Breeding Population Status of the Tricolored Blackbird in the Foothills of the Central Sierra Nevada, 2014–2022

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ABSTRACT

We report on Tricolored Blackbird (*Agelaius tricolor*) breeding surveys conducted from 2014 through 2022 in an eight-county area in the central Sierra Nevada foothills in California, including previously unpublished survey results from 2019, 2021, and 2022. The number of breeding colonies showed a slight, marginally significant decline, but the total number of breeding individuals did not decline over the study period, despite loss of habitat to development and conversion to unsuitable crops that eliminated some colonies. Numbers recorded in statewide surveys in April 2014, 2017, and 2022 varied substantially from the numbers of breeders we recorded over entire seasons in those years, illustrating the limitations of the statewide survey in assessing the species' breeding population status within this region. The lack of a trend in breeders in the central Sierra foothills differs from the San Joaquin Valley and the statewide population, which both showed substantial recent increases. A possible explanation for the lack of a population trend is that numbers were below the habitat-based carrying capacity during early years of our study, due to substantial reproductive losses over many years in the San Joaquin Valley, a source for foothill nesting birds. The lack of an increase in the number of birds in the foothills after 2018, when the size of the population in the San Joaquin Valley and statewide increased substantially, suggests that the foothill population may have reached a

limit imposed by available habitat. If so, results suggest that the size of the central Sierra foothills population may decline as habitat losses continue. We recommend continued monitoring of Tricolored Blackbird colonies and habitat losses in the foothill region and the conservation of colony sites and suitable foraging areas.

The Tricolored Blackbird (*Agelaius tricolor*) population has been in long-term decline, resulting in its listing in 2018 as a Threatened species under the California Endangered Species Act (Beedy et al. 2023, California Natural Diversity Database 2023). The species was recently identified as one of 70 "*tipping point species*," whose populations in the U. S. have declined by >50% since 1980 and could lose another half or more of their populations in the next 50 years (North American Bird Conservation Initiative 2022). Although recent surveys indicate some population recovery in the statewide population (Colibri Ecological Consulting 2022) associated with elimination of large-scale nest destruction of active colonies in agricultural fields in the San Joaquin Valley (Castañeda et al. 2023), the species' population remains vulnerable to continued land use changes and insecticide use (Beedy et al. 2023).

Over 2014–2022 (except in 2020), we and colleagues have conducted annual studies to describe the species' ecology and conservation status and determine the number of nesting birds in the central portion of the grassland-dominated region on the east side of the Central Valley and Sierra Nevada foothills (hereafter *central Sierra foothills).* We have previously presented information on breeding population size, reproductive success, nesting and foraging habitat selection, effects of foraging habitat amount on colony occurrence and size, effects of development on colony persistence, effects of direct disturbance on colonies, and predation (Airola 2021a, b; Airola et al. 2015a, b; 2016, 2018a, b; 2023). We last reported on the number of nesting birds in central Sierra foothills over 2014–2018 (Airola et al. 2018a, Airola et al. 2023).

Over the nine-year study period, Tricolored Blackbird nesting and foraging habitat in this region has been diminished by conversion to unsuitable perennial crops (orchards and vineyards), residential and commercial development, and mining (Airola et al. 2015a, 2023; Cameron et al. 2014), although recent losses have not been quantified. Additional information on the regional population status under these habitat changes is needed.

The species-wide status of the Tricolored Blackbird in California is evaluated through the comprehensive statewide survey. The survey is conducted on three days in mid-April every three years except for a recent five-year interval resulting from postponements due to the COVID-19

pandemic; Meese 2014, 2017; Colibri Ecological Consulting 2022). The statewide survey dates were selected as the period during which the species is most concentrated when breeding in the San Joaquin Valley in order to produce the most accurate range-wide population estimate (Meese 2015, Colibri Ecological Consulting 2022). Surveyors attempt to check all previously occupied sites, as identified in the Tricolored Blackbird Portal (https://tricolor.ice.ucdavis.edu/) and locate new colony sites on routes driven through suitable nesting habitat. The Tricolored Blackbird, however, typically breeds several times per year, and moves northward after their initial nesting effort to breed a second and sometimes a third time (Hamilton 1998, Robinson et al. 2018).

Airola et al. (2018a) previously compared the number of Tricolored Blackbirds recorded in the central Sierra foothills during the April 2014 and 2017 statewide surveys and numbers recorded during in our breeding-season-long surveys. Results showed that in the drier 2014, the species arrived early in the foothills, but only some of those birds initiated their first nesting attempts there (Airola 2018a). In contrast, in the wetter 2017, the size of the population recorded in the central Sierra foothills during the statewide survey was only one-third of the number that eventually nested there, suggesting that many birds bred first in the south before arriving to initiate a second nesting attempt in the foothills. We extended this comparison of population sizes recorded during 2022 on the statewide survey and our breeding surveys to further determine the accuracy of the statewide surveys in characterizing the central Sierra foothills breeding population and indicate annual patterns of breeding arrival and use in the foothill region.

Here, we add results of season-long population estimates from 2019, 2021, and 2022 to update the status of the population in this region, discuss potential population responses to habitat loss occurring over the nine-year survey period, and expand our comparisons of population sizes recorded in the statewide survey and breeding season surveys in the central Sierra foothills region. We use the term *population* in the general sense, to indicate the number of individuals and the group of individuals that occupy the central Sierra foothills region, rather than to suggest physical isolation or genetic distinctiveness.

STUDY AREA

We chose the central Sierra foothills for study because it appeared to support a substantial number of breeding Tricolored Blackbirds in a setting that was different from more intensively studied agriculture and wetland colonies in the Central Valley (e.g., see Beedy et al. 2023). This region differs from the valley both in its predominant habitat type (grassland) and breeding substrate (Himalayan blackberry, *Rubus armeniacus*). The study area is the same region surveyed consistently since 2014. It encompasses areas of

primarily grasslands east of lowlands dominated by cultivated agriculture in the central portion of the Central Valley, including portions of Placer, Sacramento, El Dorado, Amador, San Joaquin, Calaveras, Stanislaus, and Tuolumne counties. Elevations range from 15 to 550 m. In addition to grasslands, the area includes smaller amounts of urban land, oak savanna and woodland, chaparral, irrigated pasture, and cultivated agriculture (for a map of the study area see Figure 1 in Airola et al. 2023). Most of this area is privately owned, and much is used for cattle grazing.

Our definition of the central Sierra foothills differs from the foothill region used in the Tricolored Blackbird statewide survey (Colibri Ecological Consulting 2022); we included eastern Sacramento County, while the statewide survey treats the whole county as part of the Sacramento Valley region. Also, we included only those lands in the eastern (grassland-dominated) portions of San Joaquin and Stanislaus counties, while the statewide survey included all of both counties as part of the San Joaquin Valley. Individual colonies are referenced in italics by the names assigned in the Tricolored Blackbird Portal. We believe our study area encompasses a more uniform set of conditions and allows a more robust characterization of Tricolored Blackbird status in grassland-dominated areas.

METHODS

Experienced Tricolored Blackbird surveyors conducted surveys using standardize methods (Airola et al. 2018b). We drove survey routes on public roads at five-to-ten-day intervals from early April to early July during 2014–2022 (except 2020, due to the COVID-19 pandemic). Routes were designated to visit previously occupied colony sites and areas with suitable blackbird foraging habitat, consisting of areas where grassland, irrigated pasture, annual crops, and open woodland were predominant (Airola et al. 2015, 2023). On each visit we recorded the number of individuals and nesting stage and followed active colonies to determine if they were successful (i.e., some young fledged). Numbers of breeders were determined using counts and the amount of nesting habitat occupied (Airola et al. 2015a, 2018b). We also conducted all the April 2022 surveys for the portions of the statewide survey within our study area, except Placer County was surveyed by past breeding survey collaborator Deren Ross.

We evaluated whether the number of colonies, total number of breeding birds, and average colony sizes showed trends over the study period using linear regression (https://www.graphpad.com/quickcalcs/linear2/). We tested the significance of the regression slope using an F-test, in which a significant slope indicated a population increase (if positive) or decrease (if negative), with a test significance probability of 0.05. Probability values between 0.05 and 0.10 were considered marginally significant. We also compared the sizes of the populations recorded in our season-long breeding surveys to the

numbers reported within our study area during the April 2014, 2017, and 2022 statewide surveys to determine how well the statewide survey characterized the breeding population in the central Sierra foothills.

RESULTS

Numbers of Colonies and Breeding Birds

Over 2014–2022, we found an average of 26 breeding Tricolored Blackbird colonies (range = 21–31) in the central Sierra foothills (Table 1). The number of colonies declined over time (slope = −0.79) to a low of 21 colonies in 2022, but the decline was only marginally significant (R^2 = 0.44, F = 4.64, P = 0.07, Figure 1).

Colonies were most numerous in Sacramento and Placer counties, which together accounted for 56% of all colonies in the study area. In most years, two to five colonies were present in Amador, Calaveras, Stanislaus, and Tuolumne counties. Four colonies were present in El Dorado County in 2014, but as the grassland foraging habitat adjacent to breeding sites along Carson Creek in El Dorado Hills continued to be developed for commercial and residential use, the number declined to a single colony over the next two years, and then no colonies were active over the next five years. Groups initiated nesting early in 2021 (1 group) and 2022 (2 groups) at the former colony sites along Carson Creek but abandoned the sites before egg-laying. Other than one early nesting attempt that was abandoned, no nesting occurred in portions of the study area within San Joaquin County.

Table 1. Numbers of Tricolored Blackbird breeding colonies in the central Sierra foothills by county and year.

	Year								
County	2014	2015	2016	2017	2018	2019	2021	2022	Avg.
Placer	6	5	7	6	6	4	8	4	5.8
Sacramento	9	12	7	9	8	7	6	9	8.4
El Dorado	4	1	1	0	0	0	0	0	0.8
Amador	3	4	3	5	2	3	3	3	3.3
San Joaquin	0	0	0	0	0	0	0	0	0.0
Calaveras	3	2	3	4	3	4	5	3	3.4
Stanislaus	4	1	4	3	3	2	1	1	2.4
Tuolumne	0	0	2	4	2	2	2	1	1.6
Total	29	25	27	31	24	22	25	21	25.5

The central Sierra foothill breeding population fluctuated between about 36,000 and 58,000 adults per year over the nine-year study period (Figure 1, Table 2). No significant trend in numbers was evident (R^2 = 0.02, F = 0.13, P = 0.63).

Table 2. Numbers of breeding Tricolored Blackbirds by county and year in the central Sierra Nevada foothills study area.

	Year								
County	2014	2015	2016	2017	2018	2019	2021	2022	Average
Placer	12,473	19,200	19,900	9,750	25,000	9,900	8,640	6,400	13,908
Sacramento	11,000	19,300	17,150	33,800	26,600	19,200	13,250	37,625	22,241
El Dorado	5,800	2,900	1,000	0	0	0	0	0	1,213
Amador	6,375	6,320	1,140	1,500	1,200	5,520	4,900	4,200	3,894
San Joaquin	0	0	0	0	0	0	0	0	0
Calaveras	760	350	1,300	720	2,350	2,550	2,200	3,400	1,704
Stanislaus	6,601	7,000	4,550	11,000	2,600	9,300	6,500	1,200	6,094
Tuolumne	0	0	2,300	1,140	750	650	850	200	736
Total	43,009	55,070	47,340	57,910	58,500	47,120	36,340	53,025	49,789

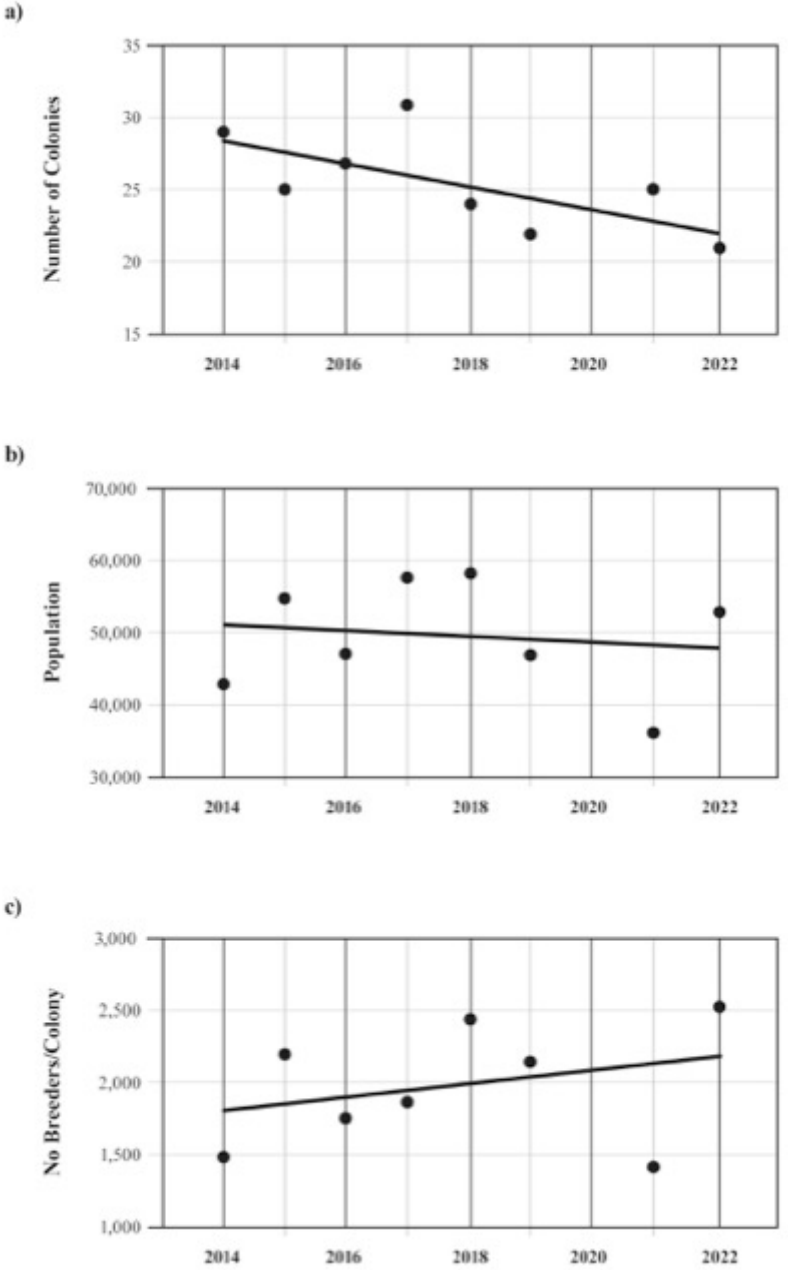

Figure 1. Annual numbers of a) colonies, b) breeding birds, and c) average number of bird colonies in the central Sierra foothills over the nine-year study period.

Sacramento and Placer counties were the most important areas in the study area, with an average of over 22,000 breeders (45% of the total) in Sacramento and nearly 14,000 in Placer (28% of total numbers; Table 2). Stanislaus and Amador counties supported an intermediate number of breeders (12% and 9% of the total, respectively). Remaining occupied counties supported low-to-moderate population sizes throughout, except El Dorado County, which had no breeders after 2016, and San Joaquin, which had none for the study period. Some annual fluctuation in numbers within counties reflected apparent movements of birds among nearby colony sites in different counties, including between Sacramento and Placer counties and between Calaveras and Stanislaus counties.

Colony sizes varied from 20 to 9,300 birds over the study period and averaged 1,910 birds over all survey years, with the annual average size varying from about 1,500–2,500 birds (Figure 2). Although a generally increasing trend in colony size was evident over the nine-year study period, the relationship was not significant ($R^2 = 0.09$, $F = 0.63$, $P = 0.46$).

Habitat Loss

Airola et al. (2023) summarized habitat losses during 2014 through 2018, which included elimination or degradation of 13 (17%) of 78 colony sites used in this period. Over 2019–2022, we located 13 new colony sites within previously surveyed areas, for a total of 91 colony sites. During 2019–2022, we observed that vegetation used for nesting was removed during the non-nesting period at three additional colony sites, and additional foraging habitat was eliminated around 10 of the previously degraded colony sites, due to continued development and mining. Thus, over the 2014–2022 period, 16 (18%) of 91 colony sites were eliminated or degraded through development, mining, or vegetation control.

Comparison of Breeding Population and Statewide Survey Numbers

Total numbers recorded within the study area during the three April statewide surveys did not match those we recorded in breeding-season surveys (Table 3). The population recorded in the 2014 breeding season surveys was only two-thirds of the number recorded in the statewide survey. In 2017, breeding survey totals were nearly 2.5 times higher than statewide survey numbers, whereas in 2022 numbers were similar, with 25% more birds found in breeding season surveys. Considerable variation also occurred between numbers recorded in individual counties in the two different surveys.

Most of the sites that were occupied by Tricolored Blackbird groups during the April statewide survey were in the settling stage (i.e., selecting nest sites and attracting mates). Many of these early-occupied sites ultimately did not become active breeding colonies, and numerous other colonies were

Table 3. Comparison of numbers of Tricolored Blackbirds recorded during 2014, 2017, and 2022 statewide surveys and central Sierra foothills breeding season surveys.

	2014		2017		2022	
County	Statewide Survey[a]	Foothill Breeding Survey	Statewide Survey[a]	Foothill Breeding Survey	Statewide Survey[a]	Foothill Breeding Survey
Placer	17,600	12,473	960	9,750	2,250	6,400
Sacramento	29,272	11,000	12,455	33,800	27,690	37,625
El Dorado	1,375	5,800	100	0	1,336	0
Amador	5,500	6,375	420	1,500	854	4,200
San Joaquin	500	0	0	0	0	0
Calaveras	404	760	1,570	720	2,240	3,400
Stanislaus	8,852	6,601	742	11,000	7,800	1,200
Tuolumne	825	0	850	1,140	200	200
Total	64,328	43,009	17,097	57,910	42,370	53,025
% difference	+50%		−70%		−20%	

[a]Sources: Meese 2014, Meese 2017; Colibri Ecological Consulting 2022

established after the statewide survey weekend. For example, 22 foothill sites were occupied during the 2022 statewide survey, but only 15 (65%) proceed to incubation. Twelve additional sites not occupied during the statewide surveys were visited subsequently by Tricolored Blackbirds and six ultimately hosted successful breeding colonies.

DISCUSSION

Breeding Population Trend

Our results show that the numbers of colonies and breeding birds in the central Sierra foothills did not significantly change over the nine-year study period. The marginally significant decline in the number of colonies was offset by a slight, but non-significant increase in average colony size. The lack of a decline in colony size in the central Sierra foothills region differs from the declining trend reported statewide over 1935–1975 (Graves et al. 2013) and as recently as through 2017 (Meehan et al. 2018). This difference may reflect the inclusion of surveys over 2018–2022 in our analysis, during which an increase in the statewide population and average colony size occurred (Colibri Ecological Consulting 2022).

Survey results show that Sacramento and Placer counties consistently supported the highest number of colonies and breeding birds in the central Sierra foothills region. These counties are also subject to the greatest development pressure in the region (Airola et al. 2023). Our annual survey results strengthen previous conclusions (Airola et al. 2023) that development of the Carson Creek Valley area south of Highway 50 in El Dorado Hills, El Dorado County, as well as in adjacent areas in Folsom, Sacramento County, appears to have reduced the amount of grassland foraging habitat to a level insufficient to sustain the Tricolored Blackbird breeding colonies that once occurred there.

The absence of colonies in San Joaquin County during our surveys is notable. Seventeen sites were reported to be occupied during 1994–2000 within the portions of our study area in the county (https://tricolor.ice.ucdavis.edu). Since then, no active colonies have been observed, despite our substantial survey effort. The species' disappearance as a breeder occurred prior to our study period when grasslands and other open habitats in San Joaquin County were widely converted to vineyards, making San Joaquin County one of California's top wine-producing counties (Volpe et al. 2010, Geisseler and Horwath 2016). Our survey results in Folsom and El Dorado Hills and evaluation of the species' recent history in San Joaquin County demonstrate the local impacts of habitat loss on the breeding Tricolored Blackbird population within the central Sierra foothills.

Implications of Differences between Breeding Population and Statewide Survey Numbers

The statewide survey is the only comprehensive survey of the species population size throughout California. The survey has been conducted in April, when Tricolored Blackbirds are most concentrated in the southern portion of their range, especially in the San Joaquin Valley (Meese 2014). Compared to our breeding survey numbers, the numbers recorded in the central Sierra foothills during the statewide surveys, covering the same areas in both surveys, were substantially higher in one year (by 50%), substantially less in another (−70%), and reasonably close in another (−20%). These results demonstrate that the statewide survey numbers, as valuable as they are in characterizing the statewide population, do not accurately characterize the breeding status of the portion of the population that breeds in the central Sierra foothills region and presumably throughout the central and northern portions of the species' California breeding range. Thus, our study results complement those of the statewide survey, as have similar season-long surveys in the San Joaquin Valley (Castañeda et al. 2023) and central California Coast (Wilson et al. 2016).

Conservation Implications

Many declining bird species may become isolated and genetically depauperate, which increases their risk of extinction (Evans and Sheldon 2008). Despite its past declines, the Tricolored Blackbird is a genetically panmictic population (i.e., lacking differentiation geographically; Berg et al. 2010, Barr et al 2020). The panmixia likely results from the wide-ranging habits of groups of individuals that move annually between multiple nesting regions and non-breeding habitats (Hamilton 1998, Airola et al. 2023, Beedy et al. 2023), which prevents geographic differentiation and promotes genetic diversity (Berg 2020). Panmixia thereby reduces the chances of inbreeding and maintains greater ability to adapt to environmental change. Tricolored Blackbirds that nest in the central Sierra foothills are believed to nest in some years (especially wetter ones) first in the San Joaquin Valley or southern Sierra Nevada foothills before moving to nest again in the central Sierra foothills (Airola et al. 2016, 2018a) such as occurred in 2017 (Table 3). In drier years, it appears that many Tricolored Blackbirds overfly the San Joaquin Valley and move earlier to the foothills or further north to initiate their first breeding (i.e., 2014, Table 3).

The central Sierra foothills region has been considered high quality habitat for the Tricolored Blackbird for several reasons. Colonies mostly occur in patches of Himalayan blackberry, which are highly protective from predators (Cook and Toft 2005, Airola 2021a) so that a high proportion of colonies successfully fledge young (Airola et al. 2018). Also, insecticide use in

this grassland-dominated region is likely lower than in agricultural regions (Airola et al. 2015, Beedy et al. 2023). This lower use could result in lower direct exposure to blackbirds or maintenance of higher insect prey populations required for reproduction. Although an initial evaluation of direct accumulation of neonicotinoid insecticides in tissues of Tricolored Blackbirds collected in agricultural regions found the insecticide in only 2 of 85 individuals sampled (Graves et al. 2022), the study did not address reduction of insect prey, which has been suspected to cause low reproduction of blackbirds at agricultural colonies in the Central Valley (Meese 2013). Colony sizes in the foothills, however, tend to be smaller than in agricultural habitats (Figure 2; Airola et al. 2023, Castañeda et al. 2023).

The lack of a decline in the number of breeding Tricolored Blackbirds in the central Sierra foothills is paradoxical, considering that a substantial amount of habitat in the region has been lost to development and conversion to orchards and vineyards (Cameron et al. 2014, Airola et al. 2023) and colonies have been eliminated in Folsom and El Dorado Hills. Our survey period, however, coincided with the establishment of a successful program to protect Tricolored Blackbird colonies in agricultural fields in the San Joaquin Valley (Colibri Ecological Consulting 2022, Castañeda et al. 2023). Prior to 2015, colonies supporting 50,000 to 150,000 breeding birds were regularly destroyed by harvest, resulting in total nesting failure. Presumably partly in response to these losses, the population declined statewide through at least 2014 (Meese 2014, 2017) and in the San Joaquin Valley through 2015 (Castañeda et al. 2023). Following enactment of protection of most agricultural colonies in 2015, the number of Tricolored Blackbirds nesting in the San Joaquin Valley, and then presumably those nesting elsewhere during a second nesting period, increased by an estimated 99,000 (127%) over 2017–2021, and total numbers recorded in the statewide survey over 2014–2022 increased by 73,000 (50%; Colibri Ecological Consulting 2022). Thus, while the population increased substantially elsewhere over our study period, the number of breeding birds in the central Sierra foothills did not.

One potential explanation for the lack of a decline in the central Sierra foothill population during our study period, despite ongoing habitat loss, is that during the early years of our study the number of breeding birds may have been constrained by colony losses to agricultural harvest in the San Joaquin Valley (Castañeda et al. 2023) rather than availability of suitable habitat. During the early years of our survey the statewide population was at its lowest recorded level (Meese 2017, Colibri Ecological Consulting 2022), which likely affected the pool of breeders available to use the central Sierra foothills. Therefore, as occupied areas were eliminated, such as in Folsom and El Dorado Hills, birds that used those sites were able to relocate to other suitable areas that were not fully occupied.

The lack of an increase in the central Sierra foothill population after 2017, when the breeding populations San Joaquin Valley and statewide increased substantially, is consistent with an explanation the population became limited by the available habitat, which prevented its increase. If this hypothesis is correct, and the population is currently at its habitat-based limit during favorable years, then a population decline may be observed in the future as suitable habitat continues to be converted to unsuitable development and orchards and vineyards. The modest decline in the annual number of colonies we observed may be an initial indication of a regional decline, particularly if efforts to protect remaining colony sites and surrounding foraging areas are not undertaken.

Other factors also may have affected numbers of breeders we recorded in the central Sierra foothills, as indicated by the variation in numbers in adjacent years (e.g., a 46% increase from 2021 to 2022). Drought has been suggested as affecting numbers found in the foothills during the statewide survey, through its effects on food supply, drinking water, and nesting habitat (Colibri Ecological Consulting 2022). We did not find declines in this region during the dry 2014–2015 years but observed a sharp decline during the dry 2021 (Table 1; Airola et al 2018a). Incomplete sampling is also an unavoidable source of variation, as in some years colonies could have moved to areas that were inaccessible to surveyors.

The ultimate fate of the Tricolored Blackbirds in the central Sierra foothills region is concerning, given the species' need for large amounts of foraging habitat (Airola et al. 2023) and the continued conversion of occupied and suitable habitat to unsuitable uses, even under established regional conservation plans (Sacramento County 2018, Placer County 2020). Our lack of detection of a population decline over our nine years of monitoring should not foster complacency, considering the complicated set of external and internal factors that appears to have produced it. Rather, these factors and the lack of a recent population increase, as has occurred elsewhere, raise concerns about the future of the species in the central Sierra foothills. Although we ended our annual breeding surveys after the 2022 season, we recommend regular periodic breeding season surveys (i.e., at least every three years, in association with the statewide survey) to track the breeding population trend. More importantly, we encourage enactment of more comprehensive conservation measures to protect the Tricolored Blackbird and its habitat in this region.

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