Breeding Status of the Tricolored Blackbird in the Grassland-Dominated Region of the Sierra Nevada, California in 2016

Peer-Reviewed Paper

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ABSTRACT

We completed the third year of a study of the breeding biology of the Tricolored Blackbird (*Agelaius tricolor*) in grassland-dominated lands on the east side of the Central Valley and lower foothills of the western Sierra Nevada in 2016. We used geographic information system (GIS) analysis of land use coverages to identify 6,809 km^2 (2,629 mi^2) of suitable Tricolored Blackbird habitat in the study area and surveyed 36% of this area in 2016. We examined the effects of precipitation on nesting substrates, breeding bird abundance, and breeding success following return of rainfall to average levels following five years of severe drought. Because of the potential for multiple breeding attempts by individuals in 2016, we quantified regional breeding bird abundance as the number of "breeding attempts" (rather than breeding individuals). We documented a total 77,830 Tricolored Blackbird breeding attempts at 50 active colonies, an increase from surveys in 2014-2015 attributable to greater survey coverage and reoccupation of the southern foothill region. Incompleteness of surveys within suitable habitat resulting from access limitations suggested that the total number of 2016 breeding attempts in the foothills likely was higher than the number we detected. The

central foothills subregion supported the largest proportion of breeding attempts in the region (58%), but a substantial number also bred within the southern foothills (29%). An area of the southern foothills that had limited suitable breeding habitat and no breeding birds detected in 2015 supported 13,250 breeding attempts in 2016, indicating a reoccupation of this region. Most birds nested in non-native Himalayan blackberry (*Rubus armeniacus*) copses and emergent wetland vegetation in the northern and central foothill regions, but mainly used non-native annual milk thistle (*Silybum marianum*) in the southern foothills. The 2016 increase in breeders in the south was associated with a dramatic increase in milk thistle abundance, likely in response to increased annual rainfall following previous years' drought. All but one of 50 active colonies studied fledged young but several colonies appeared to suffer elevated rates of mortality during severe storms. The 2016 colony locations within areas studied over multiple years further demonstrated the low between-year site fidelity of the foothill population. Direct human disturbance of colonies and previously occupied nesting habitat was rare and did not appear to affect the nesting population. We stress the importance of the western Sierra foothill region and adjacent Central Valley grassland and irrigated pasture lands to Tricolored Blackbird conservation and recommend that county general plans and similar regulatory instruments identify and protect both nesting and foraging habitats. We also recommend developing additional, perennial habitats in the southern foothills to ensure the presence of suitable nesting substrates during future drought periods.

The Tricolored Blackbird (*Agelaius tricolor*) has experienced a long-term decline in California attributed primarily to habitat loss from expansion of orchards and vineyards, urban and suburban development, and destruction of breeding colonies during agricultural operations (Beedy and Hamilton 1999, Cook and Toft 2005; Meese 2014, 2015). These declines led to its advancement to candidate status under the California Endangered Species Act in January 2016 and to a formal status review under the Federal Endangered Species Act in September 2015.

Surveys in 2014 and 2015 described the breeding status and breeding habitats of the Tricolored Blackbird in the grassland-dominated area on the east side of the Central Valley and lower foothills of the western Sierra Nevada (hereafter "foothill grasslands") (Airola et al. 2015a, b). The 2015 survey documented 55,270 individuals nesting at 26 active colonies (Airola et al. 2015b) in a 9,223 km^2 study area, representing 38% of the 2014 statewide population estimate of 145,000 (Meese 2014). A less extensive survey in 2014 documented about 43,000 breeding individuals at 29 colonies in a 5,665 km^2 study area Airola et al. 2015a). A high proportion (98%) of the 55 active colonies monitored for reproduction during 2014 and 2015 successfully fledged young. Nesting in 2014-2015 occurred primarily in upland patches of

the non-native Himalayan blackberry (*Rubus armeniacus*) and to a lesser extent in ponds supporting cattail (*Typha latifolia*) and bulrush (also tule; *Schoenoplectus acutus* var. *occidentalis*). Nearly half of the 2014 foothill grassland nesting population bred in areas that were threatened by approved and requested plans for development and mining (Airola et al. 2015a).

Most of California and most of the breeding range of the Tricolored Blackbird experienced severe drought from 2012-2015. In 2014 and 2015, precipitation in the foothill study areas totaled 51% and 71% of the 20-year annual average, respectively (Airola et al. 2015b). It appeared, however, that drought conditions were not highly detrimental to the Tricolored Blackbird in the central Sierra foothills during 2014 and 2015 due to supplemental water provided by irrigation and to the concentration of rainfall during the spring growing season (Airola et al. 2015a, b). The expansion of the survey in 2015 to additional areas that supported suitable grassland vegetation resulted in the detection of only one small colony in a small area (30 km^2) surveyed in the northern foothills and none in a more extensive area (205 km^2) in the southern Sierra foothills (Airola 2015b). Field surveys conducted in portions of the southern foothills in 2015 showed severe drought-induced effects on vegetation growth that limited the availability of nesting habitat in this region (Airola 2015b).

In 2016, we sought to estimate the number and sizes of Tricolored Blackbird breeding colonies in a larger area of the Sierra Nevada foothill grasslands, determine the fates of the breeding colonies, and estimate the area's relative contribution to the statewide Tricolored Blackbird population.

Study objectives were to:

- estimate the minimum extent of the breeding use within a larger area of grassland-dominated areas during and following a more normal precipitation year,
- evaluate survey coverage, to determine the potential for undetected colonies,
- compare numbers of breeding attempts observed in 2016 to numbers detected in 2015 in areas surveyed in both years,
- document fates of colonies and estimate the proportion that produced young,
- check previous results regarding use of nesting substrates and colony use turnover rates, and
- document potential land use conflicts with active colonies during 2016.

STUDY AREA

We define the 2016 study area as the general area encompassed within boundaries that were broadly drawn to encompass the lands dominated by

annual grasslands in the lower foothills of the western Sierra Nevada and the adjacent eastern edge of the Central Valley, California. In total, the study area encompassed 12,730 km^2 (4,915 mi^2). Elevations ranged from 15 to 550 m (50 -1700 ft) and included portions of 16 counties, from Tehama in the north to Fresno in the south (Figure 1). For comparisons, we sub-divided the study area into the *northern foothills*, encompassing 1,866 km^2 (720 mi^2) in Tehama, Butte, Yuba, and Sutter counties; the *central foothills*, encompassing 6,322 km^2 (2,441 mi^2) in Placer, El Dorado, Sacramento, Amador, San Joaquin, Calaveras, and Stanislaus counties; and the *southern foothills*, encompassing 4,542 km^2 (1,754 mi^2) in Tuolumne, Merced, Mariposa, Madera, and Fresno counties (Figure 2). We surveyed areas within these regions that were accessible by and visible from public roads (see METHODS and RESULTS for details).

We enlarged the 2016 study area to more completely characterize Tricolored Blackbird occurrence and use of this fairly homogeneous landscape. The 2016 area was nearly twice the size of the 2014 survey area and was 1.5 times the size of 2015 study area (Figure 2). The 2014 study area consisted solely of the central foothills; the boundaries of the central foothills increased by about 11% from 2014 to 2015 and then remained the same size in 2016. The portions of the study area in the northern and southern foothills were 5 and 2.5 times larger, respectively, than in 2015.

We use the term *survey area* to refer to areas of suitable habitat within the study area and subregions that were surveyed (see METHODS). In quantifying suitable habitat surveyed within the survey areas, we included both annual grassland and irrigated pasture as suitable habitat, as both had previously been shown to support extensive foraging use by Tricolored Blackbirds. The area of suitable habitat within the study area and its subregions are presented in RESULTS. We identify individual colony locations in italics, using location names found in the Tricolored Blackbird Portal (http://tricolor.ice.ucdavis.edu) to facilitate communication among those working with the species.

METHODS

Precipitation

We characterized rainfall in the study area for October 2015–May 2016, the period we considered relevant for breeding habitat conditions ("2016 water year"), to compare with previous years and the 20-year average using data derived from the California Department of Water Resources Data Exchange Center (http://cdec.water.ca.gov/). Methods were similar to those used to characterize the 2014 and 2015 water years (Airola et al. 2015b), but we expanded the number of weather stations to 17 at elevations of 8 to 500m to represent the larger 2016 study area, as well as to characterize conditions within the larger 2016 study area during 2014 and 2015.

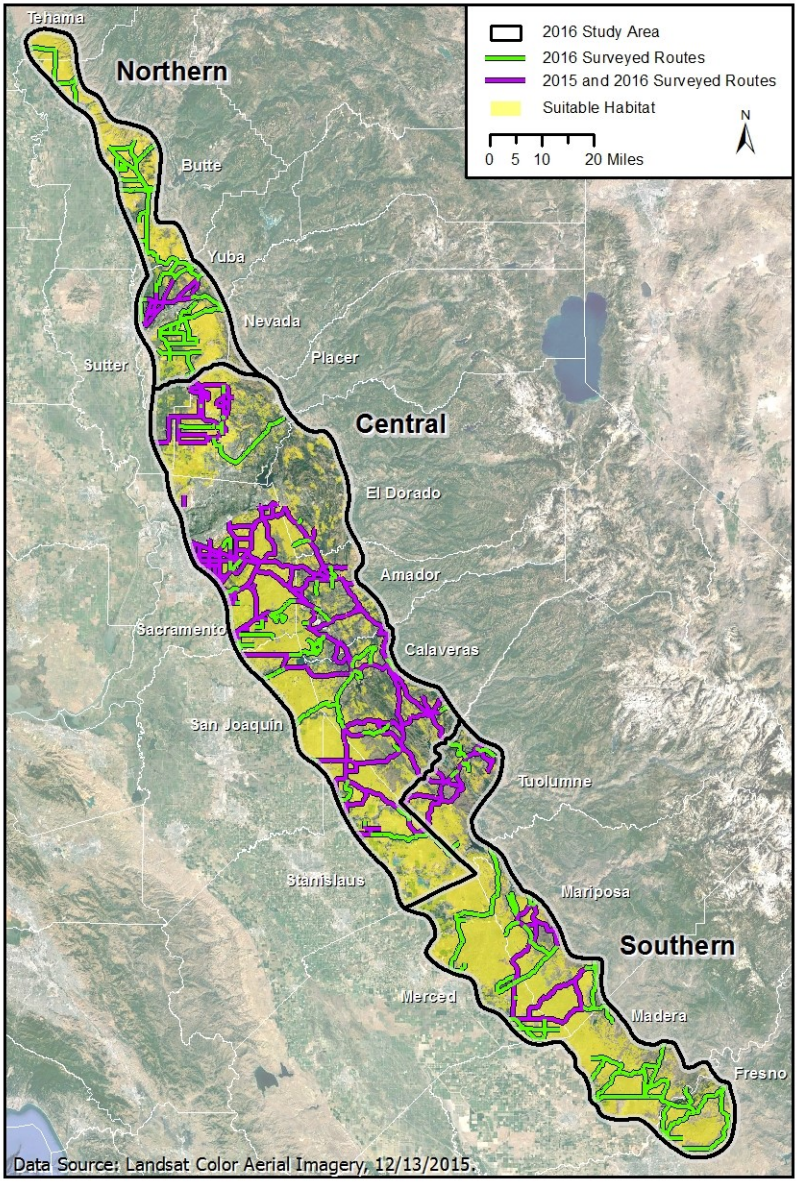

Figure 1. Tricolored Blackbird breeding survey study area and survey routes (2015-16) within the suitable habitat in the northern, central, and southern regions of the Sierra Nevada foothills. Routes are shown that were surveyed in both 2015 and 2016 (purple) and in 2016 only (green).

Therefore, precipitation reported here for previous years differs from that reported previously (Airola et al. 2015b) for the smaller study areas in those years. Because only one weather station was within the northern region, we discuss precipitation differences between the northern and central regions combined (N=10 stations) and southern region (N=7 stations).

Colony Surveys

Survey methods were as described for previous foothill surveys (Airola et al. 2015a, b). Survey effort in 2016 was of a similar intensity as that in 2015, but covered a larger area (Figure 1). Experienced observers conducted surveys for breeding birds from 2 April to 21 June 2016. The authors visited all active colonies at least once to verify breeding activity and numbers. We surveyed all 55 different sites that had been occupied in 2014 and 2015 and many other previously documented colony locations as identified in the Tricolored Blackbird Portal. We conducted intensive road-based surveys for colonies within a large area of suitable habitat. We also checked sites where observers reported Tricolored Blackbird colonies or concentrations over the 2016 nesting season in eBird (http://ebird.org/ebird/map/, Sullivan et al., in press).

Survey routes were mostly roads driven (and a few trails walked) to reach previous colony locations and that passed through suitable habitat: areas dominated by grassland and irrigated pasture (Figure 2), the primary land cover types where colonies were known to occur (Airola et al. 2015a). We checked suitable nesting habitat patches (Himalayan blackberry, cattail and bulrush wetlands, and milk thistle stands) and observed flight paths of foraging birds to locate colonies (Beedy and Hamilton 1999). We surveyed sites that were occupied in previous years (i.e., birds present at suitable nesting habitat) and other suitable sites multiple times (ave. = 4.2 visits/active site) over the breeding season to detect colonies that initiated early and late in the nesting season and to document their progress and reproductive fates.

Over the three years of our study, we found that estimating number of Tricolored Blackbirds at foothill colonies is difficult for the following reasons:

- a typical decline in the number of birds at a site after initial stages (pre-settling and settling) ,
- constraints posed by access and resulting observation distance,
- obstruction of birds in foliage,
- the tendency of breeding birds to forage out of sight of colonies, and
- the behaviors of birds during various nesting stages that influence their detectability.

Although our numbers are estimates, they were determined using consistent methods over the 2014-2016 duration of the study. We estimated

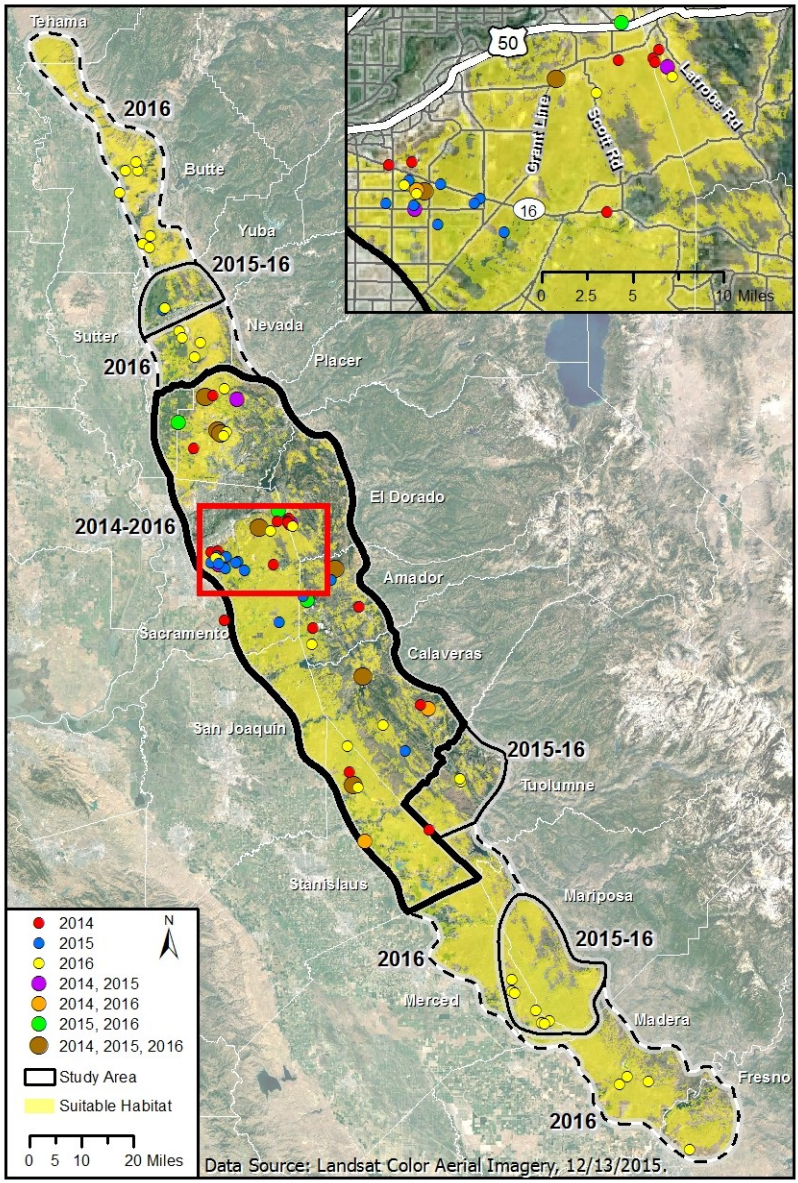

Figure 2. Study areas and colonies identified during 2014 to 2016 in the foothill grassland study area.

numbers of birds at colony sites during most visits by counting birds at and associated with the site, and then adding an additional estimate of birds that were considered likely to have not been detected because they were hidden in foliage or foraging away from the nesting site. Accounting for birds that could not be directly counted was considered necessary to get the best estimate possible, and to not bias numbers downward by only reporting birds that were directly counted. The numbers of birds used to augment counts was determined intuitively and varied among sites based on a variety of factors, including access to the site, size of the occupied area, vegetation and other conditions that affected visibility, and the behavior of birds (especially distances they were travelling to foraging sites). These additional estimates typically added 10-30% to the estimated counts. Notably, this same method of estimating the undetected portion of the population was used in 2014 and 2015, notwithstanding the simplified description (i.e., counts increased by 25%) presented Airola et al. (2015a).

As in past years, we estimated and report the numbers of birds that were active breeders (i.e, reached the incubation stage). In estimating numbers of birds at colonies, we mostly (86% of colonies) used counts from the later nesting stages (i.e., when nestlings were being fed or fledglings were present; see Airola et al. 2015a for description of stages.) At 8% of colonies, we used counts made during the incubation stage (when counts likely underestimate numbers; Beedy and Hamilton 1999) where substantial nest failures occurred subsequently. At a few colonies (6%) where counts during the incubation or nestling stages were not available, we derived estimates from combinations of counts during late settling and fledgling stages, and the area of the occupied colony site (determined from onsite estimates and measured from Google Earth [https://earth.google.com]).

Several factors unique to 2016 may have increased the potential for individuals to breed sequentially in the foothills at more than one location and thus to be counted by us more than once. Factors that contributed to possible breeding at multiple sites by the same individuals included our expansion of the latitude of the area surveyed (and thus potential to record two sequential active breeding attempts by the same birds (Hamilton 1998) and a succession of relatively intense rainstorms that appeared to disrupt nesting at several colonies, especially in the southern foothills (see RESULTS). Because we could not identify individuals, we cannot estimate the magnitude of multiple breeding attempts at different sites by individual birds. Therefore, while we report estimates at individual colonies as number of breeding individuals or breeding attempts, we refer to our estimates for counties, subregions, and the study area as the number of breeding attempts rather than the *breeding population* as was done in previous years' studies (Airola et al. 2015a, b) when the potential for multiple breeding was not as evident.

Unlike in prior years, in 2016 we noted instances of asynchronous nesting (i.e., initiation of nesting by groups of tricolors at different times) within the same colonies (see RESULTS). Asynchronous nesting was recognized when more than one period of nest building was observed at a single site or when the nestling and fledgling stages at a colony extended past the period that would be expected at a synchronous colony.

Comparison of Nesting Populations between Areas and Years

We report the number of breeding attempts in 2016 and previous years, but comparing the number of breeding attempts among various subregions and counties was complicated by differences in the areas surveyed in each year. Therefore, we compare the breeding density, calculated as the number of breeding attempts per area surveyed in each region. We focus between-year comparisons of numbers of breeders within portions of the 2016 study area where we have similar survey coverage over multiple years. These areas consisted of the central foothill region, where both the study area and surveyed area were similar (but not identical) during 2014-2016, and subunits of the 2016 southern study area subregions that were surveyed during both 2015 and 2016 (Figure 1). For the central region, we used the chi-square statistic (χ^2) to compare the observed numbers of breeding attempts in the 2016 survey area to the number that would have been expected if the density in 2016 had been the same as in 2015. (The χ^2 [statistic measures the difference between an observed value [i.e., from data] and an expected value [i.e., predicted from other data, such as our previous year's blackbird breeding density], and allows estimation of the probability that a difference is real or a result of chance.)

Colony Nesting Success

As in previous surveys (Airola 2015a, b), we attempted to determine nesting stage during each colony survey. We also characterized locations as *occupied* (breeding groups present in suitable habitat), *active* (colony reached egg-laying stage), and *successful* (fledglings observed). Occupied sites that did not become active are referred to as *abandoned*. Sites that became active, but did not produce young were considered *failed.*

As in our previous studies (Airola et al 2015a,b), we were not always able to verify whether fledglings were produced at each colony due to lack of access to private lands, difficulty in detecting young within the canopy of nesting substrates, and concern about disrupting nesting activities (Airola et al. 2015a). For similar reasons, we also did not obtain quantitative measures of reproductive success (i.e., average number of young produced per active nest) at colonies. We used a general metric which we refer to as *colony reproductive success* to quantify the proportion of colonies that were successful (i.e., fledged at least some young). As in past studies, where we were unable to visit a colony during the fledgling period, we considered all

colonies that reached the stage of feeding nestlings to have fledged at least some young, and therefore as successful colonies.

Limited access and visual obstruction by vegetation often limited our ability to verify whether or not colonies proceeded to the active stage (i.e., to the egg-laying stage) until eggs hatched and adults carried food to young. Therefore, in a few cases we could not determine if colonies had failed or were abandoned.

Survey Coverage

As in previous years, we broadly identified suitable habitat as areas of grassland and irrigated pasture land covers using Calveg maps (http://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192) to identify routes for survey and assess the proportion of potential habitat that we surveyed (see Airola et al. 2015b). We did not consider availability of suitable nesting habitat or available surface water in this generalized characterization. We evaluated the proportion of suitable habitat that was surveyed within the study area as a whole and within the northern, central, and southern subregions. We mapped road survey routes and assumed that, absent visual obstructions, we could detect breeding Tricolored Blackbirds up to 1.6 km (1 mi) away. We then excluded areas made non-visible from routes by vegetation and topography (using a digital terrain analysis with Esri's ArcGIS 10.2 3D Analyst Viewshed). To assess completeness of survey coverage, we calculated the percent of total suitable Tricolored Blackbird habitat that was visible, and thus believed to be thoroughly surveyed, on survey routes.

Colony Site Reoccupation

We evaluated the extent to which sites known to be occupied in previous years of our study were reoccupied in 2016. This analysis was confined to colonies within the central foothills where survey intensity was similar between years and where follow-up surveys were conducted at all locations occupied in previous years.

Nesting Vegetation and Colony Disturbance

We recorded the vegetation used to support nests at each colony for comparison with previous years, any loss of nest sites from previous years due to landscape changes, and documented the use of sites known to have been subjected to past disturbance or destruction. We also identified potential sources of human disturbance that occurred within or adjacent to locations occupied by breeding birds.

RESULTS

We sought to describe the relative abundance and geographic pattern of nesting by Tricolored Blackbirds in the foothill grassland region during a year of average precipitation, and compare these to the patterns documented in

the drought years of 2014 and 2015 (Airola et al. 2015a, 2015b). Therefore, we present the results for 2016 and compare those to previous years.

Precipitation

Rainfall in the 2016 study area and all subregions during the 2016 water year was similar to the 20-year average, and higher than the 56% of average precipitation in this area in both 2014 and 2015 (Figure 3). Within sub-regions, rainfall in 2016 was 2% lower than the average in the north and central regions combined, and 16% higher than average in the south.

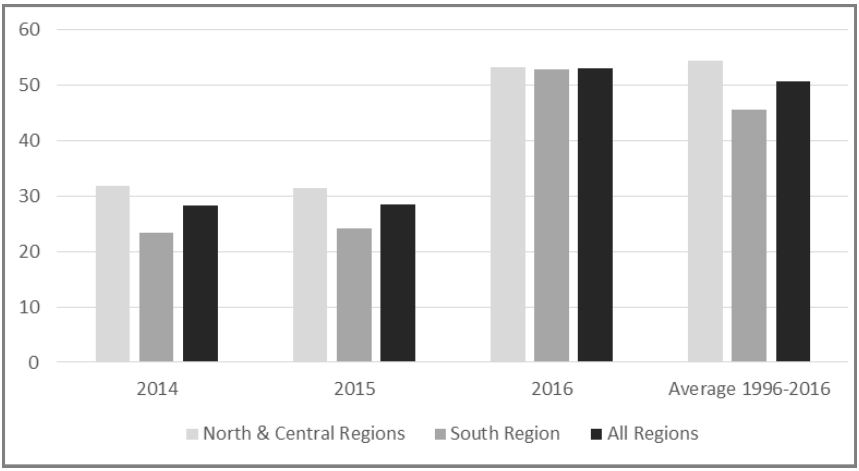

Figure 3. Annual precipitation (cm) prior to and during the nesting season (October-May) in foothill sub-regions compared to the 20-year average.

Survey Coverage

Surveys covered a total of 2,393 km (1,487 mi) of roads in the total study area, many of which were driven multiple times over the nesting season. We identified 6,809 km^2 (2,629 mi^2) of suitable habitat in the entire 12,730 km^2 study area (Figure 1), of which 15% was in the northern foothill counties, 40% in the central foothills, and 45% in the south.

Based on analysis of visibility from roadways, we surveyed 2,401 km^2 (927 mi^2) in 2016 (Table 1) which represented 36% of all suitable habitat in the study area. The surveyed areas represented 44% of the suitable habitat in the northern foothills, 43% in the central foothills, and 26% in the southern foothills. By region, 18% of the total surveyed area was in the northern foothills, 55% in the central foothills, and 27% in the southern foothills (Table 1).

The amount of suitable habitat surveyed within the expanded 2016 study area increased by 91% in 2016 over that covered in 2015, with most of the

increase (68%) occurring within the northern and southern foothills (Table 1). The suitable area surveyed in the northern region in 2016 was >14 times the size of the 2015 area. The suitable area of southern foothills surveyed increased by >3 times. Although the 2016 survey area boundary for the central foothills was similar to those of previous years, survey intensity (i.e., road transects surveyed) increased, resulting in a 32% increase in area of suitable habitat surveyed there.

Table 1. Suitable Tricolored Blackbird habitat surveyed within the Sierra Nevada-eastern Central Valley foothills grasslands study area. Suitable habitat surveyed includes grassland and irrigated pasture lands that were visible within 1.6 km of survey routes (see METHODS). Surveyed area was not quantified in 2014.

		Surveyed Area (km^2)	
Sub-region	County	2015	2016
North	Tehama		31
	Butte		200
	Yuba	30	185
	Sutter		11
	Subtotal	*30*	*427*
Central	Placer	183	214
	El Dorado	20	33
	Sacramento	424	506
	Amador	63	96
	San Joaquin	64	103
	Calaveras	99	135
	Stanislaus	169	235
	Subtotal	*1,022*	*1,321*
South	Tuolumne	42	58
	Mariposa	94	175
	Merced	69	222
	Madera		141
	Fresno		57
	Subtotal	*205*	*653*
	Total	**1,257**	**2,401**

Observed Breeding Attempts and Density

We observed an estimated total of 77,830 breeding attempts by Tricolored Blackbirds at 50 active colonies in 2016 (Table 2, Figure 2). Placer, Sacramento, and Merced counties each supported more than 10,000 breeding attempts; while Yuba, Stanislaus, and Madera counties each supported between 4,000 and 7,000; and Butte, El Dorado, Amador, Calaveras, Tuolumne, and Fresno counties each supported fewer than 4,000. For the second and third consecutive years of survey, respectively, we did not record any active colonies in Mariposa and San Joaquin counties. (However, one colony site in far western Mariposa County, *Sonny's Rangeland*, was observed to be occupied during the pre-nesting period, but not monitored thereafter, so nesting may have occurred.) No nesting birds were detected in 2016 during the first year of survey in relatively small areas of Tehama and Sutter counties included in the study area. Among occupied counties, nesting density (# breeding birds at active colonies/km^2 surveyed) was highest, by far, in Placer County (93 breeders/km^2), moderately high in Madera, Merced, and Tuolumne counties (40-50/km^2), intermediate in Fresno, Yuba, Sacramento, and El Dorado counties (21-39/km^2), and lowest in Butte, Stanislaus, Amador, and Calaveras counties ($\leq$20/km^2; Table 2).

The 50 active colonies observed in 2016 represented an increase of 92% from the 26 detected in 2015, and 77,830 breeding attempts at 2016 colonies were 41% higher than the 55,270 identified in 2015.

Northern Foothills Region. The northern region supported 12 breeding colonies and nearly 10,330 nesting birds in 2016, comprising 13% of the total number of foothill breeding attempts detected (Table 2, Figure 2). Overall density of tricolors (24/km^2) within suitable habitat in 2016 in the northern foothills was lower than in the central and southern foothills (Table 2).

The increased numbers of breeding colonies and individuals observed in the northern region during 2016 coincided with an increase in the area surveyed by over 14 times that surveyed in 2015 (Table 1). Only one colony was found in both years in the portion of the northern foothills surveyed during both years, whereas all other 2016 colonies and individuals were in previously unsurveyed areas. Although breeding density (breeding attempts/ km^2) here was substantially higher in 2016 than in 2015 (Table 2), the difference in survey effort between years precludes meaningful comparison of density.

Central Foothills Region. Most (58%) of breeding attempts observed in 2016 occurred in the central foothill region, which supported 25 nesting colonies and nearly 45,000 nesting birds (Table 2, Figure 2). Within this region, Placer and Sacramento counties supported the highest number of breeding birds for the third consecutive year, with a combined 15 colonies and 48% of the total foothill population. The density within Placer County was

the highest in the central region and the foothills as a whole, and almost double that of any other county (Table 2).

Table 2. Numbers of Tricolored Blackbird nesting colonies, breeding attempts, and breeding density by county and sub-region in the Sierra Nevada-eastern Central Valley foothill grassland study areas, 2014-2016.

Sub-region	County	Active Colonies			Breeding Attempts			Density (Breeding attempts / km^2)	
		2014	2015	2016	2014	2015	2016	2015	2016
North	Tehama						0		0
	Butte			7			3,930		20
	Yuba		1	5		200	6,400	7	35
	Sutter						0		0
	Subtotal		*1*	*12*		*200*	*10,330*	*7*	*24*
Central	Placer	6	5	7	12,473	19,200	19,900	105	93
	El Dorado	4	1	1	5,800	2,900	1,000	145	31
	Sacramento	9	12	7	11,000	19,300	17,150	46	34
	Amador	3	4	3	6,375	6,320	1,140	100	12
	San Joaquin	0	0	0	0	0	0	0	0
	Calaveras	3	2	3	760	350	1,300	4	10
	Stanislaus	4	1	4	6,601	7,000	4,550	41	19
	Subtotal	*29*	*25*	*25*	*43,009*	*55,070*	*45,040*	*38*	*34*
South	Tuolumne	0	0	2	0	0	2,300	0	40
	Mariposa		0	0		0	0	0	0
	Merced		0	7		0	10,950	0	49
	Madera			3			7,110		50
	Fresno			1			2,100		37
	Subtotal	*0*	*0*	*13*	*0*	*0*	*22,460*	*0*	*34*
	Total	**29**	**26**	**50**	**43,009**	**55,270**	**77,830**	**44**	**32**

[B] Breeding attempts are defined as the number of individuals estimated to be present at colonies during or after the incubation state of nesting. Active breeding attempts are reported because of the potential that some individuals may have bred at more than one colony during the 2016 nesting season (see METHODS).

[0] Zeroes represent counties where surveys were conducted and no nesting birds were found. Blanks indicate areas and years where no surveys were conducted.

The boundaries of the central foothill sub-region remained similar during 2014—2016, but survey intensity increased by 29% between 2015 and 2016. (Survey routes were not recorded in 2014, precluding precise comparisons,

but the area surveyed was less than in the two subsequent years). Notwithstanding the increased 2016 survey effort, the 25 colonies detected in the central region in 2016 were similar to the 29 and 25 that were found in 2014 and 2015, respectively. The 45,040 breeding attempts detected in 2016, however, were 18% lower than the 55,070 recorded in 2015. The 2016 total was similar to the number in 2014 (Table 2), when the central study region was 11% smaller and survey intensity was lowest. The number of 2016 breeding attempts observed in the expanded central foothill survey area is significantly lower than the expected number, if the density of breeders had been similar to that in 2015(($\chi^2_{1\,df}$=3.81, p=0.05). Therefore, breeding numbers in 2016 almost certainly declined in the central region from 2015, and probably were lower than in 2014.

Breeding density within surveyed areas in the Central region also declined by 34% from 54 to 34 birds/km^2 from 2015 to 2016 (Table 2). The decrease in density in 2016 while the survey intensity increased further indicates that the number of nesting individuals declined during 2016 in the central foothills.

Southern Foothills Region. Thirteen colonies and 22,460 breeding attempts were recorded in the southern foothills in 2016, comprising 29% of the total number of foothill breeding attempts (Table 2, Figure 2). The number of known breeding colonies and breeding attempts increased from zero in 2015. The increased size of the southern survey area in 2016 by more than three times that surveyed in 2015 (Table 1), however, complicates comparisons between years. Therefore, we evaluated changes in numbers of colonies and breeding attempts within the 205 km^2 area in Tuolumne, Mariposa, and Merced counties surveyed during both 2015 and 2016 (Figure 4).

Within the common area, we recorded nine nesting colonies and 13,250 breeding attempts in 2016, and no breeders in 2015. All colonies in the areas surveyed both years were found along routes that were also surveyed in 2015 (Figure 4). This substantial difference in breeding use suggests that the area was not occupied, or sparsely occupied, in 2015, and then occupied by a much larger number of breeders in 2016. This increase in use appears to have resulted from the return of near-normal precipitation (Figure 3) and the resulting increased area of tall milk thistle nesting habitat preferred by nesting birds (see *Nesting Substrate*).

Merced County supported 49% of the breeding attempts in the southern region and 14% of the total foothill breeding attempts, although density was similar to several of the other southern foothill counties. The breeding density in suitable habitat surveyed in the southern foothills as a whole was similar to that of the central region and higher than in the northern region (Table 2).

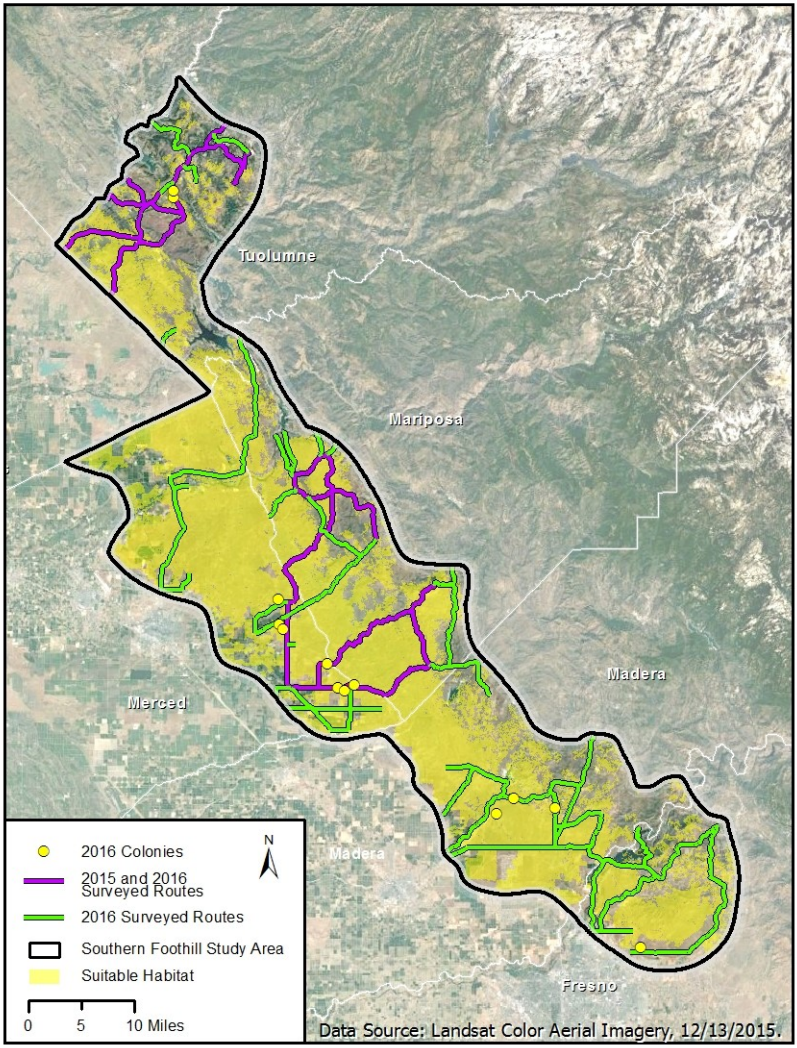

Figure 4. Survey areas and routes and colony locations in of the southern foothill region during 2015 and 2016. No colonies were found in areas surveyed in 2015.

Colony Reproductive Success and Asynchronous Nesting

We found 64 sites occupied by tricolors in the foothill study area in 2016. Active colonies were verified at 50 sites (Table 2). Six of the 14 occupied sites

that did not become active were abandoned before egg-laying. We were unable to determine whether seven others either were abandoned before egg-laying or failed after egg-laying; one site occupied early was not monitored to determine its fate. Of 50 verified active colonies, 49 hatched young and one failed while eggs were in the nest. Thirty-three colonies (66% of active colonies) were verified to have fledged young. The remaining 16 colonies were not visited late enough to assess fledging, but all these colonies were documented to have hatched young. Given that no colonies that were completely monitored failed during the nestling stage in 2016 or previous years (Airola et al. 2015a,b), it is likely that most of these colonies also fledged young.

Weather-related Nesting Failure

In addition to more rainfall during 2016 than in previous years, rain tended to occur during especially strong storms while birds were nesting. We observed several instances of partial or complete nesting failure in active colonies following intense storms. For example, the *Five Palm Trees* colony in Sacramento County was in the incubation stage on 20 April but the site was found to be completely abandoned on 25 April following an intense rainstorm. Several 2016 colonies that fledged some young, and thus were considered successful colonies, appeared to suffer substantial losses after nest building due to severe storms with strong winds. Colonies in milk thistle appeared to be especially vulnerable to storm-related mortality; for example, strong winds appeared to blow down occupied patches of milk thistle at three Merced County colonies (*Le Grand Mine, Miles Creek, Bear Creek,*), but these colonies were not completely eliminated and ultimately fledged some young. Other colonies had partial failures, but changes in numbers prior to egg-laying were hard to attribute to weather rather than general colony dynamics.

Asynchronous nesting

We observed asynchronous nesting at six 2016 colonies scattered across the foothills. Asynchronous nesting was not observed during the previous two years of survey (Airola, unpublished data). Asynchrony could have resulted from high rates of mortality during rainstorms and subsequent re-nesting (see *Weather-related Nesting Failure* below) or extended precipitation that maintained suitable nesting conditions and allowed some birds to raise two broods.

Colony Site Fidelity

In the central foothills, where the size of the study area and intensity of survey efforts were generally similar across all three years, 25 to 29 colonies were observed over 2014-16. Of 44 sites surveyed there during all three years of the study, only eight (18%) were active in all three study years and seven (16%) were active in two of three years. The remaining 29 sites (66%) were active only in one year. Of the seven sites used in two of three years, 5 (71%)

were used in consecutive years, and two (29%) were used in alternate years (i.e., 2014 and 2016). Frequency of use did not differ among sites in which the predominant nesting substrate was perennial (blackberry, willow) or annual (cattail, tule, milk thistle) (($\chi^2_{1\ df}$=0.61, p=0.44)

As noted under *Observed Breeding Attempts and Density*, in areas within the southern Sierra foothills surveyed during 2015 and 2016, all nine sites that supported nesting in 2016 were in areas where no nesting occurred in 2015.

Nesting Substrate

In 2016, Tricolored Blackbirds nested in a greater variety of nesting substrates than in the previous two years (Figure 5). In 2016, as previously, Himalayan blackberry was the predominant nesting substrate. It was used at 33 active colonies (65%) that supported 69% of the total active breeding attempts, and was the sole nesting substrate at 28 colonies (55%) that supported 59% of the attempts. Emergent marsh vegetation (cattail and bulrush) remained an important but subdominant nesting substrate, used at 10 sites (20%) and was the sole nesting substrate at four (8%).

Tricolored Blackbird use of milk thistle as a nesting substrate increased substantially in 2016 from that observed in 2014 and 2015 (Figure 5). Blackbirds used thistle at 12 colonies (24%) supporting 34% of the total 2016 breeding attempts. Milk thistle was the sole substrate used at 10 colonies (20%) that supported 17% of the total breeding attempts. Willow was used for nesting only at two colonies (4%) in 2016, which was the first documented use of this substrate over the three-year study.

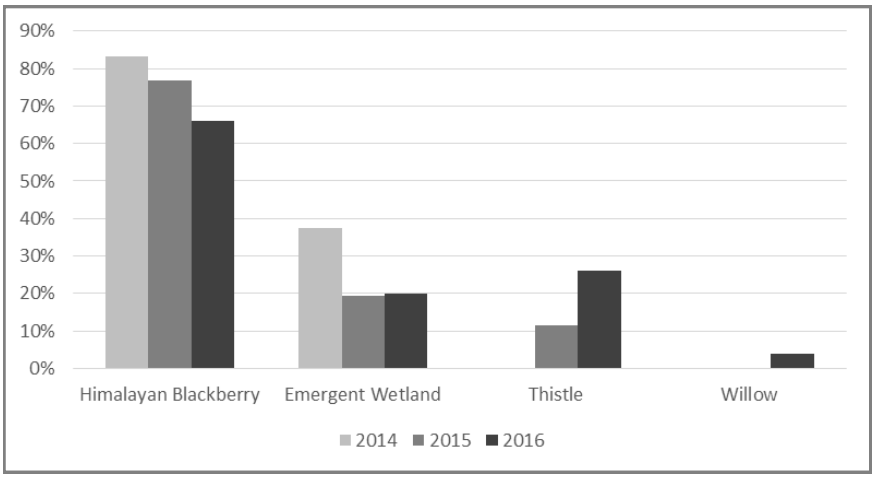

Figure 5. Use of nesting substrates at Tricolored Blackbird colonies in the Sierra Nevada foothill grasslands in 2014-2016. Percentages do not add to 100 in each year because multiple substrates were used at some sites.

Substrate use varied dramatically in different foothill subregions in 2016 (Figure 6). Substrate use in the north and central foothill region in 2016 was similar to that in previous years (Airola et al. 2015a, b), dominated by Himalayan blackberry and to a lesser extent emergent marsh vegetation (cattail and bulrush), with minor use of milk thistle and willow (*Salix* sp.). Most (69%) of the 13 newly established colonies in the southern foothills, supporting 88% of the 22,460 nesting tricolors there, nested in pure stands of milk thistle or combinations of thistle and emergent vegetation (Figure 6). The increase in the number of breeding birds here appears to have been a response to an increase in the availability of milk thistle. The large milk thistle patches occurred in many areas that had been bare ground or had minimal herbaceous growth in 2014 and 2015 (L. Young, pers. comm.).

Tricolored Blackbirds nested in several Himalayan blackberry patches in which above ground vegetation was completely dead, including *Iron Point Road,* Sacramento County, and *Milton Road #1*, Stanislaus County. The large *Iron Point Road* colony was used in 2015 and supported several waves of breeding birds (estimated in total at 6,250 birds) in 2016. The cause of the canopy die-off is unknown; potential causes include herbicide treatment or natural die-off due to drought. At initiation of breeding in April, only 10% of the above ground canopy was alive, but by late May about 25% of the canopy had regrown. Despite the presumed increased exposure to sun and rain, the colony appeared to be highly successful at fledging young. The blackberries at *Milton Road #1* appeared to have died back in response to the drying up of the adjacent creek (D. Airola pers. obs.) during the previous drought years. This colony also was successful, with fledglings at the site when it was found on 29 May.

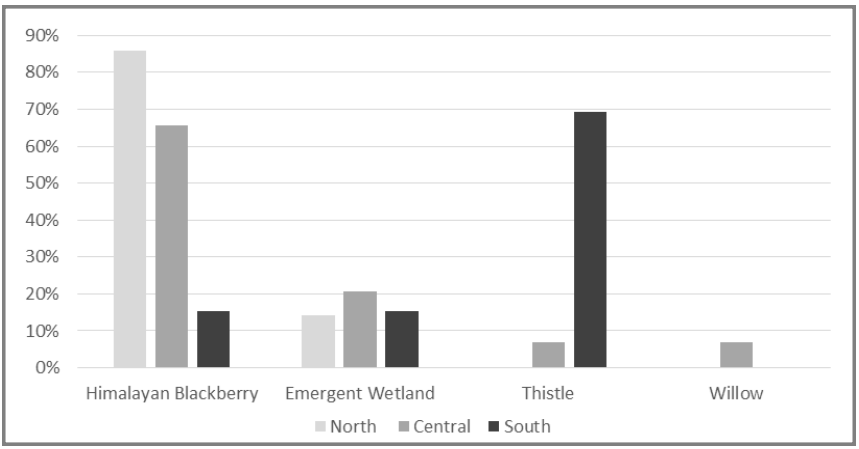

Figure 6. Proportional use of substrates for nesting at Tricolored Blackbird colonies in the north, central, and southern sub-regions of the Sierra Nevada foothills during 2016.

Flooded willow trees were used as a nesting substrate by an estimated 300 Tricolored Blackbirds at the *Papoose Pond* colony, Amador County. At *Wetsel-Oviatt Rd Quarry*, El Dorado County, nearly 1,000 birds nested mainly in willow growing without surface water, and to a lesser extent in milk thistle. While use of willow has been reported previously (Beedy and Hamilton 1999), these two sites were the only instances of willow use observed among 105 active colonies during the 2014-2016 foothill studies.

Human-caused Nesting Habitat Disturbances and Responses

Habitat Removal Prior to the Nesting Season. Only one breeding site that was active in 2014 or 2015 was disturbed between the 2015 and 2016 nesting seasons. A large proportion of the Himalayan blackberry patch at the *Yosemite Junction* colony site in Tuolumne County was removed by a landowner before the 2016 season based upon the mistaken perception that Tricolored Blackbirds were damaging his wine grape crop (fide K. Smith). The depredation was likely caused by European Starlings (*Sturnus vulgaris*); Tricolored Blackbirds have not been documented to depredate fresh grapes (Beedy and Hamilton 1999), although they have been observed eating dried grapes (R. Meese, pers. obs.). Tricolored Blackbirds returned to *Yosemite Junction* by 5 April, and were settling on 12 April, but were not seen thereafter so presumably abandoned the site before nesting.

Habitat Removal during the Nesting Season. During 2016, potential nesting habitat in milk thistle was removed at one potential colony site, *Road 29* in Madera County. About 500 tricolors were there on 10 April, and by the next visit on 27 April, the thistles had been mowed. Whether nesting occurred at this site prior to its mowing was not determined.

Use of Sonora Rd #3 Colony Following Partial Destruction in 2015. Half of the *Sonora Rd #3* colony in Stanislaus County occupied by 7,000 breeders was destroyed during the nestling stage in 2015, eliminating an estimated 1,386 to 2,345 nests (Airola et al. 2015b) Tricolored Blackbirds reoccupied the remaining blackberries there in 2016. A total of 3,700 birds bred at the site, via two “waves” of colonization that occurred several weeks apart. The lower number of birds breeding at the site may have resulted from the reduced amount of nesting habitat after the 2015 pruning. A first wave of 2,500 birds was feeding young on 10 May, and this group had mostly departed on 23 May, when few adults and fledglings were seen. A second wave of 1,200 breeders was feeding young in nests on 29 May, indicating that a substantial number of adults had been incubating on 23 May.

The second wave of breeders at *Sonora Rd #3* may have come from the nearby *Sonora Road Pond* site, where an estimated 2,000 birds were nest-building on 10 May, but only 50 were feeding young on 30 May. Birds excluded from *Sonora Rd #3* may have attempted to nest at *Sonora Road Pond*, but then abandoned and returned to *Sonora Road #3*, perhaps after

some of the first wave of breeders had departed. Thus, reduction in nesting habitat by removal in 2015 may have limited the number of birds that could initiate nesting simultaneously, thereby triggering asynchronous nesting.

Development Adjacent to Colonies. Active development at a previously approved site occurred immediately adjacent to the *Iron Point* colony in Folsom, Sacramento County. Despite construction activity within 30 m of the nesting colony, an estimated 6,250 birds nested in two successive waves and appeared to produce a large number of fledglings. Nearly all tricolors regularly flew across the construction site to grassland feeding areas and extensively used a pond constructed to store water for dust abatement on the site. It is unknown whether the eventual commercial building at the site will block movements from nesting to feeding areas, but the point may be moot as foraging areas also are approved for development (see *Land Use Changes*).

Summary of Human-caused Disturbance Effects. Over the three years of the study, we observed only two colonies (2%) where nesting habitat was disturbed during the nesting season: *Road 29* in Madera County in 2016 (where the nesting status at the time of removal is unknown) and *Sonora Rd #3* in 2015, where vigorous pruning destroyed many nests with nestlings (Airola et al. 2014b). We documented removal of nesting habitat during the non-nesting period at two additional colony sites: *Aspen IV* during aggregate mining operations prior to the 2015 season (Airola et al. 2015b) and the *Yosemite Junction* removal prior to the 2016 season. Finally, nesting habitat was maintained, but most surrounding foraging habitat was removed by development at the *Bridge* colony in El Dorado County (since renamed *Carson Creek Bridge*) in 2014-15, and Tricolored Blackbirds did not nest there in the two subsequent years (Airola et al. 2015b). Thus, over the three-year study, only two of the 105 active colonies were destroyed while they were active, vegetation was removed at two sites after nesting use following both the 2014 and 2015 seasons, and one site was cleared apparently before it became active in 2016.

Land Use Changes

Several projects previously identified as potential threats to Tricolored Blackbirds (Airola et al. 2015a) progressed in 2016. For example, a large aggregate mining project, which would mine and reclaim 353 acres supporting four colony sites and surrounding foraging habitat, was approved by the Sacramento County Board of Supervisors in 2016. Project mitigation measures include avoiding removal of occupied nesting habitat and preservation of suitable offsite foraging habitat (https://planningdocuments.saccounty.net/ViewProjectDetails.aspx?ControlNum=PLNP2014-00201). The Folsom Ranch project, which would develop a substantial amount of grassland in Folsom south of U.S. Interstate 50 that is used by Tricolored Blackbirds from surrounding colonies, also is proceeding toward development (http://www.folsomtelegraph.com/article/8/10/16/south-50-project-plans).

Most 2016 foothill Tricolored Blackbird colonies occurred on private ranchlands, but more nesting sites occurred on lands with some form of conservation status (conservation easement or ownership) than in 2014 (Airola et al. 2015a). Protected areas occurred primarily in Placer County, where five of seven colonies supporting 15,700 (20%) of the total recorded 77,830 active breeding attempts in 2016 were on designated conservation lands or other lands intended for conservation purposes.

DISCUSSION

Observed Nesting Population

Our detection of more active breeding attempts in the Sierra foothill grassland area in 2016 than in 2014-2015 likely resulted from the doubling of the amount of habitat surveyed and the widespread availability of milk thistle nesting habitat in the southern foothills in response to increased rainfall. Examination of areas surveyed consistently in 2015 and 2016 indicates a likely decline in the number of breeding attempts in the central foothills and occupation of areas of the southern foothills that were not occupied and not suitable for breeding in 2015. The 2016 foothill breeding population clearly utilized nesting habitat (primarily milk thistle) that was absent or much less abundant in 2015 (and probably in previous drought years) that grew in response to increased rainfall during the 2015-2016 season. Our results are consistent with an interpretation that the breeding population in the southern foothills was redistributed to here from elsewhere within the foothills or from other portions of the species' range.

The 2016 re-colonization of the southern Sierra foothills by Tricolored Blackbirds may have resulted from interception of birds that otherwise would have moved north to breed. It also could have been a response to diminished habitat in the San Joaquin Valley as more row crop land is converted to orchards (Holyoak et al. 2014, Meese 2016). Shifting of breeding from the San Joaquin Valley to the southern foothills could have important conservation and social consequences by offsetting habitat losses and reducing direct conflicts with San Joaquin Valley agriculture, which has required substantial effort and cost to manage (Arthur 2015).

Drought Effects and Conservation Implications

Central Sierra Foothills. Our study results showing that the nesting population in the central foothills declined during 2016 despite increased survey effort supports our previous view that the 2014-2015 drought did not have substantial negative effects on Tricolored Blackbirds there (Airola et al. 2015a, b). Abundant spring rains (especially in 2014) and availability of irrigated lands to sustain nesting habitat appeared to maintain good habitat conditions there, despite lower than average rainfall. Contrary to expectation from a drought effect, the breeding population in this region declined during the wetter 2016 water year. Reasons for the 2016 decline are uncertain, but

could be a result of an increase in suitable nesting habitat in the south, with a movement of breeding birds in response to enhanced breeding opportunities there. The central foothills also may have served in previous years as a drought refugium that attracted birds that were unable to breed elsewhere due to the lack of suitable nesting substrates and surface water, but which nested elsewhere in 2016 when conditions improved. The smaller number of nesting birds in the central foothills in 2016 also may have resulted from intense spring storms that are believed to have caused widespread nesting failures. However, they do not appear to have been concentrated in this region (see *Observed Nesting Population*).

Southern Sierra Foothills. The 2016 survey showed that a return to above average rainfall in the southern Sierra foothills increased suitable milk thistle nesting habitat which supported most of the nearly 20,000 Tricolored Blackbird breeding attempts there, including nearly 11,000 in portions of Merced County that were known to be unoccupied in 2015 (Airola 2015b). Much of the total 2016 rainfall, however, fell in a series of intense storms in March and April that while helping to grow tall dense thistle, also caused widespread partial or complete nesting failures (Meese 2016; Swarth, pers. obs.).

Tricolored Blackbirds are known to have nested in substantial numbers in foothill areas of Merced and Madera counties in the 1930s (Neff 1937) and in the 1980s and during 2005-2012 (http://tricolor.ice.ucdavis.edu/locations/colony). Some of the southern sites occupied in 2016 had also been occupied in previous pre-drought years (e.g., *LeGrand Mine*, *Bear Creek* and sites along the *Madera Canal*). Due to lack of continuous long-term monitoring, however, it is unclear whether the recent observations of habitat conditions and nesting populations there are an infrequent event or a return to typical non-drought conditions.

The apparent strong response of the birds to the increase in nesting substrate in the southern foothills is consistent with previous evidence that Tricolored Blackbirds seek suitable nesting substrates and foraging habitat annually during the pre-nesting "prospecting" period, when they are known to range widely (Airola et al. 2015a). Observations in 2015 identified abundant insect prey populations in at least some areas of the southern foothills in 2015, but a lack of nesting habitat and breeding birds (Airola et al. 2015b). The 2016 reoccupation suggests that creating nesting habitat that can remain suitable for nesting even in dry years, as suggested by Young (2015), could help maintain a more stable nesting population in the region, especially during dry years.

Colony Site Fidelity

Most (70%) of the sites used for breeding by Tricolored Blackbirds in the central Sierra foothills were used only for a single year during the three years

of this study. This low level of site fidelity does not appear to be a response to nesting habitat condition or lack of surface water, as most nesting sites were in Himalayan blackberry patches that appeared to remain unchanged over the three years of study. Holyoak et al. (2014) similarly found a high rate of between-year movement among breeding colony sites. It has been suggested by many that between-year movements from one breeding location to another result from variable insect prey distributions (Orians 1961, Beedy and Hamilton 1999, Meese 2013). More work is needed on the question of Tricolored Blackbird nest site selection to better understand why the birds tend to move between years and how site selection changes over a period longer than this study.

The frequent annual movements of breeding birds among sites may create substantial challenges for species conservation, because lands acquired for conservation purposes based on use in one year may not be used consistently (Airola et al 2015b). More information is needed on the longer-term patterns and causes of these movements to better inform conservation decisions. Some fidelity to certain larger areas appears to exist, within which a variety of breeding sites may be selected in different years (Figure 2). More study is needed to identify how nesting density and site fidelity are influenced by the availability and type of nesting habitat, the abundance and arrangement of various land cover types for foraging, and abundance of insect prey (Holyoak et al. 2014), to inform regional long-term conservation strategies. In the short term, conservation efforts should rely on a combination of preservation of high density lands and protection of as many active and recently active nest sites as possible (Airola and Young 2014).

Nesting Substrate

As in 2014 and 2015, most Tricolored Blackbirds in the foothills nested at colonies where Himalayan blackberry was the primary or sole nesting substrate. The blackberry, along with stinging nettle (*Urtica dioica*), have been shown to have higher reproductive success than other nesting substrates (Cook and Toft 2005, Holyoak et al. 2014), likely due to greater protection from predators and adverse weather and possibly their occurrence in more productive grassland foraging areas. Therefore, our results reinforce previous conclusions that non-native blackberry plays an important role in regional Tricolored Blackbird conservation, and maintenance of this species in known and suitable blackbird nesting areas is a priority (Airola et al. 2015a, b).

The occupation of the southern foothill region by Tricolored Blackbirds in 2016, after the return of higher rainfall and growth of suitable milk thistle nesting vegetation demonstrates the flexibility of the species in locating and using suitable habitat, as well as the importance of nesting habitat availability in the region. Predominant use of milk thistle in the southern foothills, where blackberry and emergent vegetation appear to be limited, especially in

drought years, demonstrates the current importance of this substrate there and the limitations imposed by its irregular occurrence. Creating areas with other nesting substrates that can persist during drought (Young 2015) is warranted to encourage more regular Tricolored Blackbird use of the southern foothills.

Effects of Human Disturbance and Land Use Changes

Our observations and informal meetings with landowners suggests that, as a group, private landowners whose lands support Tricolored Blackbird colonies have not responded to the ongoing state and federal Endangered Species Act listing process by removing nesting habitat, contrary to earlier concerns (Airola and Young 2015). Through our conversations, it appears that most landowners still do not recognize Tricolored Blackbirds on their lands and do not know of their legal status as candidates for listing as endangered by California. Therefore, they do not perceive them as a potential regulatory threat to their land uses. Thus, the Tricolored Blackbird's habit of shifting between nesting sites from year to year may also be protecting them from harm by landowners, who do not become familiar with them.

The presence of more nesting by foothill Tricolored Blackbird colonies on protected lands in 2016 than in the past (Airola et al. 2015a) is encouraging, but also could be an anomaly based on annual movements of nesting sites. Habitat protection in Placer and Sacramento counties is particularly important, considering the large Tricolored Blackbird population and substantial development pressures there. More effort is needed, however, to assess whether adequate foraging habitat is conserved to sustain the nesting population there.

Summary of the Tricolored Blackbird Conservation Status in the Sierra Foothill Grasslands

The substantial number of breeding birds and the high proportion of colonies that successfully nest demonstrate that the lower foothill region of the western Sierra Nevada and adjacent eastern Central Valley play an important role in the conservation of the Tricolored Blackbird in California increasingly (c.f. Hamilton 2000). Occupation of the southern foothills by Tricolored Blackbirds in 2016, after the return of higher rainfall and growth of suitable nesting vegetation, demonstrates the flexibility of the species in locating and using suitable habitat, as well as the importance of nesting habitat availability in the region. Creating persistent nesting habitat there that can remain suitable in dry years could substantially benefit the state's Tricolored Blackbird population, and is a high conservation priority.

Although the current population here appears to be healthy, losses of existing rangeland nesting and foraging habitats to urban development and perennial crops present long-term threats to the species and its grassland

habitat in this region (DeHaven 2000, Cameron et al. 2014). Our previous work found that 46% of the colony sites active in 2014 were in areas approved or proposed for development and mining (Airola et al. 2015a). An updated, more thorough assessment is needed to determine the adequacy of habitat protection and management measures in city and county general plans and other administrative instruments, and what additional measures may be needed to protect both nesting and foraging habitats to indefinitely sustain the Tricolored Blackbird in the foothills.

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