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

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by

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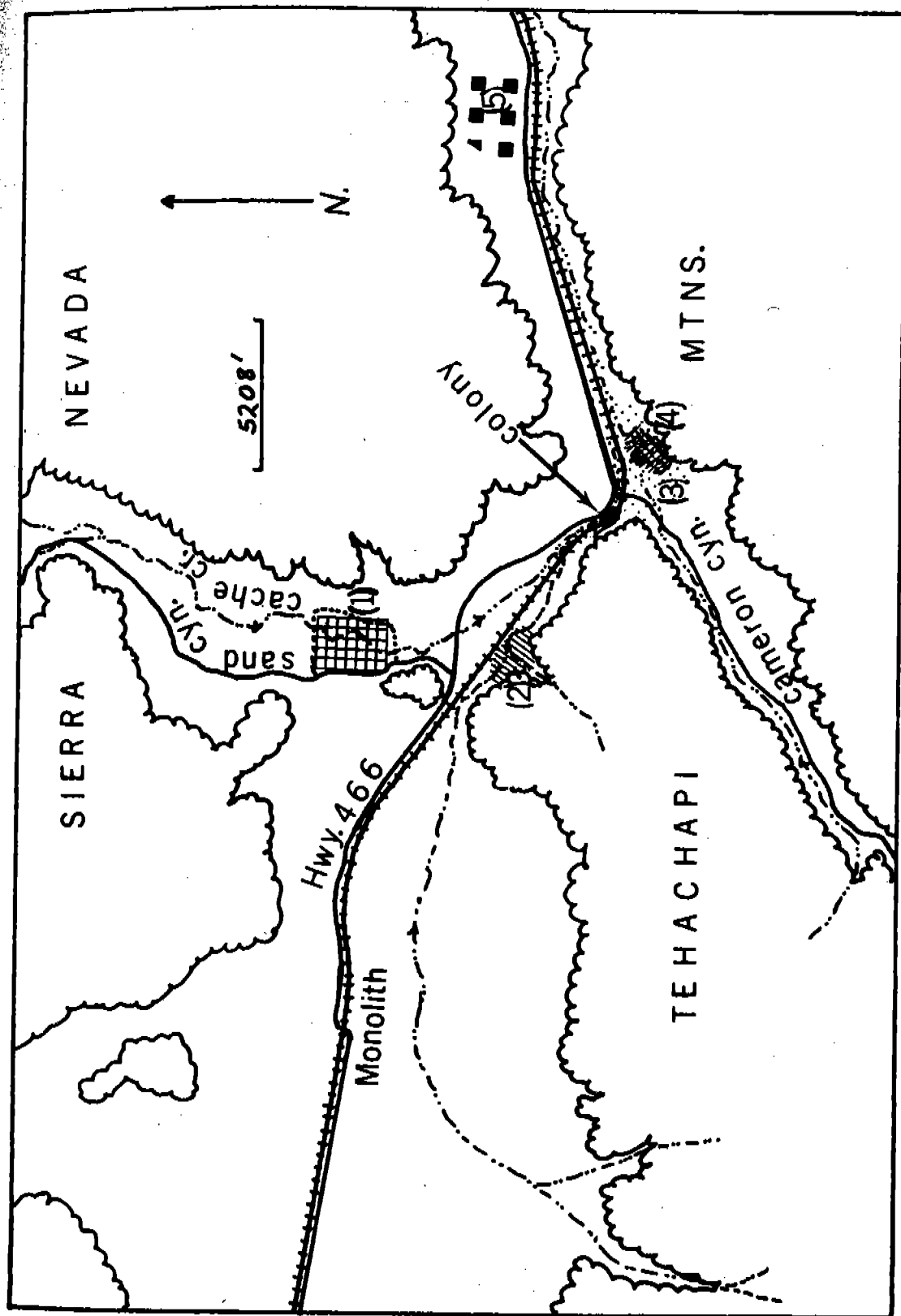
seepage from the reservoir dam (constructed in 1919) and by water pumped into it. Around the lake shore and its inlet grow abundant cultivated water iris (Iris orientalis), some cattails and numerous willows. The flat terrain immediately around the lake is covered with tall, Dallis grass and Rhodes grass (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 (north-west), 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

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).

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		Total Nests
					Young	May 5 onward	
1956							
Cache Ck.	3rd. wk. Apr.	4/19-(5/5)	4/22 - ?	max. = 5/3			2000
1957							
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
1958							
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
1959							
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
1960							
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

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.