

TRICOLORED BLACKBIRD ITINERANT BREEDING IN CALIFORNIA¹

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Abstract. To evaluate the abundance of Tricolored Blackbirds (*Agelaius tricolor*), the schedule of breeding throughout the Central Valley of California was determined in four years (1992–1994, 1997). By the end of April in 1994, all observed Tricolored Blackbirds were in the immediate vicinity of active breeding colonies. Only one colony of 600 birds was established in the Sacramento Valley north of Sacramento County. During late May and early June, more than 170,000 individuals settled in the Sacramento Valley, while attendance at colonies in the San Joaquin Valley was declining. Most breeding birds colonizing the Sacramento Valley in May and June probably already had completed nesting efforts elsewhere. This suggests that Tricolored Blackbirds are itinerant breeders. Surveys, conducted after initial settlement and before substantial movements from one breeding area to another occur, have the potential to estimate overall numbers. Inclusion of late season breeding colonies in estimates of overall abundance would result in substantial overestimates of the global population. Local and regional declines in the number of breeding Tricolored Blackbirds of an order of magnitude or more resemble population collapses but probably are attributable to itinerant breeding.

Key words: abundance, *Agelaius tricolor*, distribution, itinerant breeding, migration, philopatry, Tricolored Blackbirds.

INTRODUCTION

This study identifies breeding season movements and estimates changes in the global abundance of breeding Tricolored Blackbirds (*Agelaius tricolor*) between 1994 and 1997. A 1992 survey of colonies throughout the geographic distribution of this species produced evidence that Tricolored Blackbirds nest again in the same year at different localities. This pattern, called itinerant breeding, was first reported for Red-billed Quelea *Quelea quelea* (Ward 1971, Jaeger et al. 1986), and is implicated for the Passenger Pigeon (*Ectopistes migratorius*) and some other pigeons (Bucher 1992).

If Tricolored Blackbirds are itinerant breeders, some or all late season colonies may include individuals observed nesting earlier elsewhere, exaggerating estimates of overall abundance. To evaluate this possibility, the breeding schedule for all colonies that could be located throughout the geographic range of the species was determined again in 1993 and 1994, and sampled in 1997. This analysis focused upon the Central Valley of California (Fig. 1) where most Tricolored Blackbirds nest. Sampling of the distribution and abundance was facilitated by the rela-

tively small geographic distribution of the Tricolored Blackbird breeding range, mostly lowland cismontane California, and their conspicuous colonial nesting habits.

The status of Tricolored Blackbirds has been analyzed several times, prompted by reports of declining numbers and local population collapses (Neff 1937, DeHaven et al. 1975a, Beedy et al. 1991). Numbers, distribution, and movements of Tricolored Blackbirds between 1931 and 1936 were evaluated and interpreted by Neff (1937, 1942), who observed the largest colony ever reported, over 300,000 individuals, in a Sacramento Valley rice growing area. Orians (1961) reported colonies of more than 100,000 individuals, also near rice cultivation in Yolo and Colusa Counties, California, in 1959 and 1960. DeHaven et al. (1975a), resurveying these same areas, found no colony larger than 30,000 birds between 1968 and 1972. All investigators have found striking differences between years in the number of birds inhabiting parts of the Sacramento Valley. For example, between 1969 and 1973, DeHaven et al. (1975a) found as few as 1,000 and as many as 57,000 nesting Tricolored Blackbirds in Colusa County. Hosea (1986) found only 2,700 tricolors in Colusa County in 1981 and 1982, and none in Glenn County. Natality and mortality alone cannot account for

¹ Received 8 December 1995. Accepted 6 January 1998.

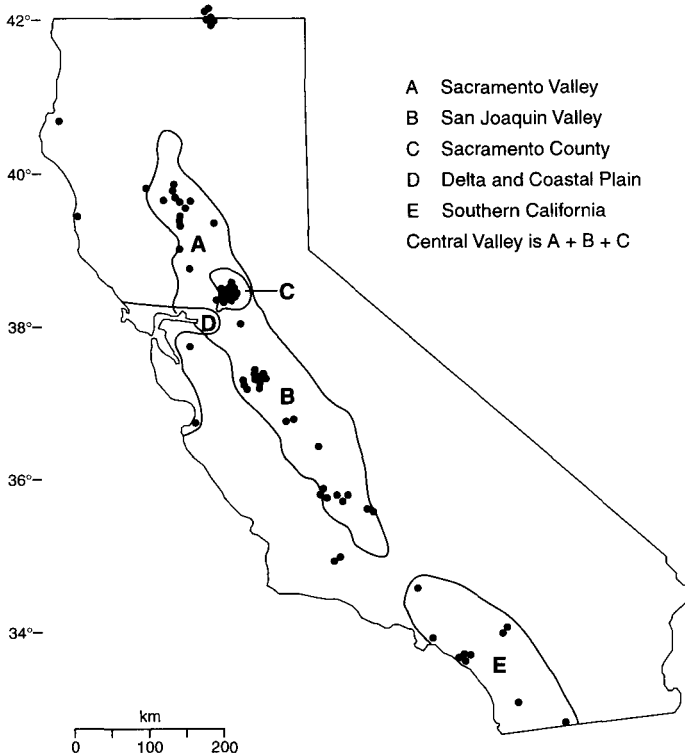


FIGURE 1. Geographic regions monitored for Tricolored Blackbirds. Breeding locations in 1994 ($n = 74$) are shown by dots.

fluctuations in abundance of this magnitude. Birds either were overlooked or were elsewhere. None of these and other historical evaluations of overall Tricolored Blackbird abundance and population changes considered the possibility that birds counted at different times and places duplicated individuals seen and counted elsewhere.

Tricolored Blackbirds winter in the San Francisco Bay Delta and along the central California coast from Monterey to Mendocino County (D, Fig. 1), the San Joaquin Valley (B, Fig. 1), and in Southern California (E, Fig. 1) (Neff 1937). In March and April they move from these wintering areas to breeding sites throughout the valleys and foothills of cismontane California and southern Oregon.

DeHaven et al. (1975a, 1975b) evaluated Tricolored Blackbird philopatry. Unless Tricolored Blackbirds are regionally philopatric, local and regional surveys cannot track changes in abundance. Of 33 Tricolored Blackbirds banded as nestlings and recovered later at breeding colo-

nies, 13 were found within 10 miles (16 km) of the banding site. The rest were recovered elsewhere, nesting up to 225 km from their hatching site (DeHaven et al. 1975b). It thus appeared that some Tricolored Blackbirds were philopatric but most were not. DeHaven et al. (1975b) did not consider the possibility of a philopatric circuit.

METHODS

Major geographic regions reported here are identified in Figure 1. Breeding colonies were identified throughout the Central Valley during the four years of this study. The search was initially directed by Beedy et al.'s (1991) summary of all nesting records.

In 1994, a two-day survey of Tricolored Blackbirds was sponsored by the National Audubon Society and the California Department of Fish and Game (NAS/CF&G Survey). To limit errors in estimation based upon movement of birds and possible duplicate counts of the same individuals, the estimate focused on the interval

22–24 April. Participants estimated both numbers of birds at colonies and flocks not associated with colonies. In this summation of these data I have included Tricolored Blackbirds settled at colonies after April 23, whether or not colonies were observed then. Later observations add to completeness because the timing of nests within colonies can be determined and the schedule of earlier activity inferred. These inferences require correction for the proportion of nests active when the colony was observed. For example, a colony where adults were feeding nestlings on 1 May must have been present on 23 April. However, the number of birds in such cases was assumed to be only at least the number of nests active and feeding nestlings as of the date of observation.

Additional colonies were located by driving roads throughout the Central Valley and surrounding foothills and investigating all Tricolored Blackbird activity during the breeding season. In addition, collaborators throughout the geographic distribution of this species reported their observations. National Wildlife Refuge (NWR) biologists helped by providing continuity of coverage at their respective locations throughout most of the length of the Central Valley. I was able to simultaneously monitor Tricolored Blackbird activity at and in the vicinity of Sacramento, Delevan and Colusa NWRs in the Sacramento Valley, and San Luis and Kern NWRs and Mendota State Wildlife Refuge in the San Joaquin Valley. Owners of private properties contacted in 1992 and 1993 also reported Tricolored Blackbird activity at colonies in 1994 and 1997. This network produced an increasingly complete seasonal record of distribution, abundance, and schedule during successive years. In all years of this study Cook (1996) independently surveyed Tricolored Blackbirds in Sacramento County (C, Fig. 1), identifying the number and schedule of adults attending colonies there.

Data and analysis here emphasize 1994 and 1997 because procedures and information obtained earlier developed our ability to locate Tricolored Blackbird colonies in the Central Valley and to accurately estimate their stage of development. All surveys were conducted on 23 April (1994) and 26 April (1997) or on the preceding and following day. From 5% (1994) to 27% (1997) of the population that could be located were observed outside the Central Valley. After

identifying active colony sites in 1992 and 1993, I revisited all of these sites at least monthly throughout the 1994 breeding season. The effort in 1994 included full time observation in the field for 30 days before breeding was initiated and continued until no more active nests could be located. In 1997 most effort was allocated to determining the location and abundance of birds at the time of the April survey, and the San Joaquin Valley was more heavily sampled than the Sacramento Valley.

Colony size was estimated during the breeding season by entering active colonies to determine the stage of nests and nest densities and to map the area used for nesting. At large colonies (> 10,000 birds) I estimated number of nests based upon linear transects. Transects are an essential component of accurate numerical estimates of colonies because at certain colonies some, many, or all nests are lost to predators or for other reasons. Thus, there may be more nests of the season within a colony at the end of the season than there were females present at any time during that season. Breeding season transects facilitate estimating the number of failed and active nests and identify the proportion of nests currently attended by adults. Twenty to 50 nests were marked along transects, and several transects were established in some large colonies. These transects provided information about the timing of nesting activities within colonies. The area occupied by nests was mapped and dimensions were measured in the field with a tape or wheel.

After the breeding season ended I re-entered colony sites to sample the number of nests more extensively along transects across the full width of colonies, refining initial estimates of density and determining their spatial configuration. Attendance values cannot be determined from these post-season measures, but the dimensions of colonies and the number of nests present during the breeding season can be accurately defined without disturbing breeding birds.

Estimates of the number of breeding females per colony were based upon the number of nests, then adjusted to include males by multiplying by 1.5 (Lack and Emlen 1939, Orians 1961, Payne 1969) to reflect the reported degree of polygyny of this species, i.e., it is a convention.

To identify when the first eggs were laid at colonies, I subtracted 12 days from the date of first hatching. I assumed a schedule of three

days for nest building (Collier 1968), three or four days for egg laying, 11 days for incubation, and nine days pre fledging from the hatching of the first nestling until the first chick will jump from the nest when disturbed. The post fledging interval of about 15 days is spent in creches in or within a few km from colonies. A successful nesting cycle can take as little as 42 days. The stage of development of some colonies was determined by observing mud plastering of nests, which occurs about two days prior to laying of the first egg (Collier 1968). Flocks of fledglings appear 25 days after the first egg (Payne 1969).

At some colonies nest initiation continued for several weeks and at some locations there were additional pulses of nest establishment, indicating re-nesting or additional settlement. I identified late nesting cohorts at colonies as additional independent breeding efforts when nest initiation continued or commenced more than 10 days after initial egg laying or if there was evidence for a new pulse of nest establishment.

Colonies were considered separate when they were physically separated from other colonies and were initiated on an independent schedule. Himalaya blackberry (*Rubus procerus*) settlements were considered to be only one colony if adjacent but not contiguous patches of these brambles were the nesting substrate. At some locations I would otherwise have identified several colonies within sight of one another in a single pasture.

RESULTS

LOCATION OF COLONIES

Collaborators and I located 112 different colony sites between 1992 and 1994, including 75 colonies in 1994 (Hamilton et al. 1995; Fig. 1). There were an estimated 332,000 Tricolored Blackbirds observed or inferred to be at colonies in northern California on 23 April 1994. In addition, Survey personnel and I observed about 37,600 birds not then settled at colonies. From late March through 1 July 1994 and 1997, I estimated the size and timing of colony settlement throughout the Central Valley. Season-long observations in 1994 located over 600,000 breeding adults, far more than the number of birds estimated to be living at the start of the breeding season. The difference between the total seasonal breeding effort and the 23 April census could be the result of errors in estimation, failure to

locate birds at census time, second and additional breeding attempts, or some combination of these effects. Based upon measures of the number of nests at colonies after the breeding season, I estimated overall error of initial estimates of breeding densities at no more than 15%, the maximum error identified by any post-season nest count at any colony.

A large proportion of all observed Tricolored Blackbird nesting effort occurs in relatively few colonies. In 1992, 1993, and 1994, the 10 largest nesting colonies included 71%, 63%, and 60%, respectively, of all breeding birds located by all observers, the declining proportion reflecting increasingly complete coverage.

Second broods. Because the analysis was based upon the breeding effort for the entire breeding season, it was possible that I would observe second broods at some locations. I observed no more than an estimated 39,200 birds nesting as possible second successful broods at sites where they initially nested in 1994. Further nesting efforts following nest failure at additional sites may account for all of the nesting observed in the Sacramento Valley north of Sacramento County.

If the subsequent broods accounted for the difference between the estimate on 23 April 1994 and that observed for the season, the later nesting effort must have been by birds that had nested at other locations earlier in the season. To further evaluate this possibility I analyzed the schedule of colony establishment (Fig. 2, and below).

Movements from wintering areas. The Delta, an alluvial plain adjacent to Suisun Bay and the confluence of the Sacramento and San Joaquin Rivers, separates the western Sacramento Valley from the San Joaquin Valley (Fig. 1). This is the wintering area for tens of thousands of Tricolored Blackbirds. Field surveys showed that there were no Tricolored Blackbirds there on 1 April 1994 and 1997. Throughout the late winter (February, March) large flocks were found in the San Joaquin Valley, especially in Merced County.

Coinciding with departure of Tricolored Blackbirds from wintering areas in late March, there were substantial settlements of breeding colonies in the San Joaquin Valley. Association with cattle feedlots and dairies near sites where breeding colonies will be established follows the exodus from the wintering areas. There also are early movements from the Delta to Sacramento

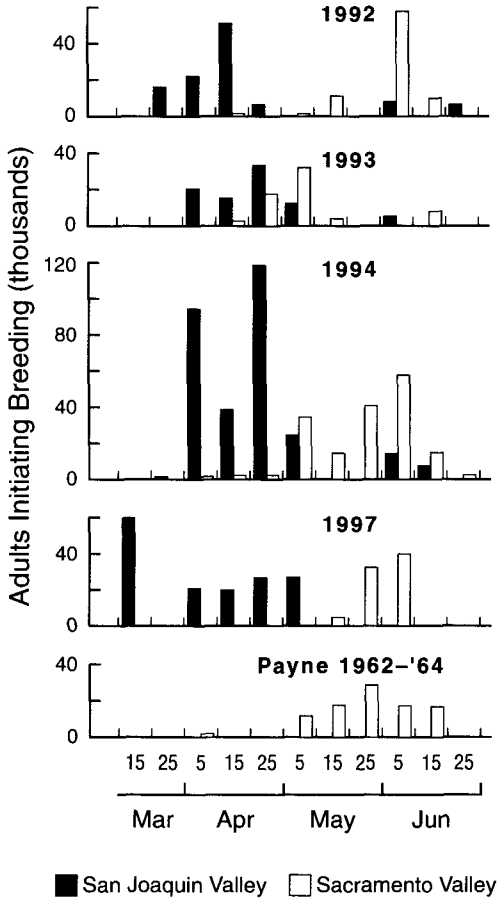


FIGURE 2. Schedule of colony establishment. Number of Tricolored Blackbirds initiating breeding by laying their first egg during 10-day intervals in the Sacramento Valley and the San Joaquin Valley—plus Sacramento County. Data from Payne (1969) are his estimated summed observations for the three years 1962–1964.

County. Initiation of breeding in the Sacramento County area was about 10 days later than in the San Joaquin Valley, but over a month before most breeding Tricolored Blackbirds arrive and settle in the northern Sacramento Valley. Substantial nesting colonies were not observed in most lowland areas of the Sacramento Valley north of Sacramento County until May. Colonies continued to be initiated there throughout the first half of June (Fig. 2).

Tricolored Blackbirds initiated breeding in the San Joaquin Valley as early as mid-March, and all birds are settled at some colony site by the end of April. Additional large settlements, such

as the late 15,000 bird cohort at a colony on San Luis NWR (first egg 9 May), may have been birds that lost nests to agricultural operations, including harvest of silage from barley fields. In 1994, silage fields contained 81% of an estimated 247,000 Tricolored Blackbirds observed nesting in the San Joaquin Valley in April. Both lodging and silage harvest resulted in the loss of about 40% of all nests in these agricultural habitats, a number that would have been 60% without protective intervention.

The Sacramento Valley also was covered county by county on 23 April 1994 by the NAS/CF&G Survey and by me in weeks before 1 May without locating any breeding Tricolored Blackbirds. In the Sacramento Valley in May and early June I visited known colony sites at 21-day intervals throughout the breeding season (1 April–1 July). There were four additional observers resident at different locations in the Sacramento Valley. Coverage there late in the season (late June, July) was hampered by access restrictions resulting in limited success in reaching colonies. Uncounted birds included two large colonies in Glenn County and two colonies in Yuba County, all active during June 1994. Thus the 170,200 birds observed in this late season coverage of the Sacramento Valley (Fig. 1) was a less complete sample of the breeding population than that of the San Joaquin Valley and in Sacramento County.

NONBREEDING BIRDS DURING THE BREEDING SEASON

Interpretations of the origin of birds arriving in the northern Sacramento Valley in late May and June depends upon whether there were substantial numbers of nonbreeding birds elsewhere before breeding birds arrived in the Sacramento Valley. The network of observers could locate less than 1,000 birds not associated with colonies during May 1994, except for briefly occupied dispersal centers, resting places from which foraging flights move radially to and fro, and all-male foraging flocks near colonies under incubation. Throughout incubation only females are present at colonies during the day. Males return late in the afternoon. Male attendance picks up at colonies after hatching when they participate in provisioning chicks.

Nonbreeders unattached to colonies. On 22 April 1994, I found one 10,000 bird mixed-sex flock of Tricolored Blackbirds foraging on rip-

ening barley heads in the San Joaquin Valley (Kings County). They were moving to and from a nonbreeding dispersal center. A 15,000 bird assemblage was observed dispersing from a base in Himalaya blackberries on the Arena Plains near Los Banos (Merced County, San Joaquin Valley) on 22 April. A small colony of about 600 birds subsequently nested there. At that time the colony at San Luis NWR, 10.2 km away, contained about 50,000 birds and was expanding steadily to reach its greatest estimated size of 105,000 birds early in May. The survey located in addition about 9,500 birds that could not be assigned to breeding colonies on 23 April. By 1 May these nonbreeding flocks were gone and I could locate no birds except those in or near colonies.

Nonbreeding birds associated with colonies. Most nonbreeding birds during the breeding season are closely associated with breeding colonies. In all four years of this study I observed some sites where males settled, sang, and displayed, but attracted only a few females or none at all. During settlement, many colonies include thousands of peripheral males that do not attract females and who abandon their territories after egg laying is completed.

At the San Luis colony (Merced County, San Joaquin Valley) about 20,000 mixed-sex nonbreeding individuals were associated with the colony following the loss to lodging of 37% of the silage substrate of 44,000 nests. In the following two weeks these nonbreeding birds disappeared and an additional nesting effort of about 20,000 birds at that colony developed, perhaps returning to breeding status birds that had lost nests to blowdown. These birds were distinguished from previous settlers by the ongoing mapping effort, which allowed me to closely estimate the number of nests added at that time.

Individuals more commonly abandon the vicinity of colonies after nest losses so there are sometimes only a few individuals commuting to foraging areas to provision the remaining nestlings at colonies where tens of thousands of birds built nests and laid eggs. I observed no desertion of colonies even following nearly complete loss of nests to predators.

Transient nonbreeders. There were occasional ($n = 9$) small nonbreeding flocks of < 100 birds in the Sacramento Valley rice districts in May 1994, prior to colony settlement there. Arrival

of large settlements in a matter of a few days was thus surprising and incompatible with ongoing observations of local abundance. Birds arriving at colonies in Colusa and Glenn Counties were associated with nonbreeding aggregations immediately preceding settlement of breeding colonies. These settlements function as if they were colonies in the sense that flocks of birds used the site as a central place during the day, with foraging flocks dispersing from and returning to them. The breeding birds colonizing cat-tails at a quarry in Glenn County first arrived from the south in a steady procession on 8 June 1994. Males preceded females in the forenoon and were followed by females that afternoon. Male display and female nest building were underway by nightfall. The source of these birds may have been the failing nesting colonies at the Capitol Outing Club, 36.9 km to the SE in Colusa County, where predation completely eliminated the reproductive effort of 60,000 adult Tricolored Blackbirds at two colonies between 30 May and 17 June.

DISCUSSION

INITIAL BREEDING

There is an initial breeding effort beginning from mid-March through early April throughout the California distribution of Tricolored Blackbirds. Early April breeding in some years includes small colonies to the north, both in the Sacramento Valley and in lower elevation montane marshes (Fig. 2). Colonies in April were initiated throughout the month. The bulk of the April breeding effort was in the San Joaquin Valley and in Sacramento County. About 50 days after the initial settlement of colonies in the San Joaquin Valley, a new wave of initial settlements occurred, mostly in the Sacramento Valley (Fig. 2).

The 170,200 birds observed arriving to begin nesting in the Sacramento Valley in May and June 1994 and influxes in other years (Fig. 2) of this study may be individuals which had previously made nesting attempts in the San Joaquin Valley or in Sacramento County.

Renesting. Birds initiating nesting at a site less than 45 days after initial egg laying may have been producing second broods following failure of their initial nests at the same site or at some other site. A nesting effort more than 50 days after initial nesting could be renesting by

individuals that already had nested successfully that year.

Many nesting attempts fail because of predation, cold or rainy weather, or as a result of agricultural operations, especially various forms of haying. These activities produce potential recruits for additional nesting efforts. Payne (1969) found a female Tricolored Blackbird laying again 10 days after losing a nest with eggs. In this case the second nest was a short distance away, but Payne's observation demonstrates the potential for prompt renesting at a second location. Because nests at some colonies fail at a high rate, any bird observed initiating nesting after 15 April could be an individual which had lost a nest at that site or elsewhere. A thorough canvas of colonies including the entire breeding season may thus identify far more individuals initiating nesting than the number of adults actually composing the population.

ITINERANT BREEDING

At the end of an intensive five-year study (1931–1936), Neff (1937) concluded that the Tricolored Blackbird is "... sheerly and illogically erratic in its seasonal movements and activities." DeHaven et al. (1975b) reported Tricolored Blackbirds to be nomadic and erratic in their breeding. Results of this study identify one basis for those perceptions. Transects, even as long as 100 km, may yield results leading to misinterpretation of trends in the overall abundance of this species if they are done when the population is elsewhere. This was the case for a part of the geographic area covered by the annual surveys. In late April there were virtually no breeding birds in the Sacramento Valley north of Sacramento.

In this study nonbreeding Tricolored Blackbirds were not seen during the breeding season except at colonies and their vicinity or at dispersal centers. I conclude that later settling individuals had previously nested in the San Joaquin Valley or in the Sacramento County area. The evidence for this conclusion is: (1) The wintering quarters in the Delta and along the coast were largely vacated by 1 April; (2) Few (about 37,000) birds could be found on 23 April 1994, except those associated with colonies; (3) In 1992 and 1994 large numbers of breeding birds initiated nesting in the Sacramento Valley during May and June (Fig. 2), but not in 1993 (33,000). The Sacramento Valley population observed in

1994 cannot be derived demographically from reproduction by and survival of birds present there in 1993; (4) The timing of breeding of the birds observed in the Sacramento Valley followed by approximately 50 days the breeding effort in the San Joaquin Valley and Sacramento County.

HISTORICAL COMPARISONS

Has the pattern of San Joaquin Valley to Sacramento Valley breeding season movements reported here been the same during the past century? Reviewing observations of Tricolored Blackbirds by region and schedule based upon all available records provides scant additional evidence for evaluation of this possibility. Neither Neff (1942) nor DeHaven et al. (1975b) assessed movements of adults during the breeding season because their analyses were based upon recoveries of birds banded as nestlings or trapped outside the breeding season. Nevertheless, Neff (1937) had the impression that Tricolored Blackbird "colonies nesting early in the season may subsequently change their habitat, and some of them may nest again at different localities." Thus, while I identified the possibility of itinerant breeding by Tricolored Blackbirds in 1992 and developed additional pertinent evidence in 1993, 1994, and 1997, Neff inferred the concept without naming it in the 1930s.

Neff's (1937) geographic coverage differed from year to year, and reevaluation of his observations neither supports nor rejects the idea of regional within breeding-season movements. He found large numbers of birds in Glenn County and elsewhere in the Sacramento Valley (Table 1) and relatively few Tricolored Blackbirds in the San Joaquin Valley. However, he did not initiate searches for breeding birds until May in most years of his study, and by mid-May most of the nesting activity I observed in the San Joaquin Valley was completed. Orians (1961) and Payne (1969) noted that rice country (Sacramento Valley) breeding colonies nested later than those in the interior Coast Range foothills to the Sacramento Valley, but they did not comment upon the source of the later nesting birds. The numbers they report for the respective areas show that the foothill birds observed cannot have been the principal source of the rice country birds. DeHaven et al. (1975a, 1975b) made no effort to canvas distribution throughout the breeding season. Indeed, they found far fewer

TABLE 1. Overall abundance of Tricolored Blackbirds for the years 1932–1936 (Neff 1937), 1968–1972 (DeHaven et al. 1975a), 1959 and 1960 (Orians 1961), 1992–1994 and 1997 (this study) by California county. The accounting method used here, highest count for any year, overrepresents abundance in those studies including more than one year because it takes the highest of the several annual estimates during each study. Counts also are not directly comparable because effort to locate colonies and the number of years was unequal in the several studies.

	Number of birds					
	1931–1936	1959–1961	1968–1972	1992–1994 Renests excluded	1992–1994 ^a Renests included	1997
San Joaquin Valley						
Fresno	150	—	0	20,200	20,200	2,550
Kern	3,000	—	3,000	71,200	72,325	17,000
Kings	3,000	—	25,000	64,000	64,000	33,000
Merced	87,000	—	26,000	104,700	129,200	13,000
San Joaquin	5,050	—	5,050	14,500	14,500	11,900
Stanislaus	18,750	—	25,300	7,075	7,075	150
Tulare	3,000	—	1,500	50,000	50,000	55,500
Total	119,950	—	85,850	331,675	357,300	133,100
Sacramento Valley						
Colusa	55,500	165,000	57,000	106,825	106,825	—
Glenn	423,000	—	18,500	83,000	83,300	—
Yuba	169,500	87,725	5,250	13,500	13,500	—
Butte	159,000	52,500	25,000	6,500	6,500	—
Yolo	57,000	105,000	31,000	1,775	1,775	—
Total	864,000	410,225	136,750	211,600	211,900	—
Sacramento County	181,500	—	50,915	89,415	111,500	31,350
Grand total	1,165,455	—	273,515	632,700	680,700 ¹	—

^a These numbers include possible reneesting which would not have been included in Neff's survey and possibly not in DeHaven's because they did not revisit and recount colonies throughout the season.

birds in the San Joaquin Valley than are reported in this study (Table 1).

It is not possible retrospectively to determine the extent to which the differences between the results obtained by these investigators and those reported here are due to observation method or are actual differences in patterns of movement. Although differences in search effort preclude close comparisons of trends in abundance, data here suggest that the intensity of the early season breeding effort may be a recent development. The erratic occurrence of Tricolored Blackbirds in the Sacramento Valley may be the consequence of their attraction to favorable breeding conditions associated with irrigation agriculture in the San Joaquin Valley. There were relatively few ($n = 20,410$) Tricolored Blackbirds in the Sacramento Valley in 1993 (Fig. 2) in spite of a search equal to that of 1992, 1994, and 1997. If breeding at these alternative locations is interdependent and development of suitable conditions in the San Joaquin Valley is delayed, the breeding effort in the San Joaquin Valley could delay or eliminate the breeding effort in the Sac-

ramento Valley. The picture suggested here of Sacramento Valley Tricolored Blackbird breeding is one of a facultative breeding assembly by birds that were both successful and unsuccessful in their earlier nesting efforts elsewhere, especially in the San Joaquin Valley and in Sacramento County.

The entire discussion begs the question of the causes of the ending of the breeding season. Along the Marin coast, August and September breeding often occurs (R. Stallcup, pers. comm.). The issue of fall breeding (Orians 1961, Payne 1969) is not considered here because neither any collaborators nor I observed any fall breeding in the Central Valley. In 1994 the breeding schedule extended from 1 April through 10 June for nest initiation and to 30 July for completion of the breeding cycle. In 1997 egg laying was initiated on 18 March in Tulare County. First eggs were laid as late as 3 July in Yolo County. Any nest in 1994 failing after 3 June ended the spring breeding season for the parents that year. In 1994 only 121,900 birds, 115,400 of them in the Central Valley and 35%

of the estimated population, were known to have initiated breeding by 16 April. An additional 15,000 birds per day, or about 50% of the estimated total population, initiated breeding somewhere during the next 10 days, so that most birds had an opportunity to nest again in the same place or elsewhere after completing a successful nesting effort. The opportunity to nest successfully twice and to have time to reinitiate nesting after loss of nests seems to be an essential feature of the Tricolored Blackbird reproductive strategy.

Local fluctuations in the abundance of Tricolored Blackbirds have been interpreted as responses to local insect abundance (Orians 1961, Payne 1969). Another possibility is that variable local abundance between years is the result of itinerant breeding movements during the breeding season after predators, agricultural operations, and adverse weather destroyed colonies. Flocks may seek suitable habitats at new locations after successfully completing nesting or failed attempts to do so.

One implication of Tricolored Blackbird itinerant breeding is that the low reproductive success in some habitats does not necessarily make these habitats reproductive sinks. Seasonal reproductive success is the sum of all successes. At some threshold level, the metapopulation becomes sustainable, despite seemingly trivial additions from certain habitats, times, and places. Perhaps the Tricolored Blackbird reproductive strategy of colonial breeding depends upon itinerant breeding.

ACKNOWLEDGMENTS

Edward Beedy, Rhys Bowen, Gerald Collier, Liz Cook, Susan Harrison, and Steve Henderson commented on earlier versions of this paper. Over 100 collaborators made independent surveys of Tricolored Blackbirds. Without their participation the estimation of global abundance and distribution would not have been possible. Numerous collaborators provided access to their private property. California Department of Fish and Game and United States Fish and Wildlife personnel participated in the evaluation of the distribution and abundance of Tricolored Blackbirds, and their assistance, advice, and access are gratefully acknowledged. Bob Barnes, National Audubon Society, Edward Beedy, Lyann Comrack, and Kevin Hunting organized the statewide surveys. This project could not have proceeded without the help of Anne Forcella,

who gathered field data, prepared summaries, and edited drafts. I thank Rhys Bowen for field support and planning help. Liz Cook provided observations from Sacramento County. I am grateful to Mark Chichester for estimates of Kern County colonies. It is a pleasure to acknowledge the support of Tara Zimmerman, U.S. Fish and Wildlife Service.

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