence. Full manifestation involved tilting the head nearly vertically, and similarly raising the tail at least 45° above horizontal, slightly lowering and quivering the wings. The display was accompanied by the female precoititional call. Full precoititional display always

preceded copulation. Invariably the male approached the female, in such cases, engaging in song and spread display ending with pre-coital display and call just before mounting. This always coincided with an abrupt freezing of pre-coital posture in the receptive female. Presumed non-receptive females commenced pre-coital display and call, but either stopped abruptly in the midst of it or fled at the approach of the displaying mate or any other male. Such negative behavior by the female consisted of a gliding, fluttering flight of several feet distance, in no way resembling sexual chasing response. Estrous females began these displays within a week after initiation of pair formation.

Female Nest Site Appeasement --- This display consisted of elevating one or both wings without extending them, often over the birds back, and quivering or "flipping" one or both wings. Such behavior appears to be identical with "wing flipping" described and pictured by Nero (1956a:29) for female Redwings. It was performed by females incubating eggs or feeding young, always near the nest. It was apparently directed toward the mate, and was usually accompanied by nest-site chatter. The posturing occurred most conspicuously upon female return to the nest, when her movements were likely to have attracted the male's attention.

The inference of appeasement motivation is based

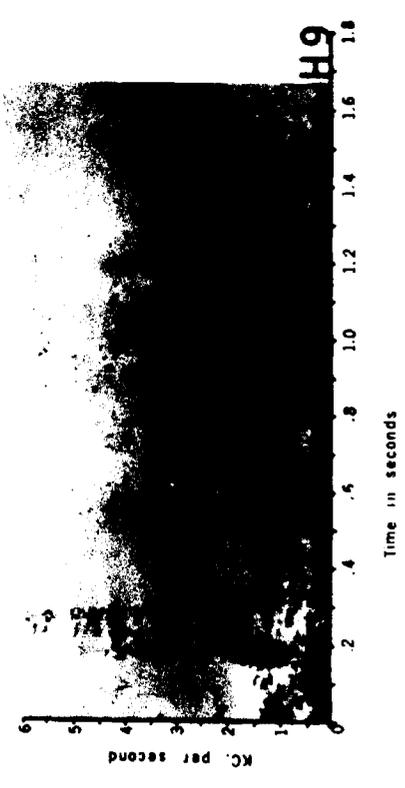
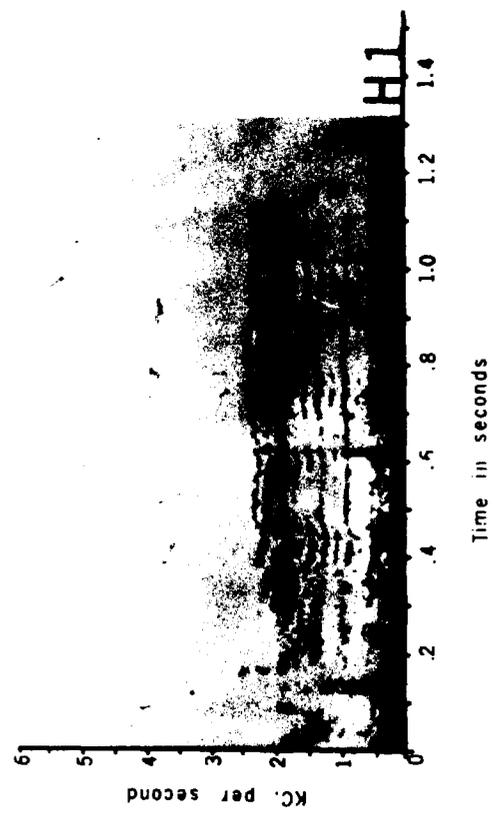
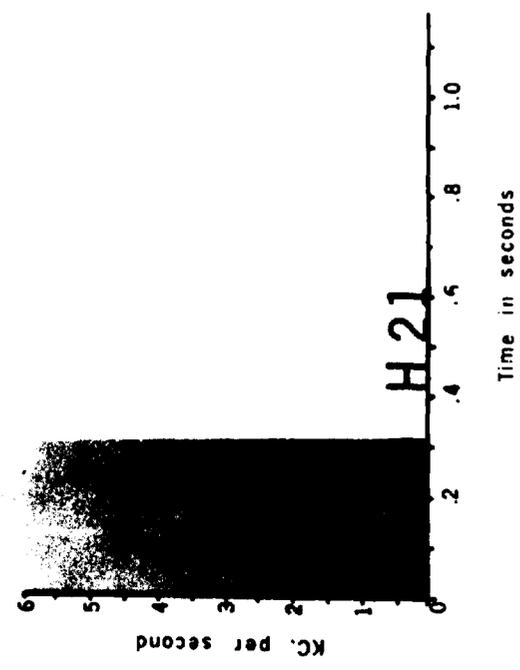
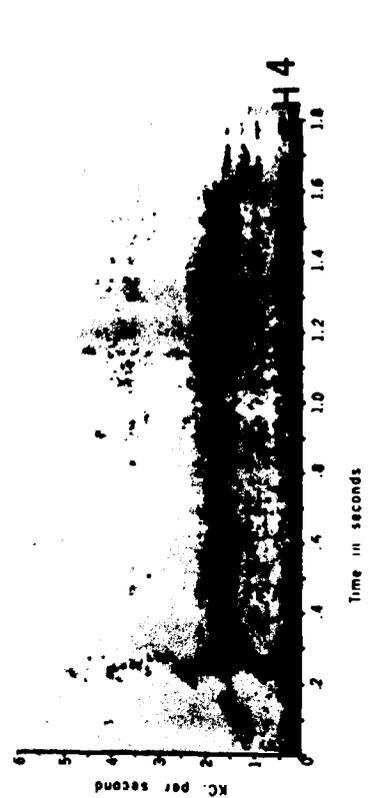
upon the coincidence of nest and male proximity to a displaying female. The phenomenon of submissive behavior by one or both avian mates as a mechanism functioning to reduce maladaptive hostility between pair members is well known (Armstrong, 1947; Tinbergen, 1951). Collias (1960) has also cited instances in which parent birds use call notes at or near the nest, which announce danger, arrival of food, and parental departures to nestlings. It is possible that the chatter call associated with this display served such an additional purpose, at least when nestlings were present.

Bill Whetting --- This was a common performance among Redwings of both sexes in the wild, and especially by hand reared captive fledglings, in which an individual wiped first one side of its beak, and then the other, on a branch or stem. It is a widespread behavior among birds, which clearly functions as a beak cleaning activity. In another context it was observed among territorial males, which often performed this behavior before or after attacking a stuffed male dummy within their territories. In such cases, the action seemed out of place, and represented a displaced activity in the sense that it was an inappropriate or unexpected response by a male in such an aggressive situation (Verplanck, 1957). It fitted the category of ambivalent behavior, postulated as involving a conflict between attack and flight (Tinbergen, 1951).

Tricolor Vocalizations

Male Song --- This is the low frequency, guttural "growl" by which the species is readily recognized in the field, and which unmistakably distinguishes it from the Redwing. A Tricolor song usually lasted between 1.5 and 2.0 seconds. It consisted of two or three brief introductory notes of variable frequency, followed by the low pitched, attenuated terminal "trill". The dominant frequency of the latter generally occurred between 1700 and 2100 cycles per second, with nearly all harmonics lying below that range, at least as low as 500 cycles per second. These qualities, plus the extremely fine or closely compacted segmentation, produced the typically rasped and guttural nature of the song (Figure 22). Phonetically it resembles "KER-AAAH", "KER-AH-OOOW" or "KER-AY-OOOW". Such variations appeared relatively minor compared to the individual, population, and geographic distinctions so typical of Redwing song. Comparison of several southern California Tricolor populations failed to demonstrate any consistent, dialectic song variations. One sharp variant did seem typical of intense, hostile Tricolor-Redwing interactions (Figure 22). This unusual song, heard in several populations, is further discussed in song-playback experiments on Tricolors (see below). The nomadic shifting and mobility of Tricolor populations, even in the breeding season, may well have been a factor

Figure 22 illustrates sonagrams of Tricolor songs and calls. Time and frequency scales are those described in Figure 18. Sonagrams H-1, H-4, and H-9 are Tricolor male songs. H-9 is the peculiar, plaintive song common in interactions with Red-wings (see text for discussion). H-21 is one version of the nest invitation call of Tricolor males. Compare with Table 42.



in favoring apparent uniformity in this vocalization simply by reducing the potential for spatial isolation of populations. Furthermore, the advantages conferred by ready intermingling and rapid integration of wandering flocks into effective breeding groups may have selected for a lower overall diversity among Tricolor songs.

As in Redwings, Tricolor males sang throughout the year. Roosting and revisitant aggregations were easily located by the "growling" male choruses, as were resting social flocks on or near feeding sites. Most of the year it was performed without attendant spread display (described below) which developed as its regular accompaniment shortly before colony establishment, as noted previously. Potential social facilitation in concert with lengthening days were doubtless responsible for reproductive maturation in males during late winter and early spring (Payne, 1965), as there are many avian examples of such interactions (Bullough, 1962). Upon initiation of territoriality, male song had clearly assumed the classical positive sexual and negative aggressive roles described previously for Redwings. Females entering territories were invariably greeted by a rapid sequence of song and nest invitations with accompanying displays, as indicated below.

While appearing to attract females and repel males at close range within breeding colonies, such readily localizable low-pitched singing clearly stimulated both

sexes to join these flocks from rather long distances. For example, Tricolors flying overhead in the company of Redwings were often observed to leave such flocks and enter a marsh in which only one or two Tricolor males were singing. On the other hand, Redwings either continued an unerring flight path, or having begun a descent to the marsh, suddenly turned and continued on their way when Tricolor songs emanated from such a marsh.

Song-flight Announcement --- This is a special call which was uttered in connection with male departure from a colony breeding site. It occurred just as the male was about to leave, or as he actually took wing. Such action involved as many as a hundred birds simultaneously calling and leaving parts of the breeding area. Phonetically it resembled one to several introductory nasal "KARGH", or sharp, rasped "CHLEK" notes, usually followed by several sharp "CHU-LAAK" notes which apparently represented its most complete rendition. Figure 23 (H-13) contains a sonagram of two harsh introductory notes showing the multiharmonic, wide spectral range and segmented termination in each brief note. It was inferred that this call clearly functioned to announce the male's departure, involving a swift steady flight away from the breeding site. It was never uttered when the male returned to his territory, in contrast to male Redwings. In the former instances, territorial Tricolor males used the

call most commonly during the early phases of nesting, and only occasionally during care of the young.

Species Contact Call --- This consisted of a monosyllabic low frequency note, which is an abrupt, guttural and sharp sound (Figure 19). The phonetic rendition of it is "WUK" or KUK". Such vocalization was uttered by individuals in airborne flocks, or those perched quietly and undisturbed in vegetation. The call appeared similar in form and apparent communicative functions to the corresponding one of Redwings, although the mean dominant frequency at 1300 cycles per second was much lower than Redwings.

Low Intensity Alarm Call --- This is a single note, similar in sound to the contact call. It was considerably louder and sharper than the latter call, showing a steep fronted spectrogram with frequency emphasis between 1500 and 2300 cycles per second (Figure 20). Phonetically the call resembled an explosive "CHECK", as for example, when a flock of Tricolors was suddenly flushed from vegetation or seemed suddenly to become aware of the observer's approach. Such contexts placed it in the category of a low level warning or an alarm vocalization as initial response to ground predators, similar to that described for Redwings. It was given by both males and females.

High Intensity Alarm Call --- This consisted of a loud, rasped monosyllable, which at times sounded weakly

disyllabic at the end of the note. Phonetically it is rendered as a faintly melodic "CHARK", but no sound recordings were obtained. Both sexes gave the call, but males seemed louder and more vociferous in their performances. Such responses were observed in cases of very close human approach, especially to nests with young birds present. It was probably a more intense reaction, a higher level, to the approach of terrestrial predator.

High Intensity Distress Call --- This is a loud and rasped "plaintive" vocalization. Phonetically it is a disyllabic "CHA-RAAH". It was heard several times when male and female Tricolors suddenly gathered at some point within a nesting colony, uttering the call as they fluttered about excitedly. Such situations simulated mobbing reactions and in one case occurred at a nest in which a kingsnake (Lampropeltis getulus) was eating the eggs. Neff (1937) reported similar distress reactions to snake predators. Nestlings a week or more old uttered a similar call when taken from the nest by hand. Such stimuli precipitated mobbing behavior, and often similar distress notes by the adult birds in a nesting colony. Females also directed the call to intruding Tricolors and immature Redwings, as described previously, interactions considered under competitive interactions below. There was simply no low intensity call heard with which I could definitely contrast this, i.e., of the type described above in Red-

wings. The high intensity here signifies an attitude of great excitement and apparent "anxiety".

Threat Growl --- This is an attenuated, rasped or buzzing note uttered exclusively by males, often repeated three or four times. Phonetically it is rendered as "KRAAAH". Each call was about 0.45 seconds long, featuring a broad frequency range from 500 to 2500 cycles per second, and four or five harmonics (Figure 20). Breeding males directed it toward other, intruding males, or rarely toward a trespassing female (especially during the care of young phase). Nearly always the result was a hasty departure by the intruder. Among non-breeding males during fall and winter the call was often heard as an apparent annoyance response on roosting sites; but attacks or supplanting of one bird by another were very rare. The only vocalization among Redwings which this growl potentially resembled was the threat or alarm hiss; but it was heard exclusively in intraspecific Tricolor activities.

Nest Invitation Call --- This is a pumped or gurgled call of two or three syllables, with a slightly rasped quality. It is phonetically rendered as "WUGUP" or "WUGUGUP". Sonograms indicate that it has a broad frequency range featuring at least five harmonics between 500 and 5000 cycles per second, with the dominant frequency close to 1000 cps (Figure 22), which apparently

produced the impression of its low pitched and guttural qualities. The call was only heard during the early phases of a colony breeding cycle, and was usually uttered by territorial males upon the entry of females into their territories. It was repeated several times as a male descended into the vegetation following the female. In the presence of the female, nest invitation display, described below, simultaneously accompanied the male's call. Occasionally a male uttered it in the complete absence of a female, one or two renditions following a song; but such instances never involved nest invitation display. The apparently instant response to female arrival, and rapid succession of events leading to nest construction, led to the interpretation of this call in a nest invitation context similar to Redwings.

Nest Site Screech --- This is a short, low, twittering trill uttered by Tricolor females. By comparison to female Redwing screeches, it is a very soft sound, usually uttered in an erratic series of three or more calls. Phonetically it resembled "TREE-TREE-TREE". Spectrographically each call features two or three segments, with four to six harmonics over a broad frequency range from 1200 to 4000 cycles per second, the mean dominant frequency lying at 1500 cps (Figure 20). This call was most common among females during nest-building, egg-laying, and feeding of nestlings. It seemed clearly to announce

presence and movements of the female, especially to her mate while she was caring for nestlings. Also during that phase of breeding, nest site appeasement display, described below, nearly always accompanied the call. As in Redwings, such contexts provided evidence for the inference that such vocalizations promoted relatively stable and non-hostile inter-mate relationships, especially in the constantly close quarters of Tricolor nest sites.

Male Precoitional Call --- This was a high-pitched, slightly melodic monosyllable uttered in series of three to ten calls. Each syllable phonetically resembles "GLEEP". Males were heard to utter the call as they pursued mates down into the vegetation substrate; and in all cases whose outcome could be observed, precoitional interaction took place with the female and copulation ensued. Frequently song, nest invitation, and precoitional calls were uttered in very rapid succession, as apparent responses to female arrivals both within a male's territory and within adjacent territories. Such situations made it difficult to determine stimuli for the female and that to which males responded; but it seemed clear that the precoitional call was used in just that context preceding copulation.

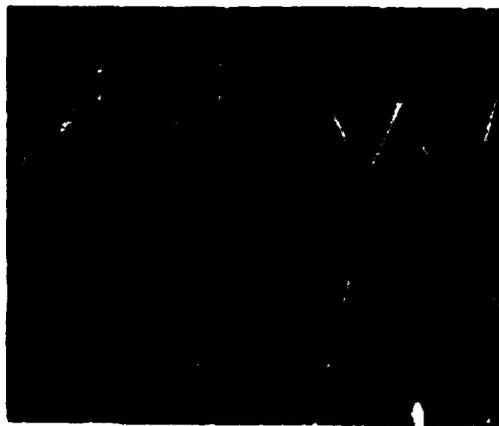
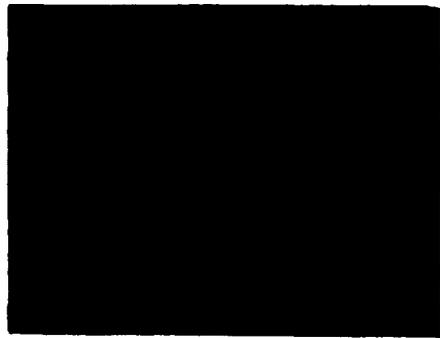
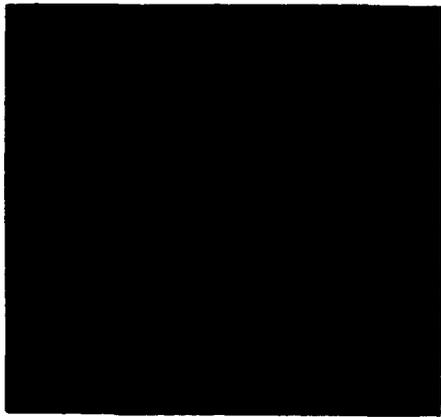
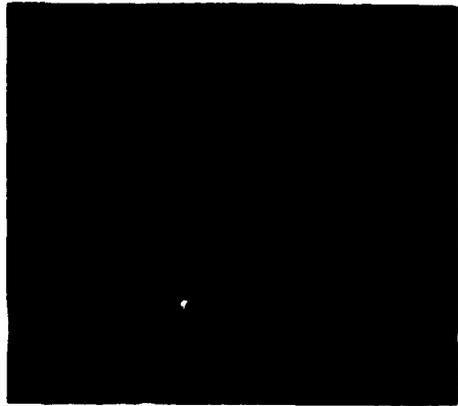
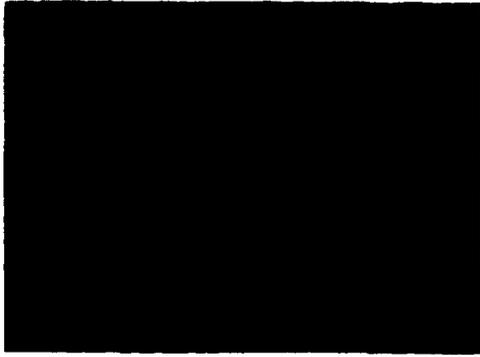
Female Precoitional Call --- This vocalization is a weak, thin, but high-pitched and brief monosyllable, uttered in series of three to ten or more calls. Phone-

tically it is rendered as "TI-TI-TI", resembling both Redwing male and female precoital calls although much fainter than either. The call seemed audible at a distance not exceeding a few feet, immediately preceded copulation, and was always accompanied by the female precoital display described below. As in Redwings, it often followed nest site screech, which was indicated previously as a common Tricolor female response to her mate's close approach or presence.

Tricolor Displays

Spread Display --- The pattern of this display in the Tricolor differs from the Redwing. At its maximum performance, the male depressed and spread his tail, spread the wings ventrolaterally and arched head and neck forward and upward (Figure 23). The neck feathers were strikingly erected. Viewed frontally, the total effect of such display is analogous to a series of three superimposed discs accentuated by the lustrous bluish cast of the plumage. The head forms the smallest part, with the puffed and arched neck representing the next and larger disc, and the wings and trunk as the broadest portion of the three. There clearly existed the potential for less intense forms of this display, such as a forward thrust of the head or partial erection of feathers. Such movements were occasional, but considerably less conspicuous than in the corresponding Redwing display.

Figure 23 is a composite illustrating Tricolor displays. The two upper photographs show full male display on WLSM and HVM, left to right respectively. The two center photos show male nest invitation display at HVM, May, 1957. The lower photo shows nest site appeasement in a Tricolor female with food in her beak on WLSM, May, 1959. See text for full descriptions.



The display was rarely observed among non-breeding birds; but its frequency, and accompaniment by song, increased during the prospecting period. During early phases of reproduction, before incubation got underway, this was the most common behavior among males on breeding sites. While song has been suggested as an effective component in reproductive maturation and in attracting Tricolors to breeding sites, once territories were organized, spread display was clearly functional in repelling or intimidation of other males; and such posturing formed the immediate response of males to female arrivals during the whole courtship phase of breeding.

Female spread display was rare or non-existent; at least none was observed in this study. Nero (1964) reports this display as rare or absent in females of some other icterids, such as the semi-colonial Yellowheaded Blackbird.

Song Flight --- This display is simply described as the swift and direct flight performed by territorial males as they departed from the breeding site. It was nearly always accompanied by the previously described flight song. While the immediate launch from a territorial perch suggested a slight hesitation and potential aerial display on the wing, this action lacked the conspicuous gliding qualities of the display described for Redwings. The abruptness of this display and associated vocalization

in male Tricolors is probably a function of restricted territory size.

Bill-tilting --- This is a rigid posture assumed by territorial Tricolor males in which beak and head pointed vertically, with plumage depressed and the chest was directed toward an opposing territorial male. It was rare, having been observed not more than two dozen times during three breeding seasons, and only then between established males before incubation had begun. Furthermore, bill-tilting behavior lasted only a few seconds when exhibited, never for the prolonged several minutes seen in Redwings. Fighting never followed it, nor was such violent physical interaction ever actually observed in Tricolor territorial defense.

Aggressive Rush --- This is an intimidation display used in territorial defense. At all levels of intensity it was accompanied by the previously described threat growl. The lowest intensity of such a display included a slight feather erection in the head, neck and trunk, and turning the head with a rapid pecking thrust toward an adversary. An increased degree of display involved hopping or climbing rapidly through the vegetation toward another male. A full rush, resulting in the immediate supplanting and eviction of an intruder included a short, rapid flight toward the intruder. Such display was most intense and frequent during initial territoriality in a

breeding season, and consisted mainly of the lowest degree of display during care of the young. Such rushing or attacking was the closest Tricolor males were observed to approach actual physical male combat, except when confronted with stuffed male dummies.

Sexual Chase --- This display was performed by territorial males when they vigorously pursued females as far as 200 yards from the colony site, occasionally actually diving at them. Such behavior was exhibited by a particular male only during the first day or two of his initial courtship interaction with a mate at the nesting site. It was clearly a component of courtship activities. No vocalization was audible during Tricolor chases. It is distinct from the corresponding behavior in Redwings in the apparently more subtle nature of the chase, distance traveled outside male territories, and probable absence of a male call.

Nest Invitation Display --- This consisted of a nearly simultaneous arching of the wings, bowing and occasional lateral "wagging" of the head, as well as partial plumage erection (Figure 23). It was one of the most common male displays noted during the first two or three days of courtship. When a female remained in the territory and appeared to be seeking a nest site, the male descended toward her and maintained this display for several seconds. It was nearly always accompanied by the

previously described nest invitation call, and most readily caught my attention then. A reasonable function of the display seemed to be enticement or encouragement for the female to remain or build in a particular territory, as well as probable sexual stimulation.

Symbolic Nest Site Selection --- Male Tricolors always appeared to follow females immediately to potential nest locations within territories. Although lacking the elaborate wandering of male and female described in Redwings, male and female Tricolors did move with specific postures to likely nest sites. The display probably assumed a stimulatory function similar to that in Redwings.

Male Precoital Display --- This display involved posturing similar to the nest invitation (Figure 23), with the exception that wings showed a slight quivering, as occasionally did the erected epaulets; and the male sometimes rapidly alternated up and downward pointing of the beak. The precoital call accompanied it, as quite distinct from nest invitation call. Function of this display is probably the same as in Redwings, assuring fixed and motionless female co-operation in copulation.

Female Precoital Display --- This posture was exhibited by estrous females with head and tail pointed up and high angles, and drooped and quivered wings. It generally occurred in male presence or after precedent male courtship display. The display clearly advertised

a female's readiness to copulate and maintained her in a potentially co-operative posture for an approaching male. Accompaniment always featured the female precoital call.

Female Nest Site Appeasement --- This was one of the most distinctive and ritualized female displays noted. The female arched her wings horizontally or upward at a moderate angle (Figure 23). It often occurred near or on the nest during building, laying and care of the young. The accompanying call was nest site screech. When incubating eggs, females were often observed to rise, perch on the nest edge, spread the wings, bow the head and even move it slowly from side to side. Such behavior was especially common in the presence of the male, who had returned to the territory to roost. Later, females with beaks full of insects to feed nestlings also performed the display. In many instances, and especially the latter, females uttered a muffled, subdued nest site screech described above. Such actions seemed clearly to be appeasement behavior which probably functioned as in Redwings for reduction of potential hostility between mates, especially in very small territories.

Bill Whetting --- As described for Redwings, this is a common behavior performed in wiping materials off the sides of the beak. It was elicited occasionally from males as a reaction to certain stuffed male dummies placed in territories. In such context, it seemed to belong to

the category of behavior inappropriate to the situation, or displaced (Verplanck, 1957). Its significance is evaluated in a discussion of field experiments below.

VII. EXPERIMENTAL ANALYSIS OF BEHAVIOR

Field experiments were based on obvious differences observed in morphology and behavior between Redwings and Tricolors. They were designed to test responses to species-specific stimuli within each species, and for presence of interspecific responses. Tests were restricted to the reproductive season or to the period immediately preceding it. At other times of the year both species were either not available on a fixed site such as a breeding marsh, or were almost totally unresponsive to any test situation, except to flee the latter scene. Where applicable, statistical tests comparing two or more samples of data for significance of response differences used chi-square contingency tables or two-sample rank tests. Both are nonparametric methods permitting simple comparisons of variable groups of data without assumptions about the normality of population (and sample) distributions (Goldstein, 1964). As stated below, calculated probabilities (P-values) indicate percent levels below which the data gathered would be expected to occur by chance, or the level of significance of differences between categories of data.

A. Experiments with Stuffed Dummies

The Redwing

Male Responses to Males

Discussion here involves aggressive responses, and

either lack of, or inhibition of same. As territoriality developed during February (Figure 10), males readily attacked "perching-postured" Redwing dummies at Lake Sherwood during 1958 and 1959, somewhat similar to the Tricolor illustration in Figure 24. During the same period, tendency to attack the dummies heightened, correlating with increased time males spent on their territories (Figure 10). This was quantitatively determined by testing HVM males during February, 1959. The increase was measured in terms of number of attacks versus number of failures to attack, as well as intensity of reaction to dummies in terms of time interval between actual dummy presentation and attack. Such presentations involved setting up a dummy during short intervals when the male left his territory, and counting presentation time zero from the moment of his return. Clearly significant differences in attacks occurred, comparing early and late February; and there were striking decreases in time lags between presentation and actual attack (Table 20).

Male Redwings tended to attack a dummy more readily within than outside their territories. This had been repeatedly observed at Lee Lake in 1953-1954. Table 21 indicates significant differences in attacks between dummies placed inside and outside territories at the north edge of HVM in 1959.

Attempts to detect species recognition of dummies

Figure 24 illustrates Redwing and Tricolor responses to dummies. The upper photograph shows a male Tricolor attacking a "spread-display" male Tricolor dummy from the rear, on his territory in the tower bulrushes of WLSM in late May, 1959 (see text for descriptions). The lower photo shows a male Redwing attempting copulation with a "precoitional-postured" dummy female Redwing, outside the male's territory at Lee Lake in late May, 1954. A second adult male can be seen on the turf in the background, having also been attracted by the female dummy.

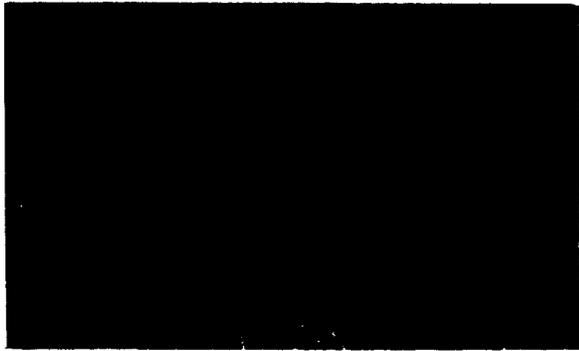
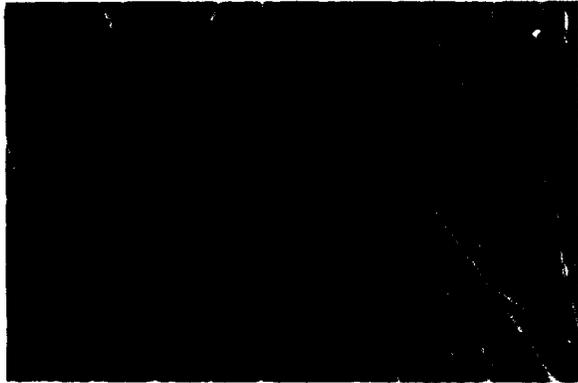


Table 20 compares male Redwing responses to perching-postured male Redwing dummies placed inside territories at HVM and WLSM during February, 1959. "N" indicates numbers of individuals tested in each group. Numbers (N) in parentheses list identifiable birds, while numbers refer to non-identifiable birds known only by day-to-day presence on a territory or nestsite. These designations are followed in subsequent tables. Time periods of early, middle, and late February are designated, respectively, "A", "B", and "C". Attack vs. no-attack test results for each period are compared for significance levels in chi-square contingency tables, as described in the text, which technique is also followed in subsequent tables. Time intervals (time lag) between presentation of a dummy and actual attack by a male were also measured, with means and standard deviations (s.d.) of these being included in the table.

Territorial Male Redwings versus Redwing Male Dummies

HVM, 1959

N = 6 (+3)

Dates

	(A) Feb. 2-6	(B) Feb. 10-14	(C) Feb. 18-23
Attack	4	5	12
No Attack	11	7	5
Mean Time Lag (Attack)	269 sec.	181 sec.	125 sec.
s. d.	101	66	59

A + B: P = < .750

B + C: P = < .250

A + C: P = < .025

Table 21 compares tendencies of male Redwings to attack perching-postured male Redwing dummies placed inside and outside their territories at HVM, March, 1959. "N" indicates the numbers of tested males, according to designations in Table 20. Two of the identifiable males were tested using perching Tricolor male dummies inside territories. P-values are derived by comparison of attack in and out of territories, and attacks on Redwing vs. Tricolor dummies.

Territorial Male Redwings

HVM: March 3-15, 1959

N = 4(+2)

Dummies

	<u>Redwing Male</u>	<u>Tricolor Male</u>
	<u>Attack</u>	<u>Attack</u>
	No Attack	No Attack
1) Inside Territory	$\frac{25}{8}$	$\frac{10}{1}$
2) Outside Territory	$\frac{2}{23}$	--

1) + 2) (Redwing) : P = < 0.005

Redwing + Tricolor (1): P = > 0.750

by territorial Redwings were also made. Redwing males readily attacked Tricolor male dummies placed within their territories (Table 21), in apparently the same way that they attack Redwing male dummies during the first half of March. This bears out the fact that Redwing males also vigorously attacked live intruding Tricolors. Tests gave no indication whether Tricolor dummies were simply misidentified as Redwings. During 1953-54 at Lee Lake Redwing males, on the contrary, had exhibited virtual lack of aggressive response toward perching-postured Brewer blackbird, and Yellow-headed Blackbird male dummies. The former species nested nearby. All such interspecific dummy experiments testing Redwing males were conducted at times other than those when stuffed male Redwings were used. Plumage modifications of dummies in experiments at Lee Lake in April, 1954, indicated that territorial males showed increased, but not significant, tendency to attack dummies with exposed epaulets, compared to those dummies having epaulets covered by black cloth (Table 22). A small number of similar tests were run at HVM during May, 1958, adding male Tricolor dummies with or without exposed or covered epaulets. Attacks were about the same on both species and both epaulet categories, with the exception that slightly fewer attacks were elicited by Tricolor dummies with covered epaulets than by Redwings in the same con-

Table 22 is the upper one, showing the tendency of male Redwings to attack dummy male Redwings and Tricolors with epaulets exposed or covered. "N" categories refer to numbers of tested individuals, according to designations explained in Table 20. Tests using Redwing dummies were conducted at Lee Lake during April, 1954. Those using Tricolor dummies took place at HVM in May, 1958. F-values are derived from chi-square contingency tables, as explained in Table 20 and the text.

Table 23 is the lower one, comparing the tendency of territorial male Redwings to attack, or not to attack, male Redwing dummies prepared in perching and aggressive postures, as indicated in the columns labeled "A", "B" and "C". "N" categories refer to numbers of tested individuals, designated as explained in Table 20. In addition, mean time intervals between actual presentation of the dummies and initial attack on them are computed, as well as the standard deviation of the means of those time intervals. F-values are derived as described in Table 20 and the text.

Territorial Redwings. A) = Lee Lake, April 15-29, 1954.

B) = HVM, May 2-20, 1958.

Dummies

	<u>Redwing Male</u>		<u>Tricolor Male</u>	
			<u>Epaulets</u>	
<u>A) N = 8 (+2)</u>	Covered	Exposed	Covered	Exposed
Attack	18	15		
			No tests	
No Attack	3	6		
<u>B) N = 4</u>				
Attack	10	7	11	7
No Attack	3	3	4	5

Cov. + Exp.: $P = < .500$

(Redwing and Tricolor)

Territorial Redwings. WLSM, April 22-30, 1959.

	<u>(A) N = 7</u>	<u>(B) N = 6</u>	<u>(C) N = 5</u>
	<u>Perching</u>	<u>Bill-tilting</u>	<u>Spread-display</u>
Attack	12	9	8
No Attack	2	5	5
Mean Time Lag (Attack)	38 sec.	78 sec.	204 sec.
s.d.	23	25	38

A + B: $F = < .500$

A + C: $F = < .750$

dition (Table 21). No satisfactory modifications of the buff or white middle wing cover areas of the two species were made for testing this character. However, one male "bicolored" Redwing (*A. p. californicus*) dummy consistently elicited attacks by territorial Redwings at the west side of the San Fernando Reservoir site on May 20, 1960. Males of the bicolored Redwing subspecies lack buff-colored middle wing coverts.

All the above experiments used dummies prepared to simulate a normal perching posture of blackbirds. Additional postures described above in intimidation displays were also tested in presentations to territorial adult male Redwings. In these, generalized perching was modified into bill-tilting posture and spread display posture and were presented to Redwings independent of previous ones using perching dummies. In both threat postures the apparent reduction in the number of attacks compared to the number of presentations was not significant, although significance was higher than in responses to covered and uncovered epaulets. However, there was a potentially significant increase in the time interval between presentation of the dummy and actual attack (Table 23). In addition intimidative dummies apparently produced considerable agitation in the test subjects. Such agitation was most conspicuous as nervous hopping about and bill whetting on branches near the dummy. Attacks on the

threat-postured dummies were always launched from the rear. These changes in tactics strongly suggested an inhibitory effect by such postures on potentially attacking males.

Male Responses to Females

Males also showed a seasonality of response to dummy female Redwings. They ignored such dummies during fall and winter, but readily attempted to copulate during the breeding season with those prepared in the precoital posture. Paralleling reactions to male dummies, male Redwings showed an increasing tendency for copulatory responses to female dummies during February and March, 1954 and 1956 at Lee Lake. The differences in responses between late February and late March are significant (Table 24); and although males increased copulations with dummies during early March, comparison with late February fails to yield a significant difference. Subsequent tests of Lee Lake males indicated comparatively consistent mating responses to dummies at least through mid-June. Males most readily reacted within their own territories; but at Lee Lake, placing a dummy on the open grassy areas adjacent to Redwing territories elicited sexual responses from nearly all passing male Redwings which had appeared to notice the dummy. This particularly included immature male Redwings, which typically approached without any precoital display, and copulated with female dummies, as reported by Noble and Vogt (1935).

Table 24 is the upper one, showing the seasonal change in the tendency of male Redwings, on actual or potential territories, to attempt copulation with female Redwing dummies prepared in a pre-coital posture (illustrated in Figure 24). "N" represents the number of males included in each test situation, designated as explained in Table 20. F-values are derived from chi-square contingency tables in which pairs of time periods, numbered 1-4, are compared, as explained in Table 20.

Table 25 is the lower one, recording copulatory responses by territorial Redwing males toward simultaneously and successively presented, pre-coital-postured Redwing and Tricolor female dummies. Successive presentations to the same individual alternated the species of the dummy presented first on any given date. "N" groups indicate numbers of males tested, designated as explained in Table 20. F-value is derived as described in Table 20 and the text.

Territorial Male Redwings. Lee Lake, 1954a; 1956b.

Precoititional Female Redwing Dummies

<u>Dates</u>	<u>N (males)</u>	<u>Response</u>	<u>No Response</u>
1) Feb. 1-10a	6	5	17
2) Feb. 19-27ab	3(+3)a;3b	23	23
3) Mar. 4-13ab	3(+2)a;3b	25	5
4) Mar. 25-31a	5	21	3

1) + 2): $P = < .100$ 2) + 3): $P = < .010$ 1) + 4): $P = < .005$ 2) + 4): $P = < .005$ 3) + 4): $P = > .750$

Territorial Male Redwings. HVM, March 1-15, 1959.

N = 5 (+2)

<u>Dummies</u>	<u>Presentations</u>			
	<u>Sequential</u>		<u>Simultaneous</u>	
	<u>Response</u>	<u>No Response</u>	<u>Response</u>	<u>No Response</u>
Redwing Female	23	5	12	
Tricolor Female	14	2	10	2

Sequential
(Redwing + Tricolor) $P = > .750$ Simultaneous
(observed/expected) $P = > .750$

Similar to results reported for Brewer Blackbirds by Howell and Bartholomew (1952), male Redwings more readily attempted copulation with dummies placed in precoital postures. Perching-postured dummies, or those with the head pointed up but the tail horizontal, elicited fewer sexual responses from males, although differences among the three stimulus categories were not treated statistically.

Tests using precoital-postured females of several other species produced variable and inconsistent results. Of greatest interest were tests using dummy female Tricolors and dark females of the Redwing subspecies, A. p. californicus. Each is quite similar to the other, and all three represented the closest specimens in general appearance to southern California Redwings used in experiments. When presented to males at HVM in March, 1959, both Tricolor dummies and those of southern California Redwings produced positive test results whose differences were not statistically significant at the seventy-five percent level (Table 25). The former tests involved use of a single dummy at one time. Simultaneous presentations of a southern California female Redwing specimen and female Tricolor dummies, or dummies of dark Redwing races, received virtually equal responses from Redwing males (Table 25), which was taken to indicate lack of any clear interspecific discriminatory reaction to these immobile

subjects. The general trend seemed to be for males to reject dummies of species rather clearly distinct from them such as cowbird and Brown Towhee (Pipilo fuscus). In the case of these latter specimens, the only full copulatory attempts were made by immature male Redwings. Territorial adult males were irregularly attracted to all such female dummies prepared in copulatory postures, but only approached within two or three feet, whereupon they abruptly ceased display and departed. Results here clearly suggested that adult male Redwings were readily attracted by pre-coital-postured stuffed females, but were stimulated to complete copulatory attempts only by plumage pattern or configuration of Tricolor or Redwing females, i.e., dummies with a general "Redwing" appearance.

Responses by Females

Female Redwings were tested much less than males. During the breeding season, in the vicinity of a nest, represented the only situations in which consistent female responses to dummies could be elicited.

Female reactions were limited to those of alarm and aggression. During the phases from nest-building through care of the young, females showed excitement and nearly always attacked with equal vigor both male and female Redwing dummies prepared in perching postures, which were placed about two feet from nests at WLSM in 1958, and at Sepulveda Dam in 1959 (Table 26). Frequency and intensity

Table 26 shows tendencies of 14 (N) different, non-identifiable nesting female Redwings to attack, or not to attack, perching-postured male and female Redwing dummies placed near nests at Lake Sherwood and Sepulveda Dam. In addition, the percent of test cases in which the females exhibited hostile behavior apparently directed toward the dummy is included.

Nesting Redwing Females
Perching Male and Female Redwing Dummies

Location---Dates

	WLSM <u>May 14-25, 1958.</u>	Sepulveda Dam <u>April 26-30, 1959.</u>
<u>Responses</u>		
Male	$\frac{10}{13}$ (N = 8)	$\frac{12}{16}$ (N = 9)
<u>Attack</u>		
No Attack		
Female	$\frac{13}{13}$ (N = 9)	No tests
Percent Hostile Display	100	100

WLSM + Sepulveda: P = > .750
(males)

Male + Female: P = > .750
(WLSM)

of attacks were judged to be of similar levels during all test periods of the breeding season. All female reactions involved fluttering about excitedly, some nest site screeches, and rarely nest site appeasement display. This is shown in Figure 26 under the percent of hostile display. Not only did these reactions resemble those directed toward live intruders of both sexes, but they also paralleled the ambivalent behavior previously described as exhibited by males toward certain types of dummies. However, dummies with modified plumage or posture were not used to test females. Identities of female test subjects in experimental sequences were based solely upon their association with specific nests.

Tests of female Redwings with perching male and female Tricolor dummies elicited aggressive responses which did not differ significantly from those exhibited toward Redwing dummies. Under the test conditions, responses appeared identical with those elicited by invading Tricolors on HVM in 1957 and 1959; but there was no indication of any special interspecific responses that would suggest species recognition by the tested females. In no test situations did female responses result in females exhibiting sexual behavior.

The Tricolor

Male Responses to Males

Seasonal responses to dummies by Tricolor males were

even more restricted than those by Redwings. Only when a breeding colony had become established and specific territories were localized, could consistent and identifiable responses be elicited. Prior to that, prospecting flocks shifted so erratically that dummies could not be reliably positioned with the expectation that Tricolors would return to the spot; and such dummies were simply ignored in all situations.

Male Tricolor dummies were always attacked more frequently when placed in nesting vegetation below the canopy. Actually all tests on WLSM in 1958 were made by placing dummies on top of the vegetation; and initial interpretation of the small proportion of attacks on these dummies was that Tricolor territoriality was extremely lax. However, experiments at Lake Sherwood during April, 1959, showed that males attacked dummies placed about a foot below the top of the marsh vegetation canopy more readily than above it. On WLSM, where the largest sample of tests was taken, the differences were highly significant (Table 27). It was clear that attacks on dummies placed down in vegetation were made immediately after the returning male appeared to have noticed the stuffed dummy, while attacks above the vegetation were delayed up to several minutes when they were made.

Covering epaulets of Tricolor dummies with black gauze produced no significant differences in attack ten-

Table 27 is divided into three parts, all showing tendencies for territorial Tricolor males to attack perching-postured Tricolor male dummies. Part "A" records tests of attacks within territories, above and below the marsh-vegetation canopy at WLSM during early April, 1959. Part "B" shows tests on HVN during mid-April, 1959, when there was intermittent interference by peripheral Red-wing males (see Figure 16). Part "C" shows results of the same tests on Tricolors engaged in caring for nestlings on WLSM during late May, 1959. P-values derived for each test situation result from comparison of attack versus no-attack responses either above or below the canopy, using chi-square contingency tables described in Table 20. "N" groups list the number of males tested in each category, according to designations provided in Table 20.

Territorial Tricolor Males. WLSM, April 6-15, 1959.

A) N = 9

Perching Tricolor Male Dummies

	<u>Attack</u>	<u>No Attack</u>
Above Canopy	3	26
Below Canopy	20	1

P = < .005

Territorial Tricolor Males. HVM, April 7-15, 1959.

B) N = 5

Perching Tricolor Male Dummies

	<u>Attack</u>	<u>No Attack</u>
Above Canopy	6	9
Below Canopy	15	2

P = < .500

Late-season Territorial Tricolor Males.

WLSM, May 21-27, 1959.

C) N = 3 (+2)

Perching Male Tricolor Dummies

	<u>Attack</u>	<u>No Attack</u>
Above Canopy	6	7
Below Canopy	10	3

P = < .500

dencies by territorial males below the vegetation canopy (Table 28). However, when dummy postures were modified to bill-tilting and spread-displays (Figure 24), and compared to reaction toward normal, perching-postured male dummies at the San Fernando Reservoir colony during April, 1960, striking differences in territorial male behavior were noted. Attack versus no-attack ratios changed dramatically for dummies presented below the vegetation canopy. Although differences in the results were not significant below the 10 percent level, the trend toward attack reduction was clear (Table 29). A noticeable increase in agitation and displacement behavior in territorial Tricolors confronted by dummies exhibiting the aforementioned threat postures. A considerable amount of shifting about, partial retreating and bill whetting was observed (Table 29). There was further measureable delay in attacking such apparently threatening dummies, compared to perching-postured ones (Table 29). Similar data for territorial phases later in breeding were not collected.

With the diurnal departure from breeding colonies by Tricolor males during incubation, and the apparently erratic return to roost on their territories, satisfactory results could not be obtained concerning their reactions to the presence of male Tricolor dummies during that period. Even in colonies whose breeding schedule was not

Table 28 shows tendencies of territorial Tricolor males on WLSM to attack perching-postured Tricolor male dummies with covered or exposed epaulets during mid-April, 1959. All tests were conducted below the top of the vegetation canopy, within the territories of the test individuals. "N" categories refer to the number of males tested, designated as explained in Table 20.

Territorial Tricolor Males. WLSM, April 12-19, 1959.

N = 5

	Epaulets	
	<u>Covered</u>	<u>Exposed</u>
Attack	13	15
No Attack	1	2

P = >.750

Table 29 compares tendencies of 12 (N) territorial Tricolor males to attack Tricolor male dummies presented in perching posture, bill-tilting and spread-display aggressive postures (illustrated in Figures 21 and 24) at San Fernando Reservoir during late April, 1960. P-values are derived by comparison of attack vs. no-attack for pairs of dummy categories, and all categories combined, following the techniques described in Table 20. Two additional aspects of the tests were included. First is the mean interval between dummy presentation and actual attack (time lag), plus the standard deviation (s.d.) of that mean. Second is the estimated percent of displacement behavior by the test individuals, involving flitting about, partial withdrawal, or bill-whetting display preceding attack.

Territorial Male Tricolors

San Fernando Reservoir, April 20-30, 1960

N = 12

<u>Dummies</u> Male Tricolors	Responses		
	<u>Attack</u>	<u>No Attack</u>	
1) Perching	16	2	
2) Bill-tilting	14	10	
3) Spread-Display	11	8	
<p>1) + 2): P = < .250 1) + 3): P = < .250 2) + 3): P = > .750</p>			
	<u>1)</u>	<u>2)</u>	<u>3)</u>
Mean Time Lag (Attack)	19 sec.	131 sec.	59 sec.
s. d.	12	73	30
Estimated Percent Redirected or Displacement Activity	8	80	65

highly synchronized, such as WLSM in 1959, territorial males adjacent to those in which females were incubating exhibited at most casual interest in male dummies, and never trespassed to attack the latter specimens. Such behavior usually prevailed even in the presence of vocal and postural agitation by incubating females (see text below) toward live or "dummy" intruders.

Return to territories and reappearance of territorial aggression, in addition to males' assisting in feeding nestlings, coincided with a resumption of attacks on dummies. Table 30, comparing some data from Table 27, shows this clearly, while additionally demonstrating that males tended to ignore dummies placed outside their territories during all breeding phases.

Male Responses to Females

Males in these categories were tested mainly on WLSM and HVM in 1959. In late March, during prospecting of breeding marshes, use of dummy females presented the same problems described for male dummies. The predominantly male flocks were unpredictable and erratic in their locations and in their responses to female dummies prepared in pre-coital (mating) posture. However, upon colony establishment males copulated nearly as readily with dummies as they did with receptive live females. All dummies were placed atop the vegetation canopy; and males showed no reluctance to approach dummies within their

Table 30 is the upper one, comparing attack-response tendencies of (early) territorial Tricolor males with those during later feeding of young on WLSM. Tests were conducted below the vegetation canopy inside and outside individual territories. "N" indicates the numbers of tested birds; and P-values are derived from contingency tables by the techniques described in the text and Table 20.

Table 31 is the lower one, consisting of two parts ("A" and "B"). It shows tendencies of territorial Tricolor males to copulate with precoital-postured Redwing and Tricolor females. Part "A" compares response vs. lack of response toward successively presented (at different times) dummies, and those presented simultaneously at WLSM during initiation of breeding. Part "B" compares response vs. no response toward Tricolor female dummies, successively presented, during breeding initiation (see part "A") and during May when tested males were feeding nestlings. "N" indicates numbers of birds tested, using designations described in Table 20. P-values are also derived as explained in Table 20.

Breeding Male Tricolors. A): WLSM, April 6-15, 1959.

B): WLSM, May 2-11, 1959.

Perching Male Tricolor Dummies

<u>Attack</u> No Attack	A) Early Territory N = 9	B) Care-of-young N = 3 (+2)
Inside Territory	$\frac{20}{1}$	$\frac{10}{2}$
Outside Territory	$\frac{0}{10}$	$\frac{0}{12}$

Inside, A + B: P = > .750

Territorial Tricolor Males. WLSM-HVM, April 6-25, 1959.

A) N = 15

Precoitional Female Dummies

	<u>Successive</u> Tricolor Redwing		<u>Simultaneous</u> Tricolor Redwing	
Response	31	25	11	7
No Response	13	7		5
Successive: P = < .750			Simultaneous: P = < .500 (observed/expected)	

Tricolor Males Feeding Young. WLSM, May 19-31, 1959.

B) *N = 5 (+3)

Successive Female Tricolor Dummy Presentations

	<u>May*</u>	<u>April (Table 31A)</u>
Response	5**	31
No Response	39	13

** Incomplete copulation attempts

April + May: P = < .005

territories. Although males usually followed females down into vegetation with vigorous courtship, culminating in copulation, such preliminary events were clearly unnecessary to elicit male copulatory attempts. With females in such conspicuous positions, a problem which arose was occasional intrusion by one or more neighboring territorial males. Such furtive copulatory attempts were met with immediate eviction by the territorial owner when he was present. Such aggression contrasted with the latter's reaction to a male intruder when no female stuffed dummy was present, which was previously described. As in Redwings, Tricolor males showed no significant differences in choice between Tricolor and Redwing female dummies, whether presented separately or simultaneously (Table 31). Female dummies of both species were often likewise approached, once they were noticed by nearby territorial males, when placed at the westedge of WLSM just outside the colony.

During later phases in breeding, reduced tendency of male Tricolors to react to, and attempt copulation with, female dummies in mating postures was striking. In both 1958 and 1959 at Lake Sherwood, while caring for young, males responded significantly less frequently to female dummies than they had earlier in the season on the same territories (Table 31). Males which gave overt signs of noticing dummies often uttered the threat growl

and exhibited incipient stages of aggressive rush; but only a few actually approached and attempted what were described as incomplete copulations. This is rather remarkable, since among birds sexually mature breeding males have always been considered to be ready for mating with any receptive female during a breeding season. Certainly such behavior contrasts strongly with Redwings during the same phases. A few Tricolor males collected at Cache Creek, but not tested with female dummies at the beginning of nestling hatching in that colony, possessed enlarged apparently functional testes. However, Fayne (1965) has recently reported that male Tricolors collected and actually identified as actively feeding nestlings had commenced testicular regression. Such evidence would provide a potential physiological basis for the observed sexual responses in this study; but further investigation will be required to determine if all males follow this pattern.

Female Responses

Reactions of female Tricolors presented more difficulties in testing than those of female Redwings, since territories of the former were so small. Territorial males were dominant over their mates, and frequently disrupted any experiments attempted with females, especially during early phases of territoriality. Actually I attempted to conduct all experiments on males or females

during periods when one or the other sex was completely absent from a territory. The phase during which females could be tested adequately and without interruption was incubation, when the male was absent much of the time. It has been previously mentioned that incubating females on HVM in April, 1957 were harassed by wandering, immature Redwing and Tricolor males. The mildest reaction by such females was nest-site screeching; but upon close nest approach by intruding alien males, females became more agitated, and gave loud, high intensity alarm calls (described above) and usually attacked the males. On WLSM in 1958 and 1959, a male perching-postured Tricolor dummy placed two feet from several nests apparently elicited nest-site screeches but no loud alarm calls, and only occasionally produced overt attacks by incubating females. Subsequently such females returned to incubating, undergoing elaborate, prolonged nest site appeasement display, lasting as long as three minutes before settling back on eggs. Females never did settle quietly on the nest as long as the dummy was present. While they were feeding young, females reacted similarly to such dummies; but again such tests were often subject to disruption by territorial males. There was no significant increase in female tendency to attack dummies once the young had hatched (Table 32). There were significant differences in Tricolor female responses to perching-postured male

Table 32 is the upper one, showing tendencies of nesting Tricolor females to attack perching-postured Tricolor male and female dummies. Part "A" compares attack vs. no-attack during two nesting phases, incubation in April, and care of nestlings during May. Part "B" compares attack vs. no-attack differentials toward male and female dummies, successively presented (at different times) during incubation. "N" indicates the number of females tested in each situation, according to the designations assigned in Table 20. P-values are derived as described in Table 20 and the text.

Table 33 is the lower one, showing tendencies by nesting Tricolor females, during care of the young, to exhibit nest site appeasement (see text description) display toward perching-postured male Redwing and Tricolor dummies. Dummies of the two species were presented successively, not simultaneously. "N" refers to the numbers of tested birds in each situation, as per designations in Table 20. F-value is derived by the technique explained in Table 20.

Nesting Tricolor Females. WLSM, 1959.

A) Tests with Perching Male Tricolor Dummies

<u>Breeding Phase</u> <u>Dates</u>	Response	
	<u>Attack</u>	<u>No Attack</u>
1) April 7-19 (N = 5) (Incubation)	25	15
2) May 5-11 (N = 5) (Incubation)	10	4
3) May 20-25 (N = 2(+2)) (Care-of-young)	11	7

1) + 2), 1) + 3): $P = < .750$, all categories.

B) Nesting Female Tricolors. WLSM, April 7-19, 1959

N = 11

<u>Dummies</u>	Response	
	<u>Attack</u>	<u>No Attack</u>
Male Tricolor (Table 32A)	25	15
Female Tricolor	24	1

$P = < .010$

Nesting Female Tricolors. WLSM, May 10-25, 1959.

N = 7

<u>Response</u>	<u>Dummies</u>	
	<u>Male Tricolor</u>	<u>Male Redwing</u>
With Appeasement	26	6
Without Appeasement	3	21

$P = < .005$

Redwing and male Tricolor dummies. Both elicited alarm as previously described; but the ratio of appeasement displays to lack of same was far lower in the case of Redwing dummies (Table 33). This suggested possibly either a more hostile or less subordinate attitude toward Redwings, and perhaps reflected species-recognition behavior. Redwing and Tricolor dummies were presented serially and not simultaneously. As in Redwings, Tricolor females exhibited no true sexual responses toward male dummies.

The responses of Tricolor females directed toward both Tricolor and Redwing female dummies were consistently aggressive, and no appeasement or sexual behavior was ever observed. Hostile reactions included agitated flitting about near the dummy, nest-site screeching and occasional attacks. Only perching-postured female dummies were used and then only in the presence of a live female with nest from whose vicinity she excluded other females and alien males as previously described. Nearly all situations in which these dummies were placed, about a foot from the nest, elicited attack from the nest owner (Table 33). Dummies placed farther away often produced confusing reactions, especially since the female in an adjoining territory or a female with her nest in the same territory, usually showed excitement and were attracted toward the dummy. Such movements frequently resulted in two or more

females flitting rapidly about the vegetation, making it difficult to recognize with certainty unmarked individuals, or else the interaction between two females terminated in a fight, with the dummy being completely ignored.

It seemed clear that female Tricolors attacked female dummies with which they were tested far more readily than they attacked males of either species; but they also seemed to exhibit about the same degree of agitated behavior in all cases. No attempts were made to offer choices by presenting male and female dummies simultaneously.

B. Vocalization Experiments

Male song formed an integral part of reproductive behavior in both species, in terms of male spatial competition and sexual attraction for females. Experiments here have attempted to measure individual and species recognition capacities. In the case of song and other reactions to call notes, results were inconclusive and confusing at best. Therefore, the relatively less complicated series of tests on males and their songs are included here.

Redwing Responses

The marked geographic variation in Redwing male song provides an excellent vehicle for testing male recognition of songs. Most tests were conducted at Lake Sherwood. Experimental subjects were tested on their territories

during the breeding season. They were exposed to five categories Redwing song as follows: a) to their own individual songs; b) to song of neighboring males; c) to the song of non-neighbor sympatric males; d) to the song of allopatric males; e) to Tricolor male song, of neighboring and non-neighbor (allopatric) males. The degrees of individual response during a test sequence were given the following designations in ascending order of intensity: 1) no apparent response; 2) orientation toward the sound source (including spread display); 3) song and spread display, pointed in the direction of the song playback for the previous response combinations; 4) approach toward the loud-speaker sound source. The greatest intensity of response involved a combination of 2, 3 and 4.

Tests on identified HVM males during March, 1959 (Figure 9) showed the following. Males responded to their own individual calls to a significantly higher degree than to songs of neighboring males at the same breeding site (Table 34). When tested with songs of Redwing males from nearby populations of WLSM and Lee Lake, HVM males responded at nearly the same level of intensity as they had shown toward their own calls (Table 34). Generally, when tested with songs of males from other geographic areas (Figure 18), these same HVM Redwings showed similar low level responses to those elicited by the song

Table 34 shows the intensity of responses by HVM-WLSM Redwing males toward five sets of recorded playbacks of Redwing song, during March, 1959. Allopatric songs came from East Park Reservoir and Napa County, central California, Meridian, Idaho, Somers, Montana, and Madison, Wisconsin. East Park Reservoir song (Colusa Co., Calif.) is also allopatric to Lake Sherwood Redwings. See text for discussion, and Figure 18 for song illustrations. Response categories, 1-4, represent increasing degrees of response intensity from no response, display, song spread, through approach toward song source, as described in text. Responses were measured simply as the maximum intensity shown by a tested male during a single test sequence. P-values are derived by comparing responses in pairs of song categories (a-e), using two-by-four chi-square contingency tables (see Table 20). "N" lists the number of tested males in each situation (see Table 20).

Territorial Male Redwings. WLSM-HVM, March 11-29, 1959.

<u>N</u>	<u>Song Playbacks</u>	Response Intensities				Total Tests
		<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	
(8)	a) Own Songs	12	3	19	31	50
(3)	b) Neighbor Males	10	5	6	5	22
6(+2)	c) Non-neighbor Males	5	5	18	27	38
3(+3)	d) Allopatric Males	13	4	6	0	23
3	e) East Park Res. Song (C-1)	6	6	12	15	33

2 x 4 Chi-square contingency tables; 3 degrees of freedom; listed values are P-values less than the indicated percent.

	a)	b)	c)	d)
e)	.25	.25	.75	.005
d)	.005	.25	.005	
c)	.50	.005		
b)	.05			

of neighboring (adjacent) males. This tendency not to respond to, or to ignore, the songs of distinctive, allopatric Redwings was consistent, with a single exception. The latter was the song of one territorial male, resident in the coast ranges of Colusa County California (Figure 18, C-1). Both audibly and spectrographically, this variant approximated the melodic qualities of the song repertoire of Lake Sherwood Redwings; and responses by HVM males occurred at levels similar to those elicited by the sympatric non-adjacent song category (Table 34). Males seemed to have mistaken this song for one from their own population. The results here compared favorably with those obtained by Weeden and Falls (1959) in testing responses of territorial male Ovenbirds (Seiurus aurocapillus) to songs of neighboring and more distant males.

For tests of simple response immediacy, it was possible to count song response alone in a particular relation to the test songs. This was done simply by examining the data and listing the number of situations in which the tested male sang at least once within five seconds after the playback, assigning lack of response as failure to sing within the arbitrary five-second limit. Results somewhat similar to those described in the preceding paragraph were obtained using the same test songs (Table 35). In addition, playbacks of HVM Tricolor male songs were used to test HVM and WLSM Redwings responses

Table 35 is the upper one, showing singing responses by tested males (see "N" in Table 34 toward the five song groups used in the previous table, plus two groups of Tricolor male song: "f)" representing local (HVM) songs; "g)" using HVM songs, with males tested at Sepulveda Dam, May 26, 1959. Responses were measured within five seconds after a playback. The F-value chart is derived by comparing one response category with another.

Table 36 is the lower one, comparing responses of breeding male Tricolors at WLSM to neighboring (1), non-neighbor (2), and allopatric (3) Tricolor male song playbacks, during three breeding phases: Early territorial period (4); incubation (5); feeding nestlings (6). "N" indicates the numbers of males tested in each group, according to designations assigned in Table 20. F-values are derived from contingency-table comparisons of response vs. no response, within five seconds after playback, results for song categories (1-3) and breeding-phase results (4-6), by the technique used in Table 20.

Territorial Redwing Male Timed Song Responses

WLSM-HVM, March 11-28, 1959.

<u>N</u>	<u>Response</u>	<u>No</u>		<u>Probabilities (<)</u>					
		<u>Response</u>	<u>Response</u>						
(5)	a)	41	12	a)	b)	c)	d)	e)	
(4)	b)	11	39	f)	.75	.005	.50	.005	.10
4(+1)	c)	52	9	e)	.25	.005	.025	.005	
3(+2)	d)	8	35	d)	.005	.75	.005		
3	e)	27	16	c)	.25	.005			
6	f)	33	10	b)	.005				
3	g)	0	10						
		(not tested)							

Breeding Tricolor Males. WLSM, April-May, 1959.

	<u>Response/No Response</u>		
	<u>Tricolor Neighbor (1) Songs</u>	<u>Tricolor HVM (2) Songs</u>	<u>Tricolor Lk. Isabella (3) Songs</u>
4) April 6-14 (territory) (N = 10)	20/6	14/4	14/2
5) April 20-26 (incubation) (N = 5)	3/6	3/10	1/7
6) May 21-31 (care-of-young) (N = 4(+2))	5/15	3/9	3/7

Categories: 1-3: 4 + 5: P = < .010
 1-3: 4 + 6: P = < .005

All other combinations: P = < .750

at the end of April, 1959. The latter paralleled levels of reaction to own-individual songs and to allopatric-non-adjacent songs for combined tests on those Redwings exposed to conflict with Tricolors (Figures 16, 28A). This tended to confirm the observer's qualitative impression that Tricolor song had been followed almost immediately by the song of an adjacent Redwing male during the extensive early-April, 1959, conflict between the two species (see below). Only ten tests were made playing Tricolor male song to Sepulveda Dam Redwings, in late May, 1959, the latter presumably not having been exposed to breeding interactions with Tricolors during that season. The total lack of responses (Table 35) in these cases seemed to indicate strikingly different attitude of that Redwing population toward Tricolor vocalization. Although the distinction in response was clear between the latter two Redwing test groups, it remains to be demonstrated more fully whether Redwings become conditioned or "sensitized" by hostile interactions with Tricolors, or simply fail to respond to Tricolor song late in the season. The group of Redwing males which I was unable to test was that which had been evicted from territories by Tricolor invasions, a situation discussed below. However, such males had either deserted their former territorial vegetation, or perched quietly on its periphery without singing or displaying. Behavior of such males

suggested they would probably have been unresponsive to song playbacks, since they gave no overt reactions to song stimuli from either nearby Redwings or Tricolors.

Tricolor Responses

As in the case of dummy responses, male Tricolors tended to react to song playbacks only during limited periods of the breeding cycle. Lack of fixed territorial positions even during the prospecting period made song testing impossible. Table 36 clearly indicates a high level of responsiveness to song playbacks by territorial Tricolor males on WLSM during April, 1959. Moreover, this level was high toward all songs, including those of adjacent males in the same colony, non-adjacent Tricolor songs recorded at HVM, and song of Tricolors from Lake Isabella, Kern County. Such measurements approximate those of neighboring, non-neighbor, and geographically disjunct populations, as outlined above for Redwings. No reduction in response toward neighboring males was apparent, in complete contrast to Redwings tested. For Tricolors, response was considered any song uttered within five seconds after the taped playback song. As did Redwings, territorial Tricolor males often responded almost instantaneously; and when more than one song was uttered during the five second interval, as rarely occurred, it was still listed as one response. However, an additional distinction became apparent upon further examination of

responses to neighboring and non-neighbor Tricolor songs. Threat growls (see "Tricolor Vocalizations") accompanied about two-thirds of the responses to playbacks of songs from neighboring WLSM males, while significantly fewer such growls accompanied song responses toward the non-neighbor Lake Isabella song playbacks (Table 37). Since utterance of a threat growl has been characterized as a more intense hostile response than absence of that vocalization, Tricolor test reactions suggest aggressive attitudes toward adjacent males of the same population, which are different from, and greater than, those obtained for Redwings. Tricolors appeared more aggressively responsive to their presumably familiar fellow members of a population, while actual territorial hostilities were uncommon.

In testing Tricolor responses to Lake Sherwood Redwing songs, two striking results were obtained. Tests using playbacks of adjacent and non-adjacent Redwing songs showed similar high levels of response from WLSM Tricolor males in early April, 1959. In such cases, males responded within five seconds after the playback about seventy percent of the time, while showing significantly fewer responses to songs of allopatric Redwings (Table 38). Likewise, number of songs per minute from the test males increased significantly when they were exposed to the same Lake Sherwood Redwing songs. In both these test situa-

Table 37 is the upper one, comparing song responses of (early) territorial male Tricolors at WLSM, to neighboring and allopatric song playbacks. Responses were noted as to presence or absence of the aggressive threat growl (see text description). "N" indicates the numbers of tested birds, according to Table 20 designations. P-values are derived by method described in Table 20 and text.

Table 38 is the lower one, comparing response vs. no response by territorial WLSM Tricolor males to non-neighbor (1), neighboring (2), and allopatric (3); see group "d)", Table 34, playbacks of male Redwing song. P-values are derived by comparing response results between group 1 and 2, and 2 and 3, according to contingency tables described in text and Table 20.

Territorial Tricolor Males. WLSM, April 6-14, 1959.

N = 10

N = 5

Tricolor Male Song Playbacks

<u>Total Song Responses</u>	<u>WLSM Songs (Neighbor)</u>	<u>Lk. Isabella Songs (allopatric)</u>
Song with Threat Growl	30	4
Song without Threat Growl	14	18

P = < .005

Territorial Male Tricolors. WLSM, April 15-22, 1959.

N = 6

Redwing Male Song Playbacks

	<u>(1) WLSM</u>	<u>(2) HVM</u>	<u>(3) Allopatric*</u>
Response	17	18	4
No Response	7	7	21

*from Table 34

1) + 2): P = > .750

1) + 3): P = < .010

tions, Tricolor responses toward songs of allopatric Redwings were significantly lower (Tables 38, 39). The latter Redwing songs were chosen from populations outside the geographic distribution of Tricolors, and which the latter may safely be assumed never to have heard. It seemed clear that the Tricolors tested were making some distinction between sympatric (previously heard) and allopatric interspecific songs. A striking correlation was noted in the nature of Tricolor song responses to the songs of local Redwings. This involved a high frequency of utterance of the peculiar, "plaintive" Tricolor song variant (illustrated in Figure 23). Such song characterized over fifty percent of these test responses, which was significantly higher than the responses to any Tricolor songs, and likewise much higher than the occurrence of this song variant in an undisturbed, non-experimental Tricolor population at the same time of year (Table 40). This type of song was regarded as occurring in high-intensity territorial Tricolor male interactions, as well as frequently following Redwing songs in interspecifically competitive situations, such as that observed at HVM during April, 1959. It is suggested that such interspecific interactions elicited the most hostile Tricolor male reactions observed. I was unable to run any tests on Tricolor populations which were known not to have experienced Redwing songs during the pre-breeding or

Table 39 is the upper one, comparing the cumulative number of Tricolor male songs noted per minute before and after each playback sequence of neighboring (1), non-neighbor (2), and allopatric (3) Redwing songs. "N" refers to the number of test playbacks (minutes) in which cumulative songs were counted for song categories, 1-3. P-values are derived by comparing "before and after" response results between the appropriate groups listed in the table, according to the technique described in Table 20.

Table 40 is the lower one, comparing normal vs. interspecific (see Figure 2, and text describing Tricolor vocalizations) songs uttered by tested Tricolor males (N=6) in responses to playbacks of adjacent Tricolor songs, and normal vs. interspecific songs counted from a one-minute segment of taped recording from an undisturbed WLSM Tricolor breeding colony during April, 1959. P-value is derived by the technique described in Table 20.

Territorial Tricolor Males: Song Response Rates.

WLSM, April 6-15, 1959

Redwing Male Song Playbacks

<u>Cumulative Songs per Minute</u>	(1) HVM (14 tests)	(2) WLSM (6 tests)	(3) Lk. Isabella (4 tests)
Before Tests	49	17	14
After Tests	75	32	16
1) + 2):	P = < .750		1) + 3): P = < .050
	2) + 3): P = < .010		

Territorial Tricolor Males: Song Types and Rates.

WLSM, 1959

Responses

<u>One-minute Tape Runs</u>	<u>Normal Song</u>	<u>"Interspecific" Song</u>
Experimental Group (N=6) April 6-12	16	19
Control Group WLSM tape April 15 (N=?)	65	8

P = < .005

breeding periods.

VIII. COMPETITION

The existence of significant intraspecific interactions among individuals of these two species has been well documented. That is, conflict of a direct nature occurs over space and other resources, with measurable results of prevalence of certain individuals at the expense of others.

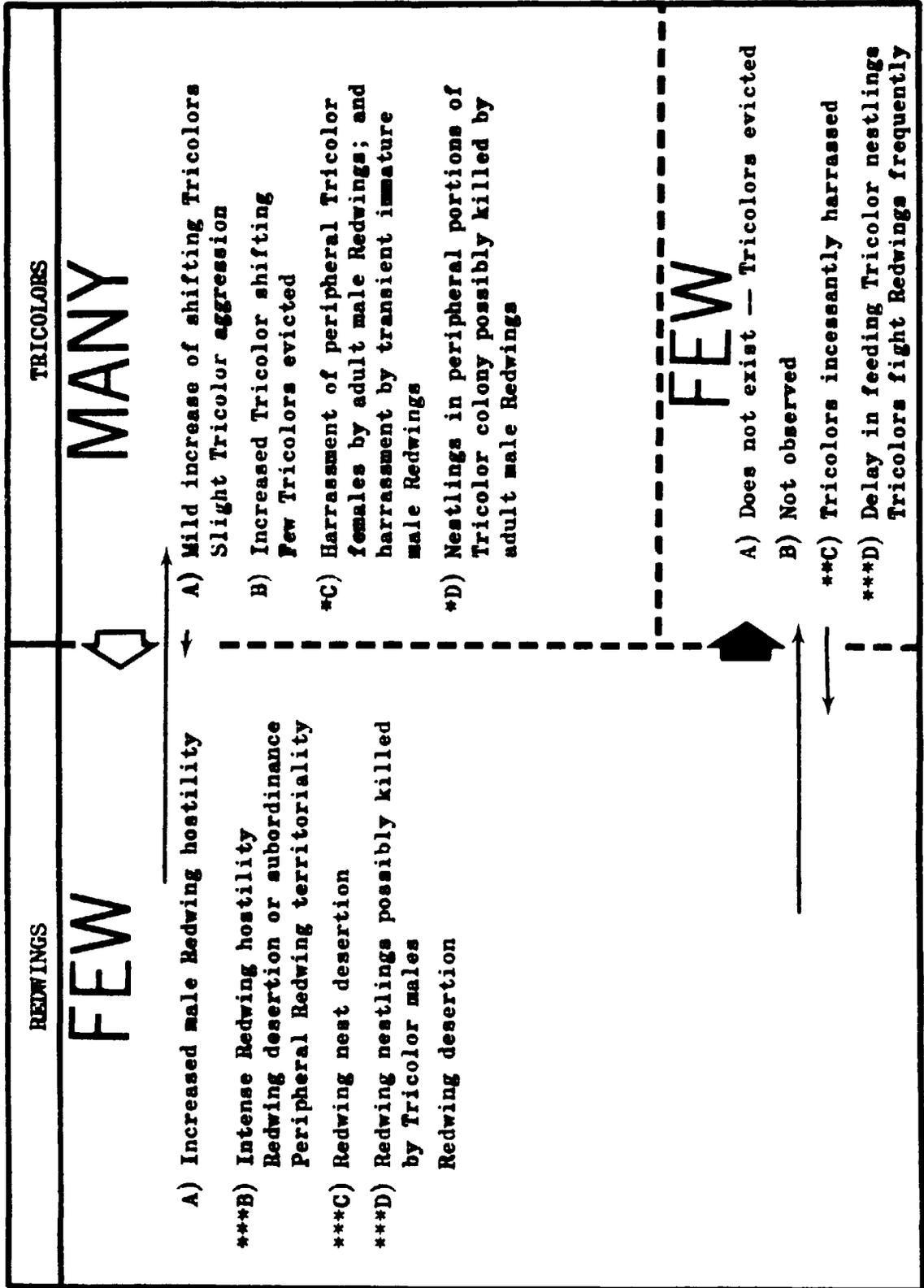
Of greater importance, and of a far more controversial nature, is whether conflict occurs between individuals of the two apparently divergent and reproductively isolated species. The question to resolve further is whether such interaction actually alters the reproductive potential of the species involved. Such a phenomenon would be defined as interspecific competition (Odum, 1959:225).

To begin with, we shall state that the Redwing and Tricolor do engage in conflicts over resources. This discussion proposes to expand on the already published outline of their general relations (Orians and Collier, 1963), as well as to document some further measurable effects of such interactions on both species.

Briefly, the major interactions and their outcomes are outlined in Figure 25. This chart covers interactions during the breeding cycle. Additionally, the non-breeding season may be summarized in the following way. Each

Figure 25 represents Tricolor-Redwing interaction in breeding sites. Redwings are always few, the Tricolor may be many or few. The number of asterisks indicates the severity of effects of the other species on breeding. The thick arrows point in the direction of the subordinate species under those conditions. The thin arrows simply signify the relative amounts of aggressive response by a species regardless of which one prevails in the situation.

INTERACTIONS



species spatially excludes the other from certain roosting sites by its mere presence; and as a result the roosting flocks of Tricolors on WLSM (Figure 8) seemed to maintain an exclusive area for the breeding colony the following spring. Correspondingly, Redwing maintenance of areas in the non-breeding period by persistent presence of resident males who part-time remained on or near their breeding territory during fall-winter (see above). These latter were also accompanied by thousands of transient roosting Redwings (Table 1); and whatever their apparent function in roosting exclusion of Tricolors, these transients had dispersed and disappeared from Lake Sherwood by the time spring breeding arrived. No evidence of fighting over food by the two species was obtained. Actually, they were often observed in single-species flocks, suggesting partial avoidance of foraging conflict.

Basically, during breeding the effects of the species upon one another varied with the particular stage of the cycle. Tricolor success in competing with Redwings for space depended on their large numbers in breeding colonies. Conflicts largely involved attempts by this species to acquire territory for nest sites. Since this seemed to occur on various dates between late March and early June, it affected the Redwings at all stages of nesting, since the latter usually established its breeding structure between the last week of March and mid-April. Tricolors

prevailed passively, without obvious counter-aggression, simply by remaining on a desired nesting site, or by invading already occupied Redwing territory, in which cases the Redwings could not handle, or expel, the overwhelming numbers. Conversely, Redwings overpowered and evicted Tricolors which occurred in numbers equal to, or only twice as great as, the Redwings. The only times when this occurred correlated with apparently unfavorable environmental conditions resulting in gradual Tricolor desertion of the site where breeding had begun. Sudden Tricolor desertion (as in 1960-1961) resulted in Redwing predominance virtually by default. The overall breeding success of Tricolors is geared to large population concentrations exploiting an apparently abundant, or at least sufficient, food source. If from no other cause, small Tricolor breeding populations co-existing with Redwings are impossible because of individual aggressive dominance of the latter. Since Redwings occur nearly everywhere Tricolors do, the latter probably can only rarely succeed in small, isolated colonies.

The situation at Lake Sherwood, particularly on HVM 1957-1959, offers revealing data on factors involved in competition. By early April, 1957, at least 150 Tricolors had established a breeding colony there, and remained on that normally-flooded marsh into mid-June (Table 11). Only six male Redwings remained territorial to breed

around the marsh edge (similar to Figure 16). However, in 1958, Tricolors (abundant on WLSM) failed to invade HVM; and at least 16 male Redwings bred there successfully (Table 5). Again, 1959 was a critical year in interactions as Tricolors invaded HVM in late March (Figure 16), commenced breeding soon thereafter, but within two weeks began to desert the drying marsh, as previously outlined.

The conspicuous correlation with these invasions by Tricolors was habitat destruction. In all three years large, successful colonies nested on west Lake Sherwood; but in 1957 and 1959, 70-80 percent of WLSM was burned in late winter (Figure 6). This was followed by the previously mentioned "overflow" of breeding Tricolors to adjacent sites. In each such overflow, Redwings were displaced after variable periods of vigorous attack on the invaders. For example, at least six male Redwings in the pond where Marsh "G" (Figure 8) is located, and nine of 16 males on HVM, were dislodged in 1959. There seems a clear reduction in Redwing reproduction attributable to disruption by Tricolor invasion. In addition, the remaining Redwings marginal on HVM in late March, 1959, appeared to start nesting during the last three or four days of March, but were disturbed and retarded until about 10 days later in April by invading Tricolors. Even if it could be established that displaced male Redwings

moved elsewhere in the Lake Sherwood region to breed successfully (for which I found no evidence), they still suffered loss of preferred territorial sites and clear retardation of breeding commencement.

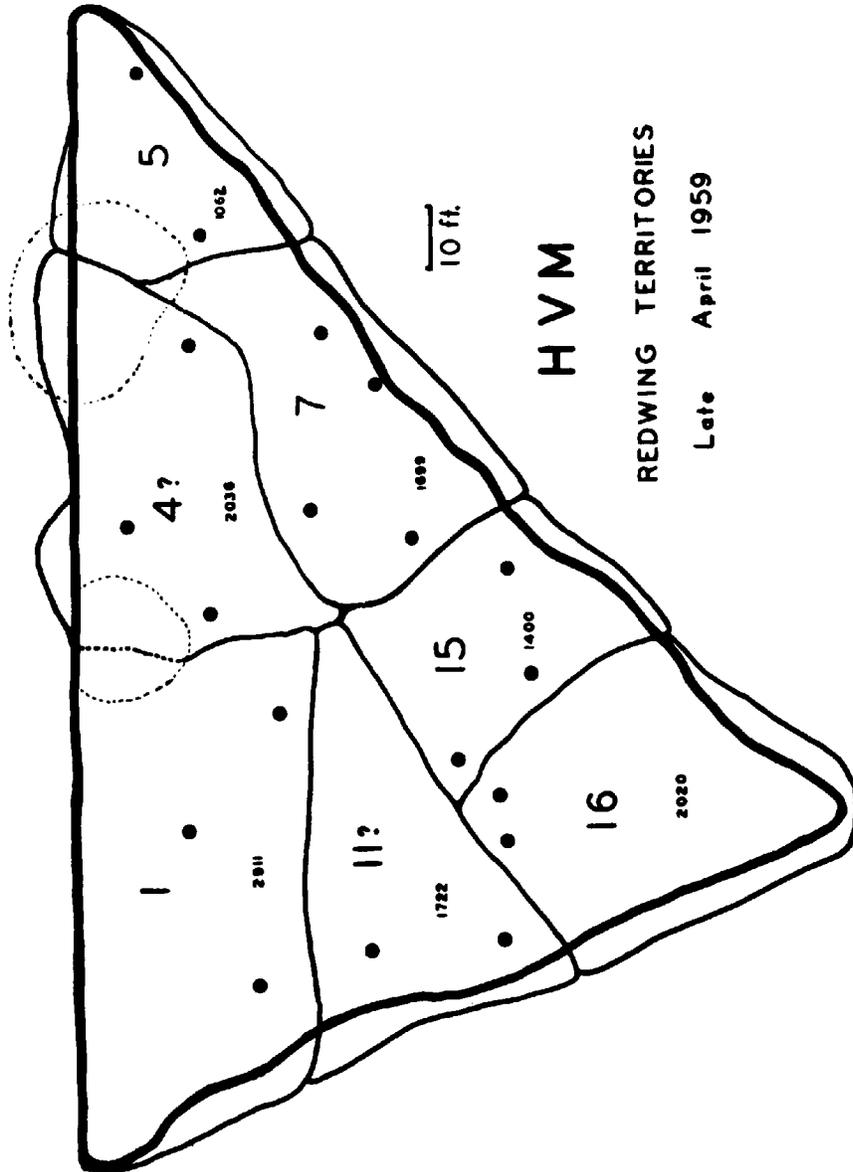
Both 1957 and 1958 were years of abundant rain as opposed to drier 1959; and established breeding populations of blackbirds did not shift or desert sites. The distinction in Tricolor tenacity on HVM was correlated with dessication of the marsh. In 1957 the species remained successfully; but they effectively had deserted by mid-April, 1959. By that date, half the marsh lacked water, and on May 1 it was almost all dry. Bulrush regrowth on WLSM (from February burning) was substantial in both 1957 and 1959; and this new vegetation was conspicuously occupied by new Tricolor nests, observed in 1959. Yet only in the drier 1959 did Tricolors give up HVM. It seems in that year, either dryness of HVM or attraction of nesting with Tricolors on WLSM, or both, were the basis of HVM desertion. Recall that the 1959 HVM invasion produced retardation of Redwing breeding there. In light of the subsequent devastating mortality of Redwing eggs and nestlings (Table 9) in a drying marsh, it seems likely that absence of Tricolor invasion would have made possible greater Redwing success in a still adequately flooded marsh earlier in the season. Wherever the deserting HVM Tricolors went, the ability of

this species to commence breeding at any time during the season suggests they may have suffered less impact on reproduction than the more "stationary" Redwings. Indeed, they may have gained some advantage if they retired to the "new" bulrushes regrown on WLSM, as these were overwater. It was clear that early Tricolor breeders there forced to nest in dry, isolated bulrush clumps, suffered great losses to predation (Table 18).

There was an unusual outcome of the mid-April, 1959, Tricolor HVM desertion. No additional Redwing males arrived to occupy the 7000 feet of central marsh. Rather, the seven marginal males simply re-occupied the deserted area for themselves (Figure 26). Why no new Redwings entered is not clear, since Orians (1961) demonstrated that complete removal of male Redwings from a marsh in Central California after the breeding season was two weeks along, resulted in reoccupation of the marsh within a week by the same number of new males. The obvious differences from HVM were that no "old" males remained on Orians' marsh, and that marsh was still completely flooded during removal and reoccupation. Both were cattail marshes.

With HVM desertion in 1959, effective aggression by Redwings toward remaining scattered Tricolor nesters increased, with even females sporadically joining in attacks on incubating Tricolors --- especially those near the

Figure 26 shows HVM subsequent to Tricolor desertion in 1959, when remaining Redwings had redivided the area. Again, large-sized numbers represent individual male Redwings (question marks signify uncertain individual identity). The small numbers indicate the size of each reconstituted territory in square feet. The black dots mark known nests active by the last week of April that year, ranging from two to four nests per territory.



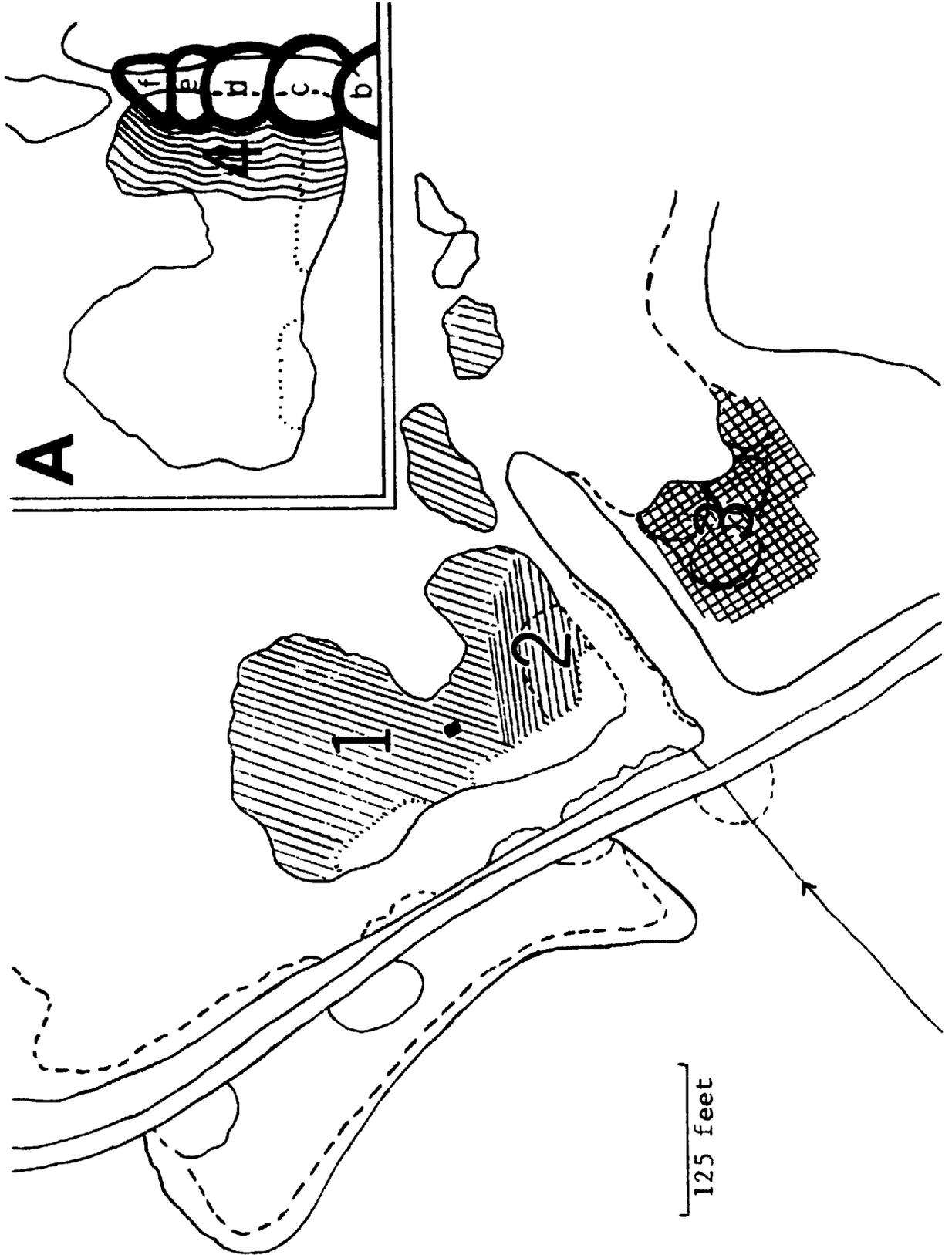
H V M
REDWING TERRITORIES
Late April 1959

northeast corner of the marsh. Their screeches and chattering resembled those directed aggressively toward intruding Redwings. This incessant harrassment, plus apparent terrestrial predation, resulted in the rearing of but a single Tricolor nestling in the marsh (Table 18). Actual Redwing destruction of nests or killing of Tricolor young were not observed.

A phenomenon common in 1958 and 1959, but not looked for in 1957, which adversely affected Redwing breeding success was establishment of the late secondary and tertiary Tricolor colonies. These occurred as a southward expansion of the WLSM colony, and as a separate invasion of SWLSM (Figure 27). In both cases, Redwing breeding area was pre-empted, presumably reducing its reproduction; and six males were displaced completely from SWLSM by June 1, 1958. These occasionally perched quietly along the south side of the marsh; and after a week they disappeared. By June 13 there was also strong circumstantial evidence for killing of several young Redwing nestlings by Tricolors in that marsh (Orians and Collier, 1963).

Invariably, presence or invasion by Tricolors relegated breeding Redwings to the margins of a marsh or other habitat. In marshes, this seemed clearly disadvantageous for the remaining Redwings, as, for example at HVM, vegetation at the edges was frequently more open and sparse,

Figure 27 is a scale diagram of west Lake Sherwood (compare Figures 3 and 8; Table 5) during the 1958 breeding season. Areas 1, 2 and 3 represent the primary, secondary and tertiary Tricolor colonies formed on WLSM and SWLSM during that season. Insert "A" represents a larger scale diagram of WLSM, in which areas "b through f" are Redwing territories. Within the same insert, the lined area "4" shows the estimated amount that males of Redwing territories "b-f" expanded their territorial areas, at the expense of incubating female Tricolors, between April 2 and 11.



and flooded with very shallow water and more subject to dessication. Even in dry fields, marginal Redwings were usually next to an open road, ditch, or field whence ground predation could easily be launched.

Tricolors, however, did not everywhere seek the most protected nesting substrate. At San Fernando Reservoir in 1960, Tricolors occupied the dry nettles, avoiding adjacent, small overwater cattail clumps, occupied successfully by Redwings. Moreover, as colony size decreased at Cache Creek, 1956-1960 (Table 12), breeding Tricolors occupied the tall stream willows, forsaking the dense, continuous cattails along the stream farther east. In both cases, habitat selection may well have been conditioned by prior successful nesting of the returning resident population. Only at Cache Creek in 1956 did Tricolor presence seem to limit Redwing numbers, when a half dozen Redwing males had small territories located among Tricolors in cattails. During May, there was constant fighting as the Redwings tried to evict Tricolors regularly trespassing on their territories. In ensuing years Redwings were absent, although hundreds of yards of cattails were unoccupied by Tricolors. Redwing success was not monitored at Cache Creek in 1956; but it may well be that the inhospitable dry desert next to the stream may have proven too harsh for Redwings, whereas Tricolors could exploit the area in moderate numbers with their

long distance foraging techniques; by moving out to wet areas and distant cultivated fields (Figure 2). This is viewed as a relatively rare example of ecological restriction of Redwings, rather than any direct conflict with Tricolors. Not even the Tricolor nested there in drier years, 1961-1962.

Among feeding Redwing and Tricolor flocks, conflict in the breeding season was not observed, except when Tricolors attempted to feed within Redwings' territories. The results were similar to those described above in other Tricolor invasions. That is, this species was able to enter and forage effectively in the territory of a single Redwing male as long as they were about six or more in number. In 1959 around HVM margins, scattered Tricolors nesting on the marsh (Figure 16) attempted to feed in the low sedges, but were always driven out by the adjacent male Redwing. However, large, shifting flocks of Tricolors foraged widely in Hidden Valley during May-June, 1959. Some of these flocks sporadically trespassed on Redwing territories along Hidden Valley Creek (see upper left quarter, Figure 3). These flocks usually ranged between five and 25 individuals; and incessant attempts by Redwing males to evict them were ineffectual. At each attack, the foraging Tricolors merely fluttered up a few feet and re-aligned in the same territory; while the territorial male ceased attacks within a few minutes

to perch, panting with wings drooped, on a cattail. Effects on Redwing food supply and breeding success were not measured; but it is reasonable to conclude that such repeated daily forays by Tricolors at least were disruptive. Since both species foraged in grain fields near this creek, under such conditions food was probably not directly limiting. However, the potential of food limitation in this type of conflict situation is obvious. The major difference in outcome of the above futile chasing is that unlike early season nesting invasions, these foraging intrusions never resulted in displacement of nesting Redwings.

Two additional instances of Redwing dominance over breeding Tricolors should be mentioned. After April 15, 1959 less than 20 Tricolors remained in central HVM, and only six clutches were eventually incubated. Of these but a single young was fledged, from a nest (#29) still overwater until early May. Both male and female Redwings attacked incubating Tricolors, causing slight delays in return to sit on eggs. Likewise, Redwings attacked Tricolors returning with food for nestlings, with similar delays in food delivery. In no case were Redwings observed as responsible for nest destruction, or for nestling starvation. All but the one fledgling disappeared from nests early after hatching. The male Tricolor of nest 29 spent fully half his time on HVM defending a

small area around the nest from Redwing male encroachments, between April 25 - May 5, while he also attempted to assist in feeding the nestling. It seemed remarkable that the single fledgling did survive this situation. A second effect on Tricolor domestic tranquility was observed between April 2-11, 1958 on WLSM. The primary colony there was highly synchronous that year; and for at least one week only incubating females were present during the day. During that period Redwing males along the south edge of the marsh made bold forays north into the fringes of the Tricolor colony. They consistently attacked Tricolor females similar to the way described for HVM. The result was that these Redwings expanded their territorial boundaries an estimated 100 percent (Figure 27). Advantages gained by Redwings in this extension and harrassment are uncertain. They did not nest in the "new" area, and increased foraging was not observed. Tricolor disadvantages may have involved nest destruction or cooled eggs (and embryo death), but neither was discovered. In view of secondary colonial expansion later in 1958 at the expense of these south-edge Redwings, any attempt at all to dislodge Tricolors is envisioned as potentially advantageous to Redwings. With the return of males and the general bustle of activity in the Tricolor colony from April 11, these male Redwings (territories "b-f" in Figure 27) retreated to approximately

their original territorial boundaries.

Reference has been made to apparent character displacement or divergence in Redwings (Orians and Collier, 1963), comparing populations highly sympatric with Tricolors to those allopatric or less frequently encountering this species on breeding sites. This simply involves the presence or absence of the middle-covert border to the epaulet in male Redwings. To the observer, those males without this buff margin (e.g., A. p. californicus of the Central Valley) are more different from the white-bordered (epaulets) Tricolor males than are other male Redwings possessing the buff (e.g., A. p. neutralis of southwestern California). Such "borderless" males might be expected to be less readily confused with male Tricolors than would Redwing males with buff edges. Observation and experiments (see above) as yet suggest no obvious recognition function for buff margin; although it may nevertheless have adaptive value in some other context.

A quantitative measure of character displacement was obtained by measuring five populations of breeding adult male Redwings as to the percentage and number (feathers) of buff-colored middle wing coverts. Buff is least in amount in the Central Valley, and in populations from Rio Hondo and Lee Lake (A. p. neutralis), and Imperial County (near Brawley = A. p. sonoriensis), buff is most extensive.

Individuals from the Lake Sherwood Redwing populations, compared to the other groups, showed a buff condition which was highly variable and intermediate to the other populations (Table 41). This site is, of course, where breeding Redwings repeatedly encountered, and frequently were in active conflict with, Tricolors. The population from Lake Sherwood appeared not significantly different from the buff-margined Redwings, but clearly reflected tendencies toward a borderless epaulet.

These data suggest that character displacement has occurred and may well still be taking place in Redwings. No such divergence was found in female Redwings, which are actually darker in the Central Valley than in southern California. In this instance they look more like Tricolor females in areas where the two species are highly sympatric than they do elsewhere. In this respect, Redwings tend to follow Gloger's Rule in that animals living in more humid regions are darker than those in drier areas. Tricolor females appear rather uniformly dark over their range, and did not conform with this rule.

Tricolor males measured from the San Joaquin Valley, Cache Creek, and Lake Sherwood, showed great uniformity in amount of white border on the epaulet. Thus, this character seems to have shown no displacement in male Tricolors. However, it is nearly impossible to find Tricolors which have remained isolated from effects of breed-

Table 41 compares mean amounts of buff coloration in middle wing coverts of territorial males in four Redwing populations. N indicates the number of specimens in each sample.

Redwing Male Epaulet Margin Coloration

Population	N	Mean Percent Buff
Imperial Valley	17	73.2
Rio Hondo Lee Lake	11	57.1
Lake Sherwood	13	30
San Joaquin Valley	12	13.1

ing interactions with Redwings. Nevertheless, observations suggest strongly that the white border may function as a species recognition mark, important in flocking of the Tricolor.

Although the role of character displacement or divergence in such recognition signals as male song remains to be fully tested, some significant correlations are worthy of mention. Table 42 shows that songs of male Redwings which live in areas of high sympatry with Tricolors have common characteristics that distinguish them strikingly from male songs in geographic regions outside the range of Tricolor breeding distribution. Redwings living within Tricolor areas usually show discrete introductory, middle and terminal song components that are more complicated than those of other Redwings. Mean song length is usually shorter in the former Redwing groups. In addition, the middle and terminal portions of songs are more liquid (melodic) and less sharp or harsh, generally lying at a higher mean frequency, than those of Redwings who never encounter breeding Tricolors. The terminal portion of song of all the latter groups of Redwings which I have heard in recordings or in the field is consistently a conspicuous, attenuated trill, consisting of as many as two dozen segments. Such a trill is absent from the song of most Redwings breeding in Tricolor distributional areas. Among populations observed,

Table 42 lists the major features of the components of Tricolor male song, and several geographic variants of Redwing song. Song categories with an asterisk belong to Redwings occurring within major distribution areas of Tricolors, and encountering them during breeding. Double asterisks indicate Redwing songs from populations breeding in areas where Tricolors are of sparse or rare occurrence.

exceptions were: Redwings at Point Conception, Santa Barbara County, and some Redwing populations in the San Diego region. In both of these areas, Tricolors are sparse or absent as breeding populations, compared with the several other study sites in central and southern California. It is suggested that such distinctions in Redwing song might function to make such male Redwings more readily distinguishable, especially for females, from the typically low and broad-frequency, attenuated terminal-growl ("trilled"; see Figure 22) song of Tricolor males. Such developments might readily have been selected for during interspecific competition in Redwings and Tricolors.

IX. ISOLATING MECHANISMS

An outcome of this study involves in part the definition and elaboration of the ecological niche of each species. Hutchinson (1958) has offered a definition of the niche of an animal species involving a "set of activities". The remarkable similarities and the subtle distinctions in activities, as well as in other characteristics, between Redwing and Tricolor invite a close examination and detailed discussion of the origin of said activities and their present status. This seems especially compelling in view of the apparent complete lack of interbreeding among highly sympatric populations of the two species. The analysis undertaken below emphasizes the behavioral niche components from three aspects. First to be considered is the spatial and environmental, intraspecific integration of components. A second aspect is the organization of these components in such a way that positive motor responses (that is, activities) are performed almost exclusively within the context of each reproductive system, producing individuals unwilling and unavailable to reproduce with the other species. A third aspect to be emphasized is the development and function of direct interspecific responses which prevent hybridization by repelling the other species.

The perspective thus gained is broadened by a further

consideration of the manner in which isolating mechanisms between Redwing and Tricolor may have arisen temporarily through historical-geological events, and how the cumulative phenomena portrayed may influence potential future relationships and success of the two species. Many of the ecological aspects discussed have been previously considered by Orians (1961); and the presentation herein expands upon some of those, particularly emphasizing the origin and functional aspects of behavioral adaptations.

A. Geographic Isolation

Consistent and complete spatial separation of these two species occurs only outside the range of the nomadic Tricolor. Extensive post-breeding movements occur in both species, resulting in their widespread intermingling as previously indicated (p. 37 ff.). The observed abrupt shifting of Tricolor flocks from one nest site to another further decreases predictability of geographic isolation (p. 173 ff.). For both species breeding habitat is widespread, although restricted and highly discontinuous throughout the ranges of both. In most areas of sympatry there exists thus a high potential for interspecific mate selection. Few members of either species probably ever complete a life cycle unaffected by experience with the other species.

There are simply no major geographic barriers west of the Sierra-Cascade Ranges, precluding presence of either

species. Elsewhere, absence of appropriate environmental conditions prevalent in central and coastal California probably restricts the Tricolor to its present range. Extensive coniferous forests of the Pacific Northwest and widespread xeric conditions from eastern Washington southward through the Great Basin represent two apparent structures on Tricolor distribution.

There is, nevertheless, clear evidence of discrete geographical races among Redwings (p. 30 ff.) suggesting that, whatever wandering occurs in this species, consistent tenacity of populations to particular sites for breeding, and desertion of these only under extreme climatic rigors, furnishes a reliable potential basis for isolation of some populations from Tricolors. Such conditions would result in significantly higher impact of intraspecific influences during most of the individuals' reproductive life, than any occasional encounters with Tricolors might produce.

B. Ecological Isolation

Both species are acknowledged as preferential marsh dwellers, neither regularly segregating by habitat selection anywhere the two are sympatric; although the Tricolors predominantly choose deeper water vegetation (p. 134 ff.). Occupation of dry land habitat is shown by both species, and appears linked to recent historical modification of the landscape. These largely result from flood control

and agricultural practices, and as yet, have produced no overt, long-term alteration of habitat selection by the blackbirds. The environmental changes described have been correlated with apparent local population increases of both Redwing (Case and Hewitt, 1963) and Tricolor (Orians, 1960), as well as with continued human destruction of palustrine habitat.

Inhabiting marshes provides two significant components of Blackbird breeding success. First, it affords well protected nest sites. Such is a fundamental necessity for open-nesting passerines. This is especially true for birds, like Tricolors and Redwings, which generally nest near the ground in concentrated habitat so readily located by predators, and whose plumages, voices and reproductively oriented displays render them highly conspicuous during critical periods (p. 188 ff.). The second component is some favorable relationship to resources. The distinctive ecological organization between Redwing and Tricolor, as previously reported (Orians, 1961; this study), is based upon methods of utilizing space and time for reproduction.

Redwings roost in varying numbers as non-breeding birds. Resident males, occupying breeding habitat for long periods prior to breeding, clearly reserved such area for themselves, relinquishing it only when driven out by a dominant male or by Tricolors, or under adverse conditions resulting in failure to obtain mates (p. 92).

A long territorial period is followed by a similarly attenuated period of mate attraction and pair formation lasting several weeks, and culminating in one or more nesting efforts by one to several female mates. These intraspecific responses inevitably have produced wide dispersal of a breeding population over any limited favorable habitat, if from no other cause than low inter-individual tolerance by males. Such habitat and spacing proclivities have resulted in the presence of Redwing populations over the North American continent nowhere greater than a few score individuals.

Stressing of successful intraspecific aggression in Redwings is shown even among subterritorial females. Spacing among the latter results both from female hostility and mediation by a territorial mate (p. 84 ff.). Invariably the strongest adult males appear to be the most competent ones in establishing and maintaining such an organization, with a peripheral surplus of subordinate adult and immature males relegated to non-breeding status (p. 65 ff.). Such a system results in the high level of polygyny recorded in this species (p. 87 ff.).

Emphasis of major male energies upon territoriality, acquisition, retention and protection of mates till termination of an extended breeding season (at least three-and-one-half months) leaves relatively reduced time and energy for male care of young. Thus, the main burden

falls upon the female, who is able to perform nesting duties, including foraging locally (Table 11), within a stable milieu provided by the male.

The avid promotion of polygyny by Redwings merits further exploration as a focal point for reviewing adaptiveness of its social system. Clearly, male behavior in excluding other males from given territories, confronts females with fewer males to select as mates than would be the case if all males had territories. Sex ratios of reproductively mature males and females have been repeatedly reported nearly equal during breeding (this study; Nero, 1956b; Orians, 1961; Wright and Wright, 1944), and all evidence gathered suggests that the mating system excludes more males than females. Redwing females appear preferentially polygynous as follows. The notable failure of any females to mate with any of the 5 HVM Redwing males 1960 and 1961 (p. 92; Table 4), while numerous males mated polygynously in successful breeding attempts on West Lake Sherwood indicates females in the area thus rejected some available males in favor of a clearly greater degree of polygyny, and, as suggested above, probably more favorable ecological conditions.

Even considering the great variability in the size of male territories (Table 5), most males appear to defend areas large enough to attract more than one mate; and indeed, the degree of polygyny was comparable between

small marsh territories and large dry-field territories (Table 3) for a given year. Observations indicated sub-territorial females were no more bothered by, or disruptive toward, each other in small than in large Redwing territories. However, Table 3 does show annual fluctuations in sex ratios for total populations at specific sites; and there is tentative correlation between slightly reduced polygyny and unfavorable conditions such as drought (p. 116). Verner (1964), and Verner and Willson (1966) have suggested that polygyny has evolved as a prevalent system in ecological situations characterized by greatly fluctuating food productivity and restricted favorable breeding habitat conditions, apparently common among Redwings, such as marshes in grasslands or brushlands.

In order to be of selective advantage, polygyny must result in the production of more offspring by males and females practicing it than by those which are monogamous in the species. Basically, females mated to polygynous males must be able to succeed in nesting without male assistance to the degree that it would be potentially available in a monogamous pairing.

Consider that females do not all arrive simultaneously in a breeding habitat. At the start of a new season, nesting of females is staggered over a period of as much as two to three weeks (p. 84 ff.). This is significant in the ecological context indicated above, as it means

that the females do not all exert synchronous demands for nest material and food energy at a particular site. Such a spreading out of nesting needs may be of value even in small populations; and they are of additional value to males. Males do assist to some extent in feeding of young. This only begins several weeks after the onset of nesting; and the staggering of nesting by females of a polygynous male will enhance his role in survival of offspring. Successful fledglings will arrive in successive broods as the season progresses. By the time this activity commences, demands of territoriality have been reduced, partly due to the fixed and recognized status among neighboring males (Tables 34, 35) and fewer intrusions by unestablished peripheral males. Males could potentially divert some energy to feeding young. Reinforcement of such apparent adaptive advantages should result in a high degree of success for polygynous males and should tend to perpetuate this mating system.

In the case of females, a polygynous one has less chance of receiving assistance from the mate than do those females which are monogamous. Her initial reception of undisturbed space probably allows her to complete initial reproductive efforts without male help. The energetically demanding function of feeding young has been suggested as possible by completely unassisted females because of the ready proximity of foraging sites

(Table 11). Moreover, the demonstrated willingness of males, "in a favorable energy balance", to feed young, especially fledglings, is a valuable asset both to the female at a time when food demands by offspring have reached a high level, and to the young fledglings at a time which is very critical in their survival. Such activities would promote survival of her genotype. Lack (1954) indicates that fledgling passerine birds generally suffer tremendous mortality upon leaving the nest. Such a male-female parental care sequence could produce vigorous offspring to withstand better the onslaughts of post-nestling environment. Under certain ecological conditions, a female placed in a potentially favorable energy balance by the various functions of mediation, protection and assistance furnished by her polygynous mate could find herself in a physiological condition to produce yet a second brood of offspring during a single breeding season. In any event, unsuccessful nesting females early in a season could still take advantage of long-term territorial maintenance.

Female conformity to the ecological and behavioral relationships (especially by the male) within the framework outlined above should result in the perpetuation and prevalence of such female ("harem") genotypes within the Redwing species. Other things being equal within the above ecological context, individuals of either sex

tending to be monogamous should produce fewer offspring "per pair" than polygynous ones.

Flexibility in such a Redwing ecological system may be augmented by apparent capacities of the species to adjust territorial and subterritorial sizes, possible adjustment of polygynous breeding ratios --- reduced in poor ecological situations, and potential adjustment of clutch size to ecological conditions. In this latter connection, there is as yet the tentative suggestion from Table 5 that female Redwings may adjust by laying smaller clutches in drought years. Overall, however, the relatively more dispersed breeding populations of southern California Redwings, compared with Tricolors, exhibited a higher mean, and somewhat less extreme fluctuations, in clutch size. This may well reflect a more general trend by Redwing populations toward an equilibrium with the environment.

In contrast to Redwings, the Tricolor has evolved a highly colonial system. Such organization permits preferential, dense crowding of large numbers of highly tolerant individuals into even more limited small areas of breeding habitat than Redwings.

Tricolors also flock and roost in large numbers during the post-breeding period. This, as with Redwings, generally occurs in marshes. However, unlike Redwings, the species does not necessarily remain perennially resi-

dent on any particular site as a function of maintaining it for subsequent breeding. The nomadic, shifting movements of Tricolor populations appear repeatedly to reflect the rapid, mass responses to ecological conditions, of which the species is capable. This is suggested as but one facet of the synchronous responses typical of Tricolor breeding efforts. Such activity may result in maintenance of a site throughout the winter, with subsequent successful reproduction, such as at Lake Sherwood (p. 123 ff.). However, the long-term occupation of potential breeding space, so characteristic of Redwings, is clearly not a requisite for Tricolors to obtain or retain a specific breeding site. This is equally true of deep-water bulrushes -- the species' "usual" habitat --- or of dry fields, into both of which habitats Tricolor flocks may immigrate over variable distances from non-breeding roost sites. Breeding at such suddenly occupied places may begin within ten days at any date during spring and summer (p. 173 ff.), even in the face of vigorous hostile reaction by already-established Redwings (Figure 26). The phenomenon is most striking when it occurs on dry croplands where the blackbirds never roost during non-breeding periods. Both Tricolors and Redwings move into such habitat, but there are conspicuous differences between them. Tricolors always move en masse, never more than two weeks prior to the start of nesting; and prolonged, in-

creasingly vigorous defense of territories is not practiced. Those Redwings which move from winter roosts always arrive in small numbers on new sites to breed as much as 10 weeks before nesting starts. Basically, either long- or short-term site occupancy by Tricolor populations can lead to effective reproduction; and either one is invariably followed by a rapid succession of events in the breeding cycle, much abbreviated by comparison to total Redwing efforts, without any of the type of elaborate preparations described in Redwings.

The rapid succession of events begins with colony-site prospecting, including all or part of a population with many males and few females. There ensues colony establishment in which the population settles in one portion of the habitat and engages in frequent foraging flights which are far more frequent than is typical of feeding activities among winter-roosting flocks (Orians, 1961). By that time, females have joined the activities in large numbers. Within a week, these two activities have merged with full manifestation of territory, pair formation, nest-building mating, egg-laying and incubation (p. 123 ff.). Whether the events in a population culminating in incubation span the "typical" seven to ten days for a single synchronous effort (resulting in a short thirty to thirty-five day cycle for the colony), or extend over varying portions of an entire breeding season,

as 1959 at Lake Sherwood (p. 173 ff.), the compression of events in the Tricolor cycle is undeniable and seems clearly designed for a rapid, opportunistic utilization of an environmental complex by many simultaneously responding individuals. Shortening of the individual female Tricolor's nesting cycle, compared to a Redwing female, involves a compression of behavioral events which initiate nesting, including rate of nest completion. Subsequent stages are quite similar, and no evidence has been obtained that Tricolor incubation or nestling periods are any shorter than those of Redwings. Even in colonies like that at Lake Sherwood, 1959, in which new individuals entered a colony almost daily between mid-April and late May, newly arrived segments of the population nested synchronously, so that the potential existed for the whole population to breed at the same time. Fundamentally, the Tricolor system would seem inevitably to require abundant environmental resources in order to support large numbers of birds with simultaneous needs (Orians, 1961). By the same token, such Tricolor populations can successfully move anywhere to breed, assuming the observed need for adequate protection from predation (p. 175 ff.), at almost anytime when the adults are reproductively mature, by virtue of their large numbers, wherever resources meet some prescribed adequacy. Given a broad temporal span of this resource availability, the species apparently

responds to the latter by a prolonged breeding season.

Spacing via territoriality in the colonial Tricolor confers order upon a potentially chaotic social system, and results in less disturbance to females who are engaged in the rapid consummation of reproductive activities leading to incubation. Male territoriality is maintained during the brief period necessary to furnish these conditions; whereupon the males are released for other activities until the young hatch. Size of male territory seems not to vary areally in any as-yet-measured way directly related to ecological favorability in the environment. Redwing male territories were over ten times as variable in size as those of Tricolors. Rather, the striking Tricolor variable was total population number, apparently correlating with ecological conditions --- as at Lake Sherwood --- no population in dry years 1960 and 1961, compared to a maximum population in wet 1958 (Table 14).

Population size did seem partly independent of inter-individual aggression among Tricolors. It is not entirely clear how population size control is effected. The latter appears to be independent of territory size or total available nesting habitat. What remains unclear is how and why some individuals breed and others do not, even though all were present prior to colony establishment and in the presence of an apparent excess of nest

sites (p. 132 ff.). Yet, consistent features of the Tricolor system are utilization of a small portion of available nesting habitat, and nesting of fewer birds than started site prospecting.

It is evident that arrival and acceptance of the nesting site by Tricolor females during colony formation takes place in a short time; and their assessment and rejection of situations may partly form a basis of Tricolor population regulation. Small territories probably can hold only a limited number of even highly tolerant female Tricolors. Whether in a synchronized or attenuated breeding colony situation, females may well accept or reject only certain territorial configurations consonant with their physiological and psychological condition, resulting from their experience interacting with the surrounding landscape, the breeding site, and advertising males.

Male Tricolor absence during incubation, especially in a large synchronized colony, results in exclusive use of adjacent foraging sites by incubating females without male competition, reduced conspicuousness of the colony, plus rest and reduced energy expense to the males. Resumption of territory by males within a few days after nestling hatching, results in relatively stable protected conditions, particularly for females, during the arduous task of parental care.

Within the framework of conditions furnished by her mate and the ecological situation, a female Tricolor can complete by herself the tasks of nest-building on through incubation. Recall that nest-building averaged less time than in Redwings. Incubation may be adequately performed without a protective territorial mate in synchronous colonies when all birds present are females so-engaged, which generally ignore or at least do not interfere with one another (p. 191). In less synchronized populations, newly arriving adults appear to avoid attempts at establishment where females are already sitting on eggs. The presence of organized surrounding territorial situations in asynchronous colonies probably discourages interloping by unestablished Tricolors, and reduces potential interference by the latter with incubating females. Only in unusual situations did any disturbance become noticeable, as intruding Redwings and Tricolors on HVM (Figure 26). Otherwise, Tricolors appeared not to suffer nest losses because of disturbance by intruders during the vulnerable period of incubation. Such vulnerability in a dense colony is possibly alleviated by males' return to roost at night, and is removed by their permanent return for parental care.

Prominent Tricolor structural, behavioral and ecological features connected with parental care differ sharply from Redwings. The species reflects fast flight (p. 40);

and both parents forage regularly over relatively long distances for the young. This may be as much as fifteen times farther away than Redwings travel from their nest sites (Figures 11, 18). Comparable food delivery rates by females (Tables 10, 17) indicate Tricolors range from six to 25 percent per hour slower than Redwings at the same sites. The percentage of male help in Tricolors is clearly a factor compensating for this disparity. Two additional factors may also operate: 1) Tricolors may deliver more food per trip by flying faster and farther to rich sources (basically indispensable because of large population and energy demands of long, fast flights), although this requires quantification (Orians, 1961); 2) Because of their longer beaks, on the average, Tricolors may be able to carry more food per trip, making longer delivery intervals possible. At any rate, singly or in concert, their characteristics furnish the Tricolor a breadth of environmental exploitation, depending on its population responses, which is unattainable by Redwings. Operation within this framework, or these patterns of exploitation, makes it advantageous --- perhaps mandatory --- for the species to forsake drought-ridden sites, and to seek favorable resources even at the risk of days or weeks of breeding postponement. For Tricolors, the postponements present advantages, considering the probable energetic disaster of mass nestling starvation or rearing

fledglings of poor vitality in poor ecological conditions.

As in Redwings, certain aspects of a polygynous mating system are significant to Tricolors. Advantages of the system are similar in both species. Tricolors, too, appear to have nearly equal male-female ratios in whole populations. Its recorded lower rate of polygyny (p. 146 ff.), probably reflects breeding by a greater proportion of adult males than in Redwings. More males would then be available for mate selection by females. The majority of unestablished peripheral males seemed to be immatures among Tricolors (p. 141 ff.). Such a situation renders more individual help for females feeding young than in the Redwing system --- again, overall --- and could thus be a potential factor in elevating the food delivery rates of Tricolors. As previously suggested, tolerance levels for greater proximity of simultaneously nesting females may not be capable of further increase in an open-nester like the Tricolor, in which females constantly encounter one another while coming and going during all phases of nesting.

Furthermore, evidence indicates that female Tricolors attempt but a single brood at one breeding locus, whether successful or not (see tower-bulrushes, p. 165, 173 ff.). It is suggested from this that once a breeding effort is attempted or completed, the female ceases for the particular season, or she shifts to another site for a second

effort. More data are needed to determine breeding status of late season new arrivals at a site like Lake Sherwood --- whether they contain females which already nested earlier in the season. Recall that Payne (1965) has reported successfully reproducing males, those feeding young, were all undergoing gonadal regression. However, exactly when that occurs during a nesting cycle would determine whether males could make more than one breeding effort per season. Circumstantial evidence for widespread failure to attempt second broods at Lake Sherwood in 1959 and for shifts of Tricolors, which had built nests, from HVM to West Lake Sherwood in 1959, strongly support these above points. Certainly single-brood attempts would be in keeping with the mobile and opportunistic nature of the species. Co-ordination of a synchronized, massive breeding effort with a food supply of limited duration, theoretically, should favor single broods in a given habitat site. In areas of more or less continuous breeding during a season, second broods as yet may have escaped detection. However, in such habitats, shift of just a few yards for the second-brood effort by a Tricolor female is certainly possible, and would constitute movement to a "new site".

For many passerines, parental feeding of young once they leave the nest is of obvious advantage, as previously noted. Fledgling care by both Tricolor parents is well

established (this study; Emlen, 1941; Orians, 1961). Whatever the greater share of nestling care borne by the female (p. 156 ff.), the dual-parent type of fledgling care (male and female) seems especially appropriate in a nomadic single-brooded species. The Tricolor parents and family can conceivably wander and forage freely about the landscape, better assuring the survival of a single brood.

In addition to the flexibility offered by the previously described components of Tricolor "opportunistic nomadism", there is limited evidence that clutch size may vary, correlating with the ecological conditions. Overall mean clutch size is smaller than in Redwings (Table 16), which may reflect an adaptation to an average lower food availability and parental delivery-rate capacities. Referring again to feeding intervals and long distances traveled by Tricolor parents, a smaller mean clutch might be yet an additional assurance for single-brood survival. However, the marked intraseasonal fluctuation of clutch size at Cache Creek, 1958, clearly correlated with the environment --- larger clutches produced in the early, wet part of the season (Table 16). Both species, living as they do in regions of limited and fluctuating resources, might be expected to adjust clutch size relative to such resources. Wagner (1957) presents a cogent argument for differential food availability to produce eggs as a proximate causal factor in

clutch-size control seasonally and latitudinally. A potentially greater variation in clutch size of Tricolors corresponds to their great mobility, compared to Redwings which exhibit a relatively more fixed and stable relation to the breeding substrate.

In addition to other advantages gained by Tricolor breeding synchrony, the period of exposure to predation is reduced. As in Redwings, greatest nest losses repeatedly occurred in drying marshes (p. 165 ff.). Even large and conspicuous colony structure in dry fields proved successful. In such situations predators simply may not have noticed or been able to locate nests. Tinbergen (1967) has shown that terrestrial predators had great difficulty locating nests even in dense gull colonies. Tricolor nests are **certainly** less conspicuous than ground nests of gulls. I have further suggested two phenomena of relatively recent historical inception as possibly affecting blackbird breeding success in Californian valley croplands. These are reduction in predator numbers by human activity, and recent invasion by blackbirds of such habitat, which may signify that predators have not become accustomed to looking for them there. The presence of fields, depending upon human agricultural practices, and Tricolors, depending upon ecological conditions, is much less predictable than presence of palustrine situations.

C. Behavioral Isolation

The whole animal's behavior is indivisible from its morphology, ecology or other aspects of its biology. Therefore, it is necessary to consider here behavior conditioned by the species' ecological and other adaptations, and how experimental analysis shed light on the significant activities of each.

Despite similarities in their non-breeding activities and habitats, both Redwing and Tricolor exhibited specific behavior which appeared consistently to attract individuals of but one species, and produce intentional aggregations of a single blackbird species with great frequency. Roosting segregation, as well as that in feeding flocks, has been demonstrated (p. 58 ff.), in contrast to any possible random intermingling of the two species. Prior to clear-cut initiation of breeding, each species showed unique behavior in its diurnal returns to roosting habitat. In such instances, their segregation was more complete than in either feeding or roosting flocks. Redwing males tended to return to incipient territories where they perched and sang intermittently. They were more dispersed than Tricolor returnees. Their presence attracted other Redwings, and general lack of aggression failed to repel those which did collect in flocks (p. 53). On the other hand, revisiting male and female Tricolors collected in dense, vocalizing (droning choruses) flocks deep in roost-

ing vegetation (p. 124 ff.).

Besides encouraging regularly intraspecific groupings, the above behavior conditions species responses in breeding initiation. In spite of increasing late-winter levels of aggression among males, Redwings continually attempted to establish themselves within that species' territorial organization at given sites. Similarly, revisitant Tricolors increased in numbers during late winter, merging into an as yet "undifferentiated" colonial assemblage.

As is doubtless true of all animals, the social organizations of the two species seemed to impel conformity, or their members would suffer reproductive failure. The evidence presented documents the firm commitment of each species to its respective ecological system, so that, even when confronted repeatedly by the other species as potential mating partners, each rejected the other. Obligation to a specific way of life for survival does not in itself preclude individual interspecific matings. There must be clear evidence of causal stimulus-response factors in behavioral rejection of one species by the other.

Dummy and song experiments furnished limited, but often conclusive evidence for intraspecific sexual (mate) selection by females. Moreover, their hostile interspecific responses were consistent. Estrous females of both species totally ignored, or aggressively rejected males of the other species. This was regularly observed

in the Lake Sherwood area, 1957-1959 (p. 242; 258). Rejection of males occurred even when the females were performing pre-coital display, an extremely vulnerable and receptive condition for copulation. Such displays were invariably initiated in an intraspecific behavioral context; and, however close such instances came to interspecific matings, no incipient copulation ever reached the stage of physical contact. Certainly dummy experiments indicated indiscriminate Redwing and Tricolor male responses to female of both species. In this regard, at HVM male Tricolors showed intensive interest in matings at least during a prolonged period, April 17-30, 1959. Redwings effectively engaged in such activities from April 17 until early June. The above suggests the greatest probability of interspecific matings existed during the last two weeks of April. Tricolors were receptive prior to that time; but then Redwing numbers were reduced, their breeding system temporarily disrupted by Tricolor invasion; and Tricolor chances of sexual encounters were more likely with other Tricolors than with Redwings. Female Tricolors were not estrous after the end of April; and, while Redwing females were estrous during much of the spring, they were only abundant after mid-April by which time many Tricolor males had already departed. These interrelationships of population numbers, reproductive phasing, and behavioral rejection seemed to be the

usual situation between sympatric Redwings and Tricolors (p. 279 ff.), again predicated on appropriate intraspecific motor responses to species-specific cues without fail.

One conceives of loud, melodic, territorially vocal Redwing males possessing positive qualities of attraction for Redwing females, quite distinctive from guttural song choruses of male Tricolors. Furthermore, Redwing vocal repertoire, including loud voice individuality, correlates well with exaggerated stationary displays and elaborate aerial displays (p. 181 ff.), all of which produce a behavioral system designed for attraction and interaction over relatively long distances including recognition and repelling competing Redwing males. Tricolor vocalizations and displays involving sexual interplay seem generally best suited to extremely close range interactions deep beneath a nesting vegetation canopy typical of this species (p. 217; 245). Similarity between Redwing and Tricolor male spread displays (p. 197; 217) probably relates to the fact that they both use them initially for long distance communication, as well as having been derived from a possible common ancestor. Marler (1957) has pointed out the relatively easier localization at long distances of low-frequency sounds made by non-visible individuals compared to those of high frequencies. Male song differences between these two species undoubtedly

relate partly to ready localization of males by females. It is reasonable to conclude that positive orientation to such distinct species-specific stimuli will discourage even estrous females from allowing males close enough for matings to occur. However, when close contact does result, appropriate communicatory signals appear sufficient to repel the other species.

The differences in intraspecific song responses correlate with the kind of inter-male spatial competition, i.e., with nomadism of Tricolors, and with the more sedentary nature of Redwings. With mobile tendencies, Tricolors, when responsive, might be expected to respond to a wide variety of male Tricolor songs, neighboring or other (p. 271 ff.). This contrasts with geographic, population variation in Redwing male song, reflecting the species' non-mobility. Male Redwings ignore distinctive geographically distant song variants, ignore neighboring male songs to which they had presumably become habituated, but show vigorous song and display responses to presumed unfamiliar non-neighbor males of the same or nearby populations (e.g., HVM and WLSM; Tables 34, 35). The great importance of territory, and long-term association of males defending territories in a Redwing population, would form the basis for these males to ignore neighbor males of "known" status, but to react hostilely to "strange" males of their own or adjacent populations, as potential terri-

tory competitors. Clearly, relatively distant male Redwings, as from geographically separated areas, not only would never compete with local Lake Sherwood males (where tests were conducted; p. 263 ff.), but also sound much different than the latter, and were responded to by song infrequently or not at all.

Song of both these marsh dwellers, and that of several American palustrine passerine species have similar physical characteristics: intermediate harsh vs. melodic qualities, complex informational components, and frequent segmented portions (buzzes, trills). Correlating with this, and the responses noted in experiments, Redwing and Tricolor distinctions in song relate to discrete information, variable components, length, and dominant frequencies. Tricolors seem to place less of a premium on individual status and recognition, especially for long-distance, precise informational conveyance in song. Such may well be accomplished with the distinctive call notes which this species uses at close range. Obviously the highly responsive nature of Tricolors with "threat growls" toward Tricolor songs of their own population points at least to recognition at a population, and perhaps even individual level. The corresponding song functions of Redwings were different, with clear individual recognition demonstrated. It is suggested that somehow the repertoire, and individual, as well as population variations of Red-

wing song reflected means of providing the recognitional cues among competing males. In the potentially "violent" territorial situation of Redwings, song of both sexes is probably useful in immediate recognition of mates without wasting time in chases and so forth. This is accomplished by greater aggressive restraint and various appeasement gestures by Tricolors. In any event, certainly for Redwings, some of these distinctive song characters have apparently become more intensified, resulting in even greater interspecific vocal divergence (Figures 18, 22; Table 42). It was indicated that males of both species either learned, or became sensitive to, songs of the other species in populations whose interspecific relations resulted in considerable competitive strife (Tables 35, 36).

While songs appeared to contain particular distinctive individual recognition value in these two species, some vocalizations, such as alarm calls, did not. In such instances, males and females seemed readily to respond appropriately to intra- and interspecific calls, according to field observations. This agrees with the concepts that such sounds, though species-specific in their exact forms, can have broad survival value to many other individuals than merely the population or species of which they are characteristic (consult Altmann, 1958; Marler, 1957).

The consistent, negative behavioral responses and reactions to dummies shown by females toward males were partly related to timing within the breeding cycle. Females possessing nest-sites or nests were already paired, and rejected the presence and approach near nest-sites by alien males of either species. Such negative hostile responses by females, combined with frustrated male mating attempts may well have produced an additive effect on interspecific male aggression. This would partly be because of greater male vs. male encounters caused by attraction of a male to a site, and partly because of the noise and agitation of rejection by the female, calling attention of an established male to an alien male's "provocative" presence. All of these negative interactions repeatedly tended to disrupt any possible sexual co-operation requisite for interspecific mating, and to reinforce females' repelling of, and territorial males' eviction of, intruding males of the other species. Actually, the successful interlopers were immature males who quietly, without display or song, attempted to copulate with equally quiet stuffed female dummies. "Stolen" intraspecific matings, though infrequent (p. 86 ff.; Nero, 1956b), have at least been noted, while interspecific ones were never seen. This suggests at least within a species that alien males may offer more "positive" or "correct" = appropriate stimuli to an estrous female with a nest-site,

than do a male's of another, similar species --- at least considering Redwing-Tricolor relations. After the initial period of the cycle leading to incubation, individual females of both species were sexually unreceptive to any males, and showed high levels of aggression to all alien males as well as submissive responses to mates. This virtually eliminated the possibility of any kind of mating with such females.

The plumage character displacement shown in Redwing males (Table 41) reflects sexual selection on the part of Redwing females. This strengthens the hypothesis of interspecific genetic isolation, by indicating natural selection for ready recognition of males by females. It suggests elimination of females who may have made mistakes in mating with Tricolor males, and elimination of males which looked more like Tricolors, at least in epaulets. In such cases, the confusing Redwing males would have been chosen for mates less often than Redwing males more easily distinguishable from Tricolors. If matings by Redwing females to male Tricolors resulted in lowered fitness, compared to females mating with Redwing males, then selection pressure would favor development of more effective recognition features (as has occurred in Redwing epaulets), or presumably extinction of Redwings might have resulted. Such was previously suggested for song as well.

Returning briefly to initiation of breeding, it was

found that Redwings show a period of three weeks of interaction between pairing birds (p. 84 ff.). Prior to that, in many areas female Redwings may roost apart from males (p. 50 ff.). However, Tricolors show flocking, roosting and breeding-initiation colonial habits in which males and females remain together in large numbers much of the time (p. 59 ff.). This may indicate that Redwing females must actively seek out males over greater distances more frequently than do Tricolor females, as a result of the frequent separation of non-breeding sexes in Redwings. It would seem that "searching or wandering" Redwing females might face a greater probability of encountering the other ("wrong") species, when preparing to reproduce, than female Tricolors. This probability would be increased by Tricolor invasions of Redwing habitat, in shifting to new sites for nesting. When Tricolors arrive at the beginning of Redwing breeding, chances for interspecific choice by Redwing females are very great, especially because of the overwhelming number of Tricolor males present. If many female Redwings are as yet unpaired, they would be more vulnerable than Tricolor females to mistakes. The reverse is true for female Tricolors. In addition to their close pre-breeding roosting association with their own males, the latter invariably outnumber greatly any male Redwings present. Thus, female Tricolors usually have much greater probability of encountering their own

males for pairing and mating. Moreover, pre-breeding flock behavior has been suggested as stimulatory to breeding condition and possibly to pair-bond formation in Tricolors (p. 182; 254). This suggests that, whenever and wherever Tricolor flocks shift, interaction between the sexes may already have produced intraspecific reproductive bonds. The value of white epaulet markings in Tricolors has been suggested as great in species recognition and maintenance of flocks (p. 326). Thus, it may facilitate females' finding and keeping track of Tricolor males. In this regard, selection should favor retention of a white border. Also, Tricolor females in a situation where they might select a Redwing male by confusing his buff-bordered epaulet with a Tricolor male's white one, may be unimportant selectively to a population for the following reasons. The number of male Redwings present is always small, and would only potentially affect female mating choice at the periphery of a Tricolor colony. Such hybrid "mistakes" by females would involve a small number of genotypes in comparison to the hundreds or thousands of Tricolors present. Thus, their total effect on the Tricolor gene pool would be very low. The major effect would probably be selection against females who made hybrid matings.

Later in a breeding cycle, relating to possibilities of interspecific hybrids, was found apparent non-interest

in copulation by Tricolor males engaged in feeding young. In addition to reducing probability of Tricolor male matings with successively estrous Redwing females later in the season (p. 84 ff.), this attitude by the males might reinforce the Tricolor system by reducing wasted expenditure of energy by them, since: 1) no estrous female Tricolors would be available; 2) maximum energy must be devoted by both parents to insure rearing healthy young. A male Tricolor may even attack alien females entering his territory during care-of-young, in absence of appropriate submissive responses by intruders; and incidence of appeasement display (p. 224) by his mate or mates is highest during that period.

Sibley's (1957) review of avian interspecific hybridization indicates high frequency of positive interspecific responses to males in species which show great sexual dimorphism and dichromism. Males of the "other" species seem to serve as superstimuli. In such examples (esp. Anseriformes, Galliformes, Apodiformes = Trochilidae, Passeriformes = Paradiseidae), little consideration is given vocal and habitat adaptations as possible isolating mechanisms; but certainly the incidence of genetic interspecific, and even intergeneric, compatibility is high. The latter has not been demonstrated conclusively in all Redwings and Tricolors. However, the consistent ecological and behavioral responses which serve as apparent iso-

lating mechanisms are abundantly documented, and, in two species which show marked sexual dimorphism.

Relating to the above presentation, the following points may be reviewed. The two species show a close phylogenetic relationship. They encounter apparently abundant opportunities for hybridization. No reliable reports of interspecific hybrids are known. In fact, the character displacement discussed above furnishes strong evidence for the evolution of recognition characters resulting in assurance against mistaken interspecific identifications or choices. This sequence of points seems to make most reasonable the conclusion that the isolation between the two species fundamentally results from partial or complete genetic incompatibility. Regardless of the admitted great similarities between the two species, reflection upon the large number of adaptations which have resulted in two markedly different social systems make it further reasonable to conclude that the distinctions are based upon multiple genetic differences. This would surely increase the likelihood of interspecific genetic incompatibility, as well as the intensive intraspecific behavioral focus.

D. Evolution of Isolating Mechanisms

Present reproductive isolating mechanisms must ultimately be considered in light of the historical development of the two species. Several initial basic premises

should be established. First, it is reasonable to conclude that the divergence of Redwing and Tricolor species occurred, on the basis of their great similarities, within relatively recent geological past. Therefore, it is logical to seek causal factors for these phenomena within the realm of recent geological events. Further, the widely dispersed Redwing appears to be a more generalized species in the genus Agelaius, and is more likely to have been the evolutionary product of broad North American continental conditions and changes with which the species must have been faced since its inception. The sort of adaptive complex described in the Tricolor shows it to be more specialized, especially to the ecological conditions of the California Central Valley, as Orians (1961) and other "agelaiologists" have reported. Thus, a comparison of the two species suggests that the Tricolor probably diverged and specialized to coloniality from a Redwing or "Redwing-like" form. Modern relationships between these two species additionally suggest that geographic isolation was a prerequisite for Tricolor divergence, since the latter species only succeeds in competitive situations with Redwings when present in large numbers. Basically, without prior isolation, it is difficult to envision a divergent modification toward coloniality in the midst of constant pressure from a sympatric population, featuring highly territorial individuals such as Redwings.

We may profitably begin by considering the probable evolution of the specialized Tricolor in the appropriate temporal and spatial conditions that could have favored divergence from its progenitors. A consistent hypothesis may be erected in which geographic isolation for black-birds and geological events coincide, if one examines particular aspects of Pliocene-Pleistocene epochs in the California region. Today the Central Valley is characterized by dry, hot summers, and remarkable fall-winter flooding resulting from substantial precipitation in the Coast and Sierra Nevada Ranges, west and east respectively.

It is basically an elongate basin of riverine lands and flood basins, virtually treeless and lacking rain during the agricultural growing season (Jahns, 1954; Wahrhaftig and Birman, 1965). Such conditions are even more pronounced in the northern half, the Sacramento Valley portion, than the southern San Joaquin portion. These conditions during spring and summer, accompanied by large, diverse arthropod populations, have been suggested as major necessary features conditioning the success of the nomadic-colonial Tricolor (Orians, 1961).

Conditions requisite for isolation of the Central Valley as a potential center of adaptive radiation, to permit development of the Tricolor colonial system from a Redwing or other such palustrine ancestor, probably developed in the recent past as a result of the following

sequences. Peabody and Savage (1958), in discussion of salamander evolution in California Coast Ranges, suggest that the southern half, the San Joaquin Valley, was inundated by marine waters during most of the Cenozoic, with the low-lying land of the future Coast Ranges present as a series of offshore archipelagoes. Wahrhaftig and Birman (1965) agree, and further state that the Sacramento Valley has been a riverine basin above sea level at least since the Miocene, perhaps 20 million years. This valley was probably then, as it is today, an excellent habitat for marsh-dwelling birds. However, the same authors indicate that the San Joaquin Valley did not emerge until at least the early Pleistocene. Also, it was at approximately that period when much of coastal southern California (including the Ventura and Los Angeles Basins), as well as the aforementioned Coast Ranges emerged from the sea, largely from mountain-building activity which still continues today (Flint, 1957). Evidence from paleobotany (Axlerod, 1957) and tectonics (King, 1965) suggests that during the Pleistocene, at the latest, the Central Valley as we know it today was structured by widespread orogeny and uplift along the Pacific coastal region. Whatever absolute dating Pleistocene, at the latest, the Central Valley as we know it today was structured by widespread orogeny and uplift along the Pacific coastal region. Whatever absolute dating assigned to the Pleistocene (discussed below), its span

in time is identified by an alternating series of cold (glacial) and warm (interglacial) periods. These characteristics, along with particular fossil types, are suggested as the best criteria for recognizing the epoch in the geological record.

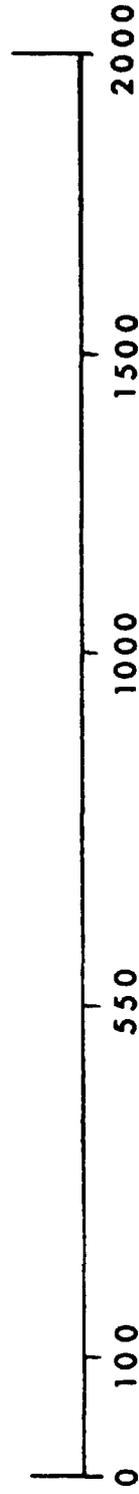
It is outside the province of this study to attempt to resolve the perplexing controversies over absolute dating of the Pleistocene epoch. Many older methods have proven inaccurate or not applicable to the problem (erosion rates, etc.; Flint, 1957). For periods older than about 70,000 years before present (B.P.), conflicts have arisen especially in many contradictory results obtained by using various isotopic geochemical methods. Results from these yield a range from 300,000 to 3.5 million years back to the beginning of the Pleistocene (Broecker, 1965). The latter author states that dating within 70,000 years of the present is reasonably consistent with refined carbon-14 methods. Figure 28 shows that I have adopted a compromise dating, and above evidence suggests the epoch was indeed longer than a million, and probably closer to at least three million years (see Broecker, 1965, 1966; Wahrhaftig and Birman, 1965).

Figure 28 suggests the following glacial and interglacial tentative time periods to serve as a basis for further discussion of blackbird evolution in the Pleistocene. Dating back from the present, modern climatic con-

Figure 28 shows two lines relating to periods of glacial and interglacial conditions during the Pleistocene epoch. Data is from Broecker (1965). The lower line graphs probable time relationships of glacial (G) and interglacial (I) periods. Letter abbreviations from the left to right mean: R = recent; W = Wisconsin glacial period; S = Sangamon interglacial; I = Illinoian glacial; Y = Yarmouth interglacial; K = Kansan glacial; A = Aftonian interglacial; N = Nebraskan glacial; dashed lines and question marks mean uncertainty as to length of period. See Flint, 1957, for full descriptions of the periods. The upper line contrasts potential periods of isolation during glacial periods with potential periods of re-invasion of the Central Valley during interglacials. Zero means no isolation and probability of entry is great. Number 1-5 indicates a relative amount of time the Valley was isolated compared to other glacial periods. Shortest period of isolation was during the Wisconsin; longest period was during the extended Nebraskan (oldest).



Correlated Periods of Possible California Central Valley Isolations
for Tricolors



Time in Thousands of Years Before Present (B.P.)

ditions have existed for the last 5,000 years; and the last glacial retreat occurred about 11,000 years ago. The most recent North American continental glaciation began no earlier than 70,000 years ago (the "Wisconsin", in North American terminology), and reached its maximum about 19,000 years ago (Broecker, 1965; 1966). It is well correlated temporally with the latest ("Tioga") glaciation in the Sierra Nevada, which was covered at the maximum by an ice cap extending at least from 36 to 40 degrees north latitude (Wahrhaftig and Birman, 1965). During the same period glaciers virtually encircled the north end of the Central Valley in the High Cascades and Coast Ranges. In addition, there was a small number of valley glaciers in the transverse San Bernardino Mountains to the south during this time (Jahns, 1954; Wahrhaftig and Birman, 1965). In such a relatively recent climatic and geological situation, it is again reasonable to conclude a substantial degree of isolation in the whole Central Valley. There are evidences of at least three previous glaciations, both continentally and in the Cordillera. However, erosion, orogeny and other factors tend to obscure precise measurements of time and extent of glaciers. Yet all evidence points to the fact that there were earlier glaciations, at least back three million years (Curry, 1966). They produced cooler climates, probably reduced evaporation, local arctic conditions at glacier edge, and vege-

tation shifts such as lowered altitudinal occurrence of highland conifers. Soil deposition and fossils indicate the interglacials marked retreat of ice and climates as warm as, or warmer than, today. Figure 28 shows extrapolations of sedimentation rates (see Broecker, 1965) suggest quite long glacial and interglacial periods back to the "Nebraskan", presumably the first continental glacial age in North America. Furthermore, conditions in Yosemite Valley of the western slope of the Sierras during the second recorded glaciation there (correlated with the continental "Kansan"; = K, in Figure 28) were perhaps three times as severe as in the Tioga glacial period (Norris, 1958).

Central Californian climate during glaciation was probably somewhat wetter and cooler than at other periods. As in other areas not immediately adjacent to the ice packs, climate appears not to have been severe or arctic (Flint, 1957). Interglacial periods have already been likened to modern climates. East of the rain shadows cast by the Sierras and southern Coast Ranges, deserts were developing during the Pleistocene (Axlerod, 1950; 1958). This trend was accelerated during the drier interglacial periods. Coinciding with glacial periods in the Sierras and elsewhere, were the Fluvial Periods in the Great Plains and in the xeric regions south and southwest of the Central Valley (Morrison, 1965). Such

periods typically showed large lakes in the interior basins of these regions; and Morrison records at least 150 of these lakes. These conditions correlated with a southward shift of cyclonic storm patterns, and reduced evaporation as a result of cooler conditions relating to continental glaciations during the same periods. Riparian and palustrine vegetation appear to have increased substantially in such pluvial periods and areas.

We may summarize the possibilities for Tricolor evolution, as a result of the above environmental complexes. Pliocene California had a warm climate, with essentially the Sacramento Valley region as the most extensive habitat area (not submerged) potentially suitable for marsh-dwelling blackbirds. This region was probably widely confluent with other regions to the north and east via connecting valleys in the surrounding, gently sloping uplands (King, 1965). Thus, any "Redwing-form" would not have been restricted by geography in such situations. The advent of the Pleistocene epoch brought substantial raising of the Pacific coastal landscape, such that the whole Central Valley gradually emerged in shape and form similar to that seen today. This furnished extensive flood-basin habitat. However, disruption of the previously warm climatic conditions was produced by interspersal of a series of cold periods resulting from continental and montane glaciation. Therein lies the story of poten-

tial isolation of the Great Central Valley. Data suggest that, whatever the epoch's length, its early glacial periods may have been long (Figure 28) and severe, even in the Sierra Nevada, and in mountains farther north. Long glacial periods relatively early in the Pleistocene, with Central Valley climate somewhat cooler than at present (but not severe) at least in summer, with widespread flooding and drying in marsh and riparian habitats, without interference by "typical" and territorial Redwings, would furnish a highly favorable situation for the development of the Tricolor's colonial habit. This makes reasonable the assumption of abundant insect reproduction, similar to the present such as the lepidopterous, orthopterous and odonate forms noted earlier, conditioned by levels of precipitation. Present Tricolor-Redwing sympatry would thus be a result of one or more secondary contacts by invasion or re-establishment of "typical" Redwing populations during one or more interglacial periods. Figure 28 clearly shows at least three of these of rather lengthy duration. Certainly the Redwing character displacement previously mentioned would seem to point to reinvasion of the Valley during some earlier interglacial period. It would seem to me that this exposition presents a highly reasonable theory for the separation and evolution of the Tricolor, acknowledged problems and inadequacies of precise Quaternary dating notwithstanding.

Correlative circumstantial support of the above theses has been provided from evidence on other species pairs whose origin is thought to be the result of Pleistocene conditions in the western part of the continent. Yellow-billed Magpies (*Pica nuttallii*) occur only west of the Sierra-Cascades and mainly in the Central Valley, while the closely related Black-billed Magpie (*P. pica*) stays almost completely east of the Sierras and is at best a casual visitor to California within *P. nuttallii*'s range. Also, the California Quail (*Lophortyx californicus*) is a bird mainly of the brushy lowlands, not moving east of the Sierras or southern Coast Ranges; while its close relative, Gambel's Quail (*L. gambelii*) is restricted to the deserts east of those mountains. Similar to the latter case, is that of the coastal Nuttall's Woodpecker (*Dendrocopos nuttallii*) and its desert relative, the Ladder-backed Woodpecker (*D. scalaris*), which are occasionally found together in oak woodland or riparian areas just west of the desert. These three species pairs also seem likely to have diverged during the combinations of Pleistocene glacial-interglacials and xeric vegetation development (Miller, 1951; Orians, 1961). However, unlike the Redwing and Tricolor, these species pairs show moderate amounts of hybridization (Sibley, 1957; Linsdale, 1938; L. R. Short, oral communication). This may be related to the fact that the overall morphology, and espe-

cially behavior, have diverged to a lesser degree between these species pairs than they have between Redwings and Tricolors. Relationships of one other group of birds is pertinent to this discussion. This pertains to an apparent recent secondary contact between two strikingly divergent subspecies of Agelaius phoeniceus. These are A. p. gubernator and grandis, occurring near Toluca, in the state of Mexico. Studied by Hardy and Dickerman (1965), the two forms are distinctive morphologically, vocally, and to some extent in habitat selection. The subspecies grandis is thought to have crossed surrounding mountains within the last 40 years, and to have established itself in the Valley of Mexico as a result of human disturbance of habitat, making the latter available to it. While these are clearly only races of the same species, hybrids are extremely rare and the situation would seem to point toward a transition in which an incipient late-Pleistocene speciation has been discovered in its early stages, as it were, even within the same species which may well already have given rise to A. tricolor. The ecological bases for such incipient divergence are as yet obscure for these Mexican Redwings; but the parallel is nevertheless remarkable. Such a situation makes reasonable a quite recent divergence of Tricolor and Redwing.

E. Future Relations

With continued pressure and even greater impact on

the blackbirds by human population, the only outcome can be further restriction of the two species' habitats. Nowhere is this more apparent than in southern California. Correlated with this will likely be increased and more intensive agriculture in restricted sites farther from metropolitan areas. However, little short of wholesale extermination (considering climatic and political vicissitudes) of these blackbirds, as for example, because they were insufferable crop depredators, can be foreseen as endangering the survival of either species. Their remarkable capabilities for successfully inhabiting dry-land areas, in the presence of adequate food, are clear.

The Tricolor system has even been suggested as benefiting, and potentially expanding its numbers, as a result of increased specialized agriculture in the Californian Central Valley (Orians, 1960); and a similar situation in the Boat-tailed Grackle (Cassidix mexicanus) in Florida was reported by Selander and Nicholson (1962). It seems reasonable that as long as nesting habitat and foraging habitat are not destroyed, or the two sites do not become located simply too far apart even for Tricolors, the species will thrive. Of course, nowhere could this species afford to breed in small numbers, either because of habitat limitations or foraging distances, since Redwings would disrupt their breeding and evict them. With the perennial need for irrigation of the Central Valley in

dry summers, for intermittently flooded livestock pastures, and for cheap, intensive agriculture prevalent there, elimination of Tricolors' habitat is improbable. The Redwing is even more environmentally adept in terms of surviving human impacts.

It seems reasonable that the outcome will simply be a gradual extension of what one already observes. As humans predominate, there will be an accelerated local disappearance of the species. It seems unlikely that even California can tolerate more than a certain upper limit of human density; and it is likely that a bit of marsh, even on a golf course or in a public park, will remain after some density threshold has been reached, or surpassed.

X. SUMMARY

A thorough study was made of natural history, ecological and behavioral attributes of the closely related, typically palustrine Tricolored and Redwinged Blackbirds in southern California. The former is restricted mainly to central and coastal California, while the Redwing is widespread over pancontinental North America. The major objective was description and analysis of behavioral adaptations in the two species, as they were observed and measured in intra- and interspecific niche relationships. Intensive investigation occurred between 1957 and 1961, with sporadic work covering the rest of the period, 1953-1967.

Both species are highly social, a striking phenomenon during the non-breeding season when large roosting flocks used protected marsh areas for shelter. During that period, major activities involved roosting behavior, and shifting, scattering diurnal movements to, from, and within diverse foraging areas. Variable numbers of both species were encountered in mixed- and single-species flocks. Throughout fall and winter, blackbird flocks bivouaced in roosting vegetation intermittently during the day, as did much of the roosting population. Such flocks repeatedly showed preference to join aggregations of their own species. The breeding system evolved by

each species conditioned its responses and use of roosting vegetation as the breeding season approached. Redwing males were typically highly aggressive defending large territories, between 500 and 11,000 square feet in area, intensely in fairly dispersed populations. These activities began gradually, as much as 10 weeks before onset of nesting with pair formation commencing about three weeks before nesting. The Redwing is highly polygynous, and mated females undertook alone all nesting duties. Activities of male and female Redwings focused within or near the territory for nearly all reproductive behavior. Males furnished stable, protected sites for nesting, occasionally assisting in rearing young --- especially fledglings. The nesting season lasted from late March at least through June, during which time females attempted to rear one or more broods. Clutch size was somewhat variable, with an overall mean of 3.42. Breeding success approximated that expected in open-nesting passerines, except in marshes which were exposed to high terrestrial predator pressure by dessication, in which cases nestling and fledgling crops suffered great losses. Escape from predators by open-field nesters observed may have resulted from small predator populations, or their unfamiliarity with such habitats as Redwing nesting sites. The Redwing social system has selected for the strongest adult males to acquire harems in limited, favorable nesting substrate.

High levels of aggression dispersed the population and excluded weaker males, including all immatures.

Behavioral cues --- both visual and auditory, and specific motor responses --- both vocal and behavioral represented adaptive features specifically for that type of system. Conspicuous postures, loud and distinctive individual songs and call notes characterized both sexes. Rapid long distance recognition of individuals was typical. Vocal and postural components were highly significant in this species, and experiments with stuffed dummies showed frequent lack of discrimination in species or conspicuous plumage characters. Sex discrimination was always excellent, except by immature males.

The Tricolor is as gregarious a breeding species as it is a winter rooster. Its social system organized into dense coloniality more rapidly, and somewhat differently than the Redwing. Control of population sizes came through adjustment of total colony numbers attempting to breed at a site. Usually a substantial percentage of birds initially prospecting a site departed before breeding began. This is suggested as partly due to female acceptance or rejection of sites and males attempting to set up territories. With only about a week of buildup, Tricolor breeding commenced suddenly on a given date, with formation of territories (mean size ca. 35 square feet), pairing and nest-building, which were soon followed by

egg-laying and incubation. Females performed all nesting duties alone, as in the Redwing, except feeding nestlings. A territorial male was absent during incubation, but returned to assist the female feeding the young. A male usually had no more than two mates, either because those are all he can assist or else females simply could tolerate no more than two of them per 35 square feet available. Tricolor colonies from a few hundred to several thousand birds necessarily exploited food resources for miles around the colony site to supply their nestlings, which, adult flight capacities, parental cooperation, and nomadic opportunism in selecting favorable sites permitted them to do. In unfavorable conditions, whole Tricolor colonies deserted sites even as late as egg-laying stages. Synchrony of Tricolor breeding populations facilitated exploitation of short term rich resources; but if abundance of the latter was prolonged, a population breeding season might last as long as in Redwings. Tricolors abbreviated events at the start of a season, which shortened individual and synchronous-colony reproductive efforts, a major modification from the Redwing system. Circumstantial evidence pointed to a single-brooded condition in Tricolors; and males are known to undergo testes regression, when they have reached the stage of feeding young. Experiments indicated reactions to stuffed dummies similar to those of Redwings, depending

on the reproductive phase; but there were some clear distinctions in responses to vocalizations. There seems a reduced premium in Tricolors for individual recognition solely by song. Evidence has accrued for strong, long-distance flock attraction as a major adaptation in Tricolor male vocalizations; but individual interactions are also extremely close-range and feature high degrees of ritualized appeasement behavior by females. Laxity in male aggression, except beneath the breeding vegetation canopy, slight decrease in male aggression and a great reduction in male sexuality during incubation and care of the young phases were also noted. As in population variations and apparent opportunism of Tricolors generally, some evidence of marked clutch-size variability with ecological fluctuation was noted. Otherwise, clutch size, at an overall mean of 3.17, was significantly lower than in Redwings. Predation effects were similar to those in the Redwings, that is, marshes exposed to terrestrial predators were devastated; and the dense Tricolor populations in them suffered great losses. Again, field-nesting colonies probably escaped high predation either because of a typically rapid, synchronous breeding effort (30-35 days), or low predator populations. Competition existed because often the two species, sympatric nearly everywhere Tricolors live, contest resources, usually in the form of space, and sometimes food. In such encounters,

the Tricolor prevailed because of overwhelming numbers, occupying contested territory without requiring any counteraggression. Redwings reacted as would be expected in Redwing intrusions, but soon deserted territories if Tricolor invasions persisted. Tricolors must compete this way only in large numbers. The more aggressive Redwing dominated and evicted them when their invading numbers were small. Character displacement in Redwing plumage, and perhaps song suggests potential genetic incompatibility and selection for more ready recognition of them by the Redwing female in recurrent competitive situations.

The two species are only incompletely isolated by geography within the Tricolor range. Their ecological isolation involves different temporal and spatial exploitation of environment, and permits frequent co-existence without overt, strict habitat selection. Natural or human environmental modifications produced all the particular ecological conflicts observed. Behavioral isolation among sympatric forms appeared to be interspecifically highly developed in part because of a requisite strict adherence to the appropriate aspects of each social system for reproductive survival, and in part because of potential reproductive incompatibility. Historically, the Tricolor system probably evolved from some form of Redwing-type in the Californian Central Valley in the partial or complete isolation of that region during Pleistocene

glaciations. Such a situation probably favored the colonial nomadism in exploitative responses to environmental nesting and food resources, such as vast marshy and riparian habitat associated with explosive occurrence of arthropod populations. Secondary contact with Redwings by reinvasion of the latter has occurred and continued divergence has been favored in these two distinctive avian species at least because of devastating numerical impact by Tricolors on Redwings.

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