California Fish and Game 102(4):162-174; 2016

Breeding chronology, movements, and life history observations of tricolored blackbirds in the California Central Coast

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The tricolored blackbird (*Agelaius tricolor,* hereafter, tricolor) has experienced population declines and is currently under review for listing under both the California and Federal endangered species acts. Tricolors form the largest breeding colonies of any extant North American land bird, and are mostly found within the California Central Valley. However, smaller numbers of tricolors breed in other parts of lowland California, including the California Central Coast where the species is little-studied. From 2012 to 2014, we studied radio-tagged tricolors at four breeding colonies in Monterey County. The relative cover of the tricolors' primary grassland foraging habitat within 5 km of colony sites was lower than reported elsewhere. Birds arrived at colony sites from early-April to mid-May and remained up to 90 days. Nest-building occurred between 5 April and 18 June, with asynchronous nest-building at individual colonies occurring over periods up to 35 days. The largest colonies each year ranged from 600 to 800 birds. Twenty-five percent of radio-tagged birds moved between the study colonies during the breeding season, suggesting itinerant breeding. After breeding, 15% of tagged birds were observed near colony sites while 21% dispersed up to 37 km north and northeast towards known over-wintering areas (northern San Joaquin Valley, San Francisco Bay-Delta, and coastal Marin County). We also recorded, apparently for the first time, 1) arboreal foraging in oak woodlands, 2) use of lichen (*Ramalina* or *Usnea* spp.) as nest material, and 3) likely predation by long-tailed weasels (*Mustela frenata*). Given the observed variability in nesting chronology, our findings suggest that surveys of prospective breeding colonies should occur throughout the entire breeding season to accurately assess presence

or absence of nesting tricolors. Additionally, inter-colony movements of tricolors suggest that continued use of any one location may depend upon the suitability and productivity of nearby colonies. Management regimes for the species must therefore ensure cooperation among multiple land-management entities controlling nearby tricolor habitats.

Key words: tricolored blackbird, *Agelaius tricolor*, California Central Coast, itinerant breeding, radio-telemetry, arboreal foraging

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The tricolored blackbird (*Agelaius tricolor*, hereafter, tricolor) is a medium sized passerine that forms the largest breeding colonies of any extant land bird in North America (Neff 1937; Cook and Toft 2005). It occurs in its greatest abundance in California's Central Valley and surrounding foothills, where the largest breeding colonies occur and where the species has been most intensively studied. Smaller breeding colonies occur in the coastal and Sierra Nevada foothills of southern and central California and very small numbers of breeding birds occur in Oregon, Washington, Nevada, and Baja California (Neff 1937, Cook and Toft 2005, Meese et al. 2014).

A century ago the species was considered one of the most abundant birds in California; however, the tricolor has experienced a dramatic population decline from an extrapolated 2-3 million birds in the 1930s (extrapolated from Neff 1937) to about 145,000 birds in 2014 (Meese et al. 2015). This decline led to a 6-month emergency listing of the species as endangered under the California Endangered Species Act in December 2014 (State of California 2014) and the species is currently in formal status review for listing under both the Federal and California Endangered Species Acts (USFWS 2015; State of California 2015).

The tricolors' decline appears to be tied to loss of food supplies and habitat. Tricolors require insect prey during the breeding season for egg formation and nestling development (Payne 1969), and breeding colonies are often in proximity to insect-rich grasslands or rangelands, the bird's primary foraging habitat. Loss of grassland foraging habitat has been implicated in the decline of the species (DeHaven et al. 1975; Beedy and Hamilton 1997) and lack of insect prey has been implicated with recent chronic poor reproductive success (Meese 2013). Beedy et al. (1991) reported wetland loss and fragmentation as a principal reason for the tricolors' decline. Tricolors historically nested in largest numbers in cattail (*Typha spp.*) or bulrush (*Schoenoplectus spp.*) marshes in the California Central Valley. However, this area experienced wetland losses >90% between 1850 and 1980 (Frayer et al. 1989) and today the largest colonies typically appear in non-native upland substrates, primarily Himalayan blackberry (*Rubus armeniacus*), milk thistle (*Silybum marianum*), and cultivated triticale fields near dairies (Meese et al. 2014).

Triennial statewide tricolor breeding surveys, conducted since 1994, are the primary means for monitoring this species' numbers. The three most recent surveys indicated that the breeding population in the Central Coast declined by 91% between 2008 and 2014, the largest proportional decline in the state during that period; over half the nesting birds counted in this seven-county region in 2014 were in Monterey County (Meese 2014). Besides the triennial statewide breeding surveys and a breeding bird atlas of Monterey County (Roberson and Tenney 1993), no other tricolor research has been reported for the Central Coast region.

To improve understanding of the species' life history and population decline, we undertook breeding and post-breeding season studies in the Central Coast region during 2012-2014. Our objectives were to document numbers of breeding birds, habitat use, breeding chronology, and movements.

Materials and methods

Study areas.—We studied four tricolor breeding colonies in Monterey County, California, April to July each year from 2012 to 2014 (Figure 1). Two colonies, Cienega Pond (36°26'27.20"N, 121°47'35.89"W) and Ohlone Pond (36°28'9.02"N, 121°47'37.64"W), were at 446 m and 435 m elevation, respectively, within the Santa Lucia Mountains near the town of Carmel Valley. These two colonies occur on the Santa Lucia Preserve (SLP), a 20,000 acre private residential development containing an 18,000 acre protected natural area managed by the Santa Lucia Conservancy, a non-profit land trust. The Cienega Pond breeding substrate was primarily bulrush (*Schoenoplectus spp*.) with smaller amounts of cattail (*Typha spp.*), which together covered about 30% of the 10,277 m^2 pond. The Ohlone Pond breeding substrate was dominated by bulrush, which covered about 70% of the 2,503 m^2 pond.

Two additional colonies, Fort Ord Nettle Patch (36°36'3.96"N, 121°43'3.00"W) and Laguna Seca Pond (36°34'17.04"N, 121°46'4.80"W) were located about 20 km north of the SLP colonies, in the Sierra de Salinas range, near the edge of the Salinas Valley at 129 m and 116 m elevation, respectively. The Fort Ord Nettle Patch was located within the Fort Ord National Monument managed by the Bureau of Land Management and the Laguna Seca Pond was located within the Laguna Seca Recreation Area managed by the Monterey County Parks Department. The Fort Ord Nettle Patch breeding substrate was stinging nettle (*Urtica dioica)*, which covered 310 m^2, and the Laguna Seca Pond breeding substrate was a mix of cattail and bulrush, which covered about 73% of the 11,488 m^2 pond.

The four colonies ranged between 9 km and 12 km from the Pacific Ocean and the maximum inter-colony distance was 20 km. All colonies were adjacent to grasslands and all except Fort Ord Nettle Patch were within 200 m of an equestrian facility. Cienega Pond and Laguna Seca Pond were also adjacent to golf courses. In 2014, these four colonies contained an estimated 25% of the birds found in the entire seven-county Central Coast region (Alameda, Santa Clara, San Mateo, Santa Cruz, Monterey, San Luis Obispo and Santa Barbara Counties) according to triennial statewide survey data (Meese 2014).

Habitat characterization.—Tricolors most often forage for insect prey within 5 km of colonies (Orians 1961, Beedy and Hamilton 1997, Airola et al. 2015). To characterize available upland foraging habitats within 5 km, we utilized the California Wildlife Habitat Relationships (WHR) System classification (Meyer and Laudenslayer 1988) available in the 2013 Existing Vegetation - CALVEG polygon GIS data for Zone 6, the Central Coast. We aggregated the WHR vegetation classes into groupings of similar physiognomic structure, with the assumption birds in different areas would utilize the groupings similarly. These groupings were: forest (montane hardwood, montane hardwood-conifer, redwood), grassland (annual grassland), shrubland (chamise-redshank chaparral, coastal scrub, mixed chaparral), other (barren, lacustrine), urban, and woodland (blue oak woodland, coastal oak woodland, valley oak woodland).

Breeding chronology and abundance.—We monitored tricolor nesting activity and abundance at the breeding colonies beginning the first 10 days of April each year, from the start of nesting until breeding activity ceased and most birds departed from

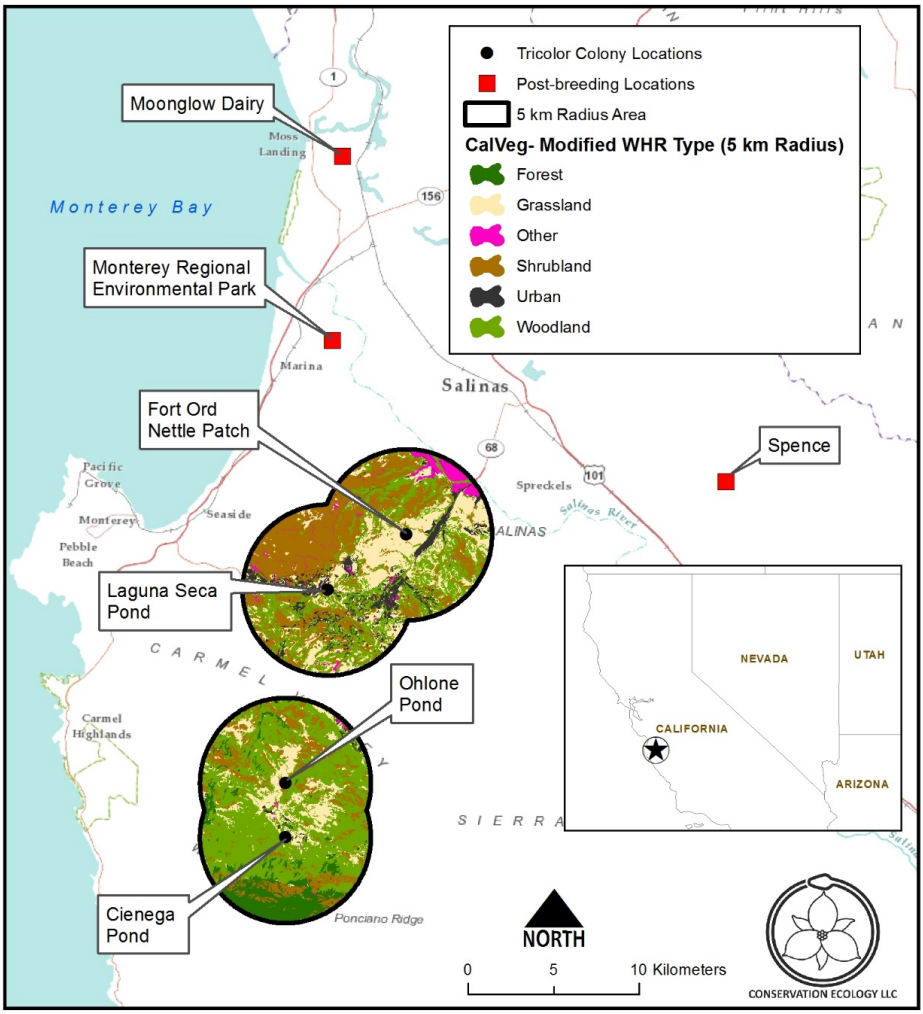

Figure 1.—Locations of tricolored blackbird breeding colonies, surrounding habitat types, and post-breeding locations. Monterey County, California.

colonies. For each 10-day interval, colonies were visited one to seven times. Observations at nesting substrates were conducted for at least 20 mins from a distance of 5 m to 15 m away. The birds did not flush or show defensive or nervous behavior in response to our presence. Tricolors carrying nesting material (and partially constructed nests) were indicative of active nest construction. Colony abundance was estimated during each visit as the sum of all birds visible on nesting substrate, birds flying to and from the colony, and birds foraging in nearby areas visible from the colony. On most occasions, birds were counted by a single observer. Counts by multiple observers were averaged.

Movements.—We used radio-telemetry to document tricolor breeding and post-breeding movements. Tricolors were captured one week after breeding began in the study area, using walk-in traps baited with cracked corn (Meese and Simmons 2010). Advanced Telemetry Systems model A1030 transmitters weighing 1.8 g (about 3% and 5% of mass of

males and females, respectively) were attached to birds using the backpack method described in Rappole and Tipton (1991). Over the three year study, transmitters were attached to a total of 48 birds: 22 (46%) males and 26 (54%) females (5 males and 5 females in 2012; 8 males and 10 females in 2013; and 9 males and 11 females in 2014). Estimated battery life of transmitters was 90 days and the unobstructed, straight-line detection distance was about 2 km. Captured birds were also banded with aluminum USGS bands on the left leg and Darvic color bands on both legs. All tricolor radio-tagging and banding occurred at Ohlone Pond and birds were banded and released within 1 hour of their capture.

During monitoring visits to colony sites, radio-tag detection was determined by scanning transmitter frequencies using the Advanced Telemetry Systems model R410 receiver and a 3-element Yagi antenna. As the breeding season progressed each year and fewer tagged birds were detected at colonies, we began conducting broader vehicle-based searches within the Santa Lucia Preserve and western Monterey County. These broader searches involved scanning tag frequencies using an omnidirectional antenna mounted to the roof of a moving vehicle, then stopping and searching specific areas of interest with the unidirectional Yagi antenna. Searches targeted grasslands, vegetated ponds, ranches, equestrian facilities, and dairies in the vicinity of: California State Route 1, between Andrew Molera State Park and the town of Moss Landing (a driving distance of about 70 km); Carmel Valley Road, between the towns of Carmel-by-the-Sea and Carmel Valley (about 20km); and California State Route 68, in the vicinity of Toro County Park, Fort Ord National Monument, and Laguna Seca Recreational Area (about 8 km). These broader searches generally occurred at least once per 10-day interval. On 22 June 2013 we searched for radio-tagged birds by airplane, scanning colony sites (and vicinities), the Salinas Valley southeast to King City, and coastal areas between Watsonville and Monterey (about 2,000 km^2). Transmitter locations detected from the air were later (within 2 days) searched from the ground, using the vehicle-based methods. For temporal analyses of observations, we chose one date representing the transition from breeding to post-breeding, generally reflecting 1) the end of nest building activity, 2) substantially declining numbers of birds at colony sites, and 3) movements of tagged birds away from colony sites (>5 km).

Results

Foraging habitat.—For the four colony sites combined, the three most dominant habitat types within 5 km were woodland (43%), shrubland (25%), and grassland (21%); forest, urban, and other habitat types made up the remainder (<11% combined).

Breeding chronology and abundance.—Annual first-arrivals of birds to colony sites occurred between early-April and mid-May, and colonies were occupied for <30 days to 90 days (Figure 2). Nest-building occurred between 5 April to 18 June at four sites in 2012, but at only two sites in 2013 and 2014 (Table 1). Ohlone Pond was the only site with nest building observed each year. In 2012 and 2013, nest building was observed at active colonies over periods of 5 to 35 days.

The largest colonies each year contained: 600 birds at Laguna Seca Pond in 2012, 800 birds at Ohlone in 2013, and 600 birds at Laguna Seca in 2014 (Figure 2). For all colonies combined, the highest number of birds during a single 10-day interval each year was: 910 birds during late-May 2012, 827 birds during mid-Apr 2013, and 600 birds during mid-May 2014.

Breeding and post-breeding movements.—Over the three years, the latest nest-building activity was on 18 June, the earliest pronounced movements (5 km or

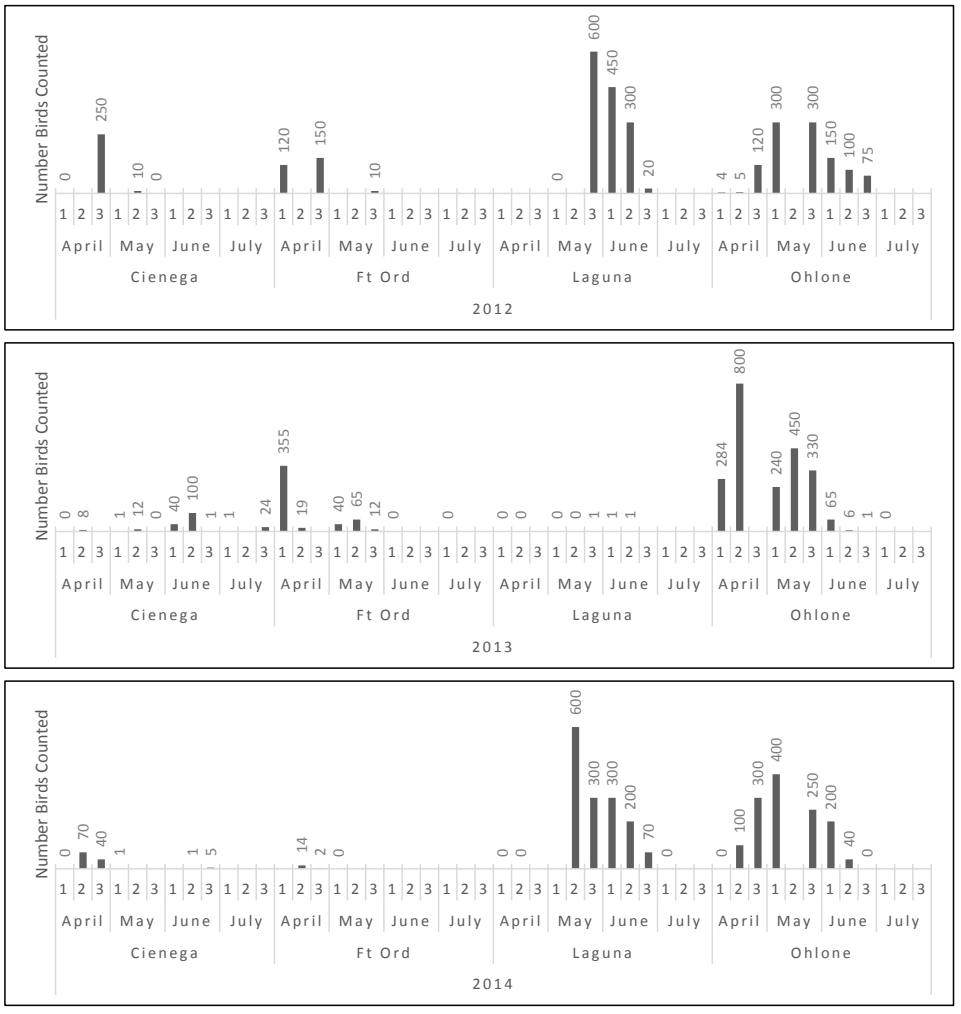

Figure 2.—Maximum number of tricolored blackbirds counted during 10-day intervals at four breeding colony locations, 2012 - 2014. A count of zero indicates the site was surveyed, but no birds were observed.

more) of tagged birds away from colonies was 22 June, and the last 10-day interval of June was when most colonies were completely abandoned. Thus, we considered movements of tagged birds occurring on or before June 19 to represent the breeding season and movements on or after 20 June to represent the post-breeding season.

Twelve birds (25% of total tagged) moved among colony sites during the breeding season (Table 2). These birds moved from Ohlone Pond to Cienega Pond (3 km), or to Laguna Seca Pond (11 km). Three of the 12 returned to Ohlone Pond during the same breeding season. Proportionally more males (32%) than females (19%) made inter-colonial movements.

Post-breeding locations of 17 radio-tagged birds were recorded between 22 June and 30 July (Table 3). Seven birds (15% of total tagged) were only observed at or near the breeding colonies. Six of these birds were observed within the Santa

Table 1.—Nest-building dates at four tricolored blackbird colonies.

	Tricolor Study Colonies			
Year	Cienega Pond	Ft Ord Nettle Patch	Laguna Seca Pond	Ohlone Pond
2012	9 April	9 April	31 May	2 May
	24 April	24 April	2 June	10 May
	30 April		18 June	14 May
	7 May			17 May
				18 May
2013	5 April			10 April
	10 April			19 April
				13 May
				15 May
2014			12 May	18 April

Lucia Preserve, within 3 km of the Ohlone Pond capture site, and were located at Ohlone Pond, Cienega Pond, in and around the grazed pastures of nearby equestrian facilities, and in surrounding annual grasslands. Another bird remained at the Laguna Seca Pond where it was previously observed during that year's breeding season.

Ten (21% of total) radio-tagged birds dispersed from breeding sites and were found at three locations to the north and northeast (Figure 1, Table 3). Six of these birds were observed near the Monterey Regional Waste Management District (MRWMD) wastewater treatment plant (36°42'8.63"N, 121°46'5.96"W), in grazed pasture and grasslands, 26 km North of Ohlone Pond. Two birds were located at the Moonglow Dairy adjacent to Moro Cojo Slough (36°47'51.91"N, 121°45'49.59"W), near the town of Moss Landing, in grazed pasture, 37 km north of Ohlone Pond (including one bird previously observed at the MRWMD site during the same year). Two other birds were located outside the town of Spence, CA (36°37'53.64"N, 121°30'33.06"W) along the base of the eastern foothills of the Salinas Valley, among agricultural fields and grazed pasture, 31 km northeast of Ohlone Pond.

Additional life-history observations.—On four occasions during late-April to early-May of 2012, one occasion in late-July 2013, and three occasions mid-April to early-May 2014, we observed tricolor flocks of 12 to 100 birds foraging in coast live oak (*Quercus agrifolia*) and valley oak (*Quercus lobata*) trees within the Santa Lucia Preserve. Several of these flocks were mixed with red-winged blackbirds (*Agelaius phoeniceus*) and European starlings (*Sturnus vulgaris*). Additionally, during mid-April of 2012, about 20 tricolors were observed foraging in the crowns of coast live oak trees near the Fort Ord Nettle Patch (Don Roberson, Monterey Audubon Society, personal communication.). We believe this arboreal foraging behavior observed in 2012 represent birds feeding on California oakworm caterpillars (*Phryganidia californica*), a species known to fluctuate widely (Furniss and Carolin 1977) and which was relatively abundant that year (C. R. Wilson and R. J. Meese, personal observation.)

On one occasion in late-April 2012, about 30 tricolors were observed returning to Cienega Pond from the direction of an extensive woodland and forested area, many carrying nesting material consisting of lace or beard lichen (*Ramalina or Usnea* spp.). We believe this is the first reported use of lichens as nest materials by this species.

Finally, during early-May 2012, we observed a group of three juvenile long-tailed weasels (*Mustela frenata*) hunting on the ground within the Fort Ord Nettle Patch, while nesting tricolors were present. Although predation was not observed and the weasels were not observed climbing vegetation in the vicinity of nests, it appeared they were likely searching on the ground for nestlings or fledglings that had fallen from nests.

Table 2.—Locations of radio-tagged tricolored blackbirds that moved among breeding colonies during the breeding season. Individual birds are labeled M (male) or F (female) followed by capture sequence number. CP = Cienega Pond, LS = Laguna Seca Pond, OP = Ohlone Pond. No tagged birds were observed at the Fort Ord Nettle Patch.

	Individual Birds											
	2012					2013				2014		
Date	F01	F02	F03	M01	M05	F08	M10	M11	M13	F17	M14	M22
3 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
4 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
6 May	OP	OP	OP	OP	OP	-	-	-	-	-	-	-
7 May	OP	OP	OP	OP	OP	OP	OP	OP	OP	-	-	-
8 May	OP	OP	OP	OP	-	-	-	-	-	OP	OP	-
9 May	-	-	-	-	-	-	-	-	-	OP	OP	-
10 May	OP	OP	OP	OP	OP	OP	OP	OP	OP	-	-	-
12 May	-	-	-	-	-	-	-	-	-	OP	LS	-
13 May	-	-	-	-	-	OP	OP	CP	OP	-	-	-
14 May	OP	OP	OP	OP	-	-	-	-	-	OP	LS	-
15 May	OP	OP	OP	OP	-	OP	OP	CP	OP	-	-	-
16 May	OP	OP	OP	-	-	-	-	-	-	-	-	-
17 May	OP	OP	-	OP	-	-	-	-	-	-	-	-
18 May	OP	OP	-	OP	-	OP	OP	-	OP	-	-	-
20 May	-	-	-	-	-	OP	OP	OP	OP	OP	-	-
21 May	OP	OP	-	-	-	-	-	-	-	OP	-	OP
22 May	OP	OP	LS	LS	-	OP	OP	-	OP	OP	LS	CP
23 May	LS	-	LS	LS	-	-	-	-	-	OP	-	-
24 May	LS	OP	LS	-	LS	OP	OP	-	OP	-	-	-
26 May	-	LS	-	LS	-	-	-	-	-	-	-	-
27 May	-	-	-	-	-	-	-	-	-	OP	-	-
28 May	-	-	-	-	-	OP	OP	-	OP	OP	-	-
29 May	-	OP	-	-	-	-	-	-	-	OP	-	-
30 May	-	LS	LS	-	LS	OP	LS	-	OP	-	-	-
31 May	-	LS	LS	-	LS	-	-	-	-	-	-	-
1 June	-	OP	-	-	-	-	-	-	-	OP	-	OP
2 June	-	OP	LS	-	LS	-	-	-	-	OP	-	-
3 June	-	-	-	-	-	-	-	-	-	OP	-	-
4 June	-	-	-	-	-	CP	-	-	-	-	-	-
6 June	-	-	LS	-	-	-	-	-	-	OP	-	-
7 June	-	-	-	-	-	CP	-	-	-	-	-	-
8 June	-	-	-	-	LS	-	-	-	-	-	-	-
9 June	-	-	-	-	-	-	-	-	-	LS	-	-
11 June	-	-	-	-	-	CP	-	-	-	-	-	-
12 June	-	-	-	-	-	-	-	-	-	-	LS	-
14 June	-	-	-	-	-	CP	-	-	-	-	-	-
17 June	-	-	-	-	-	-	-	-	-	CP	-	-
18 June	-	-	-	-	-	CP	-	-	CP	-	LS	-
19 June	-	-	-	-	-	-	-	-	-	-	LS	-

Discussion

The four tricolor colonies studied here were adjacent to grasslands; however, the percent coverage of grasslands within a 5 km radius of each colony was lower than reported elsewhere. For example, in a recent study in the Sierra Nevada foothills, Airola et al. (2015) found tricolor colonies occurred in areas containing 55% grassland and 21% combined woodland-forest-shrub cover within a 5 km radius. Our coastal study site exhibited 21% grasslands and 68% combined woodland-forest-shrub cover within a 5 km radius. Lack of grassland

Table 3.—Post-breeding locations of radio-tagged tricolored blackbirds. Individual birds are labeled M (male) or F (female) followed by capture sequence number. LS = Laguna Seca Pond, MOON = Moonglow Dairy/ Moro Cojo Slough, MWMD = Monterey Regional Waste Management District, SLP = Santa Lucia Preserve, SPEN = Proximate to the town of Spence.

	Individual Birds																
	2012	2013												2014			
Date	F02	F04	F07	F08	F12	F13	M06	M07	M08	M10	M11	M12	M13	F17	F22	M14	M19
22 June	-	MWMD	SPEN	-	MWMD	-	-	SPEN	MWMD	MWMD	-	MWMD	-	-	-	-	-
23 June	-	MWMD	-	-	MWMD	-	-	-	MWMD	MWMD	-	MWMD	-	SLP	-	LS	-
25 June	-	MWMD	-	SLP	MWMD	-	SLP	-	MWMD	MWMD	SLP	MWMD	SLP	-	-	-	-
28 June	-	-	-	-	MWMD	-	-	-	MOON	MWMD	-	MWMD	-	-	-	-	-
30 June	-	-	-	-	-	-	-	-	-	-	-	-	-	-	SLP	-	-
1 July	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LS	-
2 July	MOON	-	-	SLP	-	-	SLP	-	-	-	SLP	-	-	-	-	-	-
3 July	-	-	-	-	MWMD	-	-	-	MWMD	MWMD	-	MWMD	-	-	-	-	-
7 July	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LS	-
8 July	-	-	-	-	MWMD	-	-	-	MOON	-	-	MWMD	-	-	-	-	MWMD
10 July	-	-	-	SLP	-	-	SLP	-	-	-	-	-	-	-	-	-	MWMD
14 July	-	-	-	-	-	-	SLP	-	-	-	-	-	-	-	-	-	-
22 July	-	-	-	-	-	-	-	-	MOON	MWMD	-	MWMD	-	-	-	-	-
23 July	-	-	-	SLP	-	-	SLP	-	-	-	-	-	-	-	-	-	-
28 July	-	-	-	SLP	-	-	SLP	-	-	-	-	-	-	-	-	-	-
29 July	-	-	-	-	-	MWMD	-	-	-	-	-	-	-	-	-	-	MWMD
30 July	MOON	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

cover near breeding colonies may result in reduced availability of required insect prey and smaller colonies, since insects preferred by foraging birds are more often found in grasslands (Payne 1969). Tricolors in our study appeared to offset reduced grassland foraging opportunities by foraging for larval insects in woodland habitats, and such arboreal insect-gathering has not, to our knowledge, been reported before. Also, the abundance and use of woodland habitat in our study may explain the opportunistic gathering of lichen as a nest material.

In Monterey County, tricolor nesting at most colonies is known to begin around mid-April, with an occasional colony starting as early as late-March (Roberson and Tenney 1993). However, we observed colonies forming as late as late-May, and nest-building continuing as late as 18 June. Additionally, there was variability in how long individual colonies were occupied, ranging from <30 to 90 days. This variability in colony initiation and duration has important implications for surveys meant to determine site occupancy, specifically that site surveys extending throughout the breeding season (late-March to late-June) are necessary to accurately assess the presence or absence of breeding tricolors in a particular area.

Tricolor reproductive success is known to be strongly positively-associated with insect abundance in surrounding foraging habitats (Meese 2013). Low rainfall has been implicated in low insect abundance (Orians 1961) and loss of suitable nesting substrate due to pond drying (Roberson and Tenney 1993; Meese 2014). During 2013 and 2014, Monterey County and much of California experienced extreme drought and water levels at our breeding pond locations were markedly lower than in 2012. Consequently, the maximum numbers of tricolors observed in 10-day periods each year, and number of observed nest-building events, declined over the three-year study. These observations are not unexpected, given the state's drought and overall downward population trend of tricolors indicated by the Tricolored Blackbird Statewide Surveys from 2008 to 2014 (Meese 2014).

At least 25% of radio-tagged birds in our study engaged in inter-colony movements during the breeding season. Although we did not confirm if these radio-tagged birds actually nested, their movements among colonies suggests itinerant breeding (i.e., breeding more than once per year in different locations) as described by Hamilton (1998). Based largely on banding studies, tricolors are known to be itinerant breeders in the Central Valley, first breeding at locations in the San Joaquin Valley and then moving north to new breeding locations within the Sacramento Valley, low Sierra foothills, and northeastern California (Hamilton 1998). Nevertheless, our study appears to be the first to: 1) use radio-telemetry to study movements of tricolors, 2) document apparent itinerant breeding movements outside of the Central Valley, and 3) document such movements over relatively short distances of 3 to 11 km. The selective advantages of such movements are unknown and require additional study, but perhaps some birds were unable to acquire sufficient resources at one colony site for the entire breeding season, or were prospecting among colonies to assess availability of nesting and foraging resources or access to mates. Whatever the motivation for the movements, itinerant breeding may be more common than previously reported. The availability of multiple proximate nesting locations may allow the species to compensate for early-season nesting failures and variation in habitat and forage conditions over time (Beedy and Hamilton 1997).

Some previous workers have reported tricolors as synchronous breeders, with most eggs in a colony being laid within one week (e.g., Orians 1961). However, five of eight colonies in our study had nest-building intervals >1 week (9 to 35 days). Our study colonies were thus frequently asynchronous and breeding occurred over extended periods. However, our study colonies had relatively small numbers of birds compared to colonies studied by others (e.g., Orians 1961, Payne 1969), and small colonies may simply facilitate gathering

finer details on the nesting cycle. We did not observe predation of either eggs or nestlings, thus we believe that most of the observed nest-building asynchrony was due to the periodic arrival of additional breeding birds from other locations, as the telemetry results suggest.

Tricolors are present in Monterey County year-round, and during fall and winter they form nomadic mixed-species foraging flocks near dairies, horse and cattle feedlots, and open grasslands (Roberson 2002). Unfortunately, due to the limited battery life of the transmitters used in our study, we were able to follow tagged birds only briefly at the beginning of the post-breeding season. During this time, the birds exhibited a variety of post-breeding movements, with at least 13% remaining at the Santa Lucia Preserve and foraging in horse pens, pastures, and lawns associated with equestrian facilities, and with nighttime roosting in the nearby emergent-marsh ponds on the property. The remainder of post-breeding observations (23% of total tagged) were at northerly points within Monterey County, in rangelands, agricultural fields, or near dairies. Two tagged birds were found at the Moonglow Dairy, which is a well- known tricolor enclave during fall and winter months (Roberson and Tenney 1993; Roberson 2002). We suspect that some of the tagged birds eventually moved farther north and northeast to known wintering areas in the northern San Joaquin Valley and San Francisco Bay-Delta area (DeHaven et al. 1975), or coastal locations in Marin County (Meese et al 2014). Tricolors are also known to concentrate in rangelands along Highway 1 between Point Sur and Andrew Molera State Park during fall and winter months (Roberson 2002). The breeding colonies at the Santa Lucia Preserve are the closest known to this overwintering area, but none of our tagged birds were found along this section of Highway 1. Post-breeding movements and overwintering ecology of tricolors need further study before significant insights to aid in conservation of the species can be developed.

Our study shows that, at least in this part of the species' range, inter-colony synergism may also be integral to tricolor productivity. Therefore, management to maintain or enhance disparate nesting and foraging habitat is essential given the decline of tricolor populations and continued threats to the species (Meese and Beedy 2015). The breeding colony locations in our study area, including much of the surrounding existing and nascent foraging habitats, are currently managed by three different entities. Coordination and cooperation amongst these entities will be essential to slowing the rate of population decline of tricolors on the Central Coast.

Acknowledgments

We thank the following: M. Stake, B. Edwards, and C. Cumberworth for their assistance with fieldwork; K. Kyle for his advice regarding study design and assistance acquiring funding from the Audubon California Tricolored Blackbird Conservation Fund to purchase telemetry equipment; J. Cornelius for her advice regarding avian radio-telemetry techniques; the board and staff of the Santa Lucia Conservancy for general funding and logistical support; M. Dedon, M. Sutton, and Lighthawk for donating aircraft flight-time for aerial telemetry surveys; the residents of the Santa Lucia Preserve (particularly the Zulberti and Blatman families), Monterey County Park District, B. Delgado, and Fort Ord National Monument for their cooperation regarding access to study sites; and D. Roberson for contributing tricolor observations and insights.

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Submitted 31 August 2016
Accepted 14 November 2016
Associate Editor was N. Clipperton