FORAGING HABITAT AND ITS EFFECTS ON THE TRICOLORED BLACKBIRD'S BREEDING DISTRIBUTION AND ABUNDANCE IN THE SIERRA NEVADA FOOTHILLS, CALIFORNIA

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ABSTRACT: The grassland-dominated eastern Central Valley and Sierra Nevada foothills of California, from Placer to Stanislaus counties, supported at least 43,000–55,000 breeding Tricolored Blackbirds (*Agelaius tricolor*) annually from 2014 to 2018—about 30% of the statewide population. We found that within 5 km of a colony, the extent of land cover used for foraging, grassland–herbaceous, and to a lesser extent annual crops and irrigated pasture, exceeded their proportions in this region as a whole, suggesting that nesting Tricolored Blackbirds select colony sites where these habitats are more abundant. Other land-cover types were underutilized for foraging, suggesting avoidance. The probability of Tricolored Blackbird occupancy of blocks of 100 km^2 was strongly associated with the extent of the selected land-cover types. The relationship between average density of the breeding population and the extent of the selected land-cover types was significant but weaker, implying that other factors are important in determining density. From 2014 to 2018, development and mining eliminated or degraded 9 of 79 colony sites and made 4 others unsuitable by reducing the extent of nearby foraging habitat, although the total breeding population in the region did not decline. We recommend that conservation measures for the Tricolored Blackbird in federally and state-approved habitat-conservation plans in Placer and Sacramento counties, which support the largest breeding populations in the central Sierra foothills but where urban development is rapid, be reevaluated on the basis of recent colony locations and recognition of the critical role of grassland, annual crops, and irrigated pasture as foraging habitat.

The Tricolored Blackbird (*Agelaius tricolor*) has long been in decline throughout its range in California (Graves et al. 2013, Clipperton 2018) and was listed as threatened under the California Endangered Species Act in 2018 (Beedy et al. 2018). The major historical cause for the species' population decline has been loss of wetlands and grasslands (Beedy et al. 2018). The primary recent threats in agricultural lands of the Central Valley have been destruction of nesting colonies in agricultural crops (substantially reduced since 2015 through financial incentives; Castañeda et al. 2023), conversion of grasslands and field crops to vineyards and orchards, and reduction in insect populations (and possible direct mortality) caused by insecticides (Cook and Toft 2005, Meese 2013, 2017, Meese et al. 2015, Beedy et al. 2018, Clipperton 2018).

From 2014 to 2018, surveys within the central portion of the grassland-dominated foothill region of the eastern Central Valley and lower Sierra Nevada ("central Sierra foothills") identified a minimum annual breeding population of 43,000–58,500 Tricolored Blackbirds (Airola et al. 2018b), which represents about 30–33% of the estimated statewide population (Meese 2014, 2017). The numbers nesting in these foothills appear to be more stable than in other areas of the species' range, owing to low levels of human disturbance, limited pesticide use, a low rate of predation, and the availability of irrigated pastures that may moderate the effects of drought (Airola et al. 2015a, 2016). Some foothill lands that support nesting and foraging habitat for the Tricolored Blackbird, however, are subject to conversion to crops that do not provide foraging habitat, residential development, and mining (Cameron et al. 2014, Airola et al. 2015a, Soulard and Wilson 2015). Nearly half of the Central Sierra foothills population nests in Sacramento and Placer counties, where development pressure is high (Airola et al. 2018b).

The importance to the Tricolored Blackbird of water sources, and of grasslands and alfalfa as foraging habitat, has been confirmed (Cook and Toft 2005, Airola et al. 2015a, Wilsey et al. 2019). Other land covers, including irrigated pasture and non-irrigated hay and grain fields in combination with grasslands, may be important to the species (Airola et al. 2018b) but have not been extensively evaluated. Neither the minimum extent of suitable foraging habitat required to support a nesting colony nor the relationship between the extent of suitable habitat and number of breeding birds in a colony has been quantified, but both measures are crucial for the species' conservation.

We summarized the locations and sizes of Tricolored Blackbird colonies in the central Sierra foothills from 2014 to 2018 (Airola et al. 2015a, b, 2016, 2018a, b). We also mapped and quantified the extent of various land covers within the study area, and we used the average number of breeding Tricolored Blackbirds in 100-km^2 grid cells to evaluate the relationship between the extent of land cover and Tricolored Blackbird occupancy and abundance. We apply this information to provide guidance for conservation planning in this and similar grassland-dominated regions within the species' range.

STUDY AREA AND METHODS

Study Area

Our study area encompassed 33,750 km^2 at 15 to 550 m elevation in the lower foothills of the western Sierra Nevada and the eastern edge of the Central Valley, California, in Placer, Sacramento, El Dorado, Amador, Calaveras, San Joaquin, Stanislaus, and Tuolumne counties (Figure 1). We selected this area because it had been surveyed consistently over five years (2014–2018). In this area, lying east of the predominantly flat, cultivated agricultural lands of the Central Valley, the cover of annual grasslands is >50%. Less extensive land-cover types are oak woodland, scrub, urban, and agricultural, among others (Airola et al. 2015a, 2018b; Figure 1; see Results). Individual colonies are referenced in italics by the names assigned in the Tricolored Blackbird Portal (https://tricolor.ice.ucdavis.edu/).

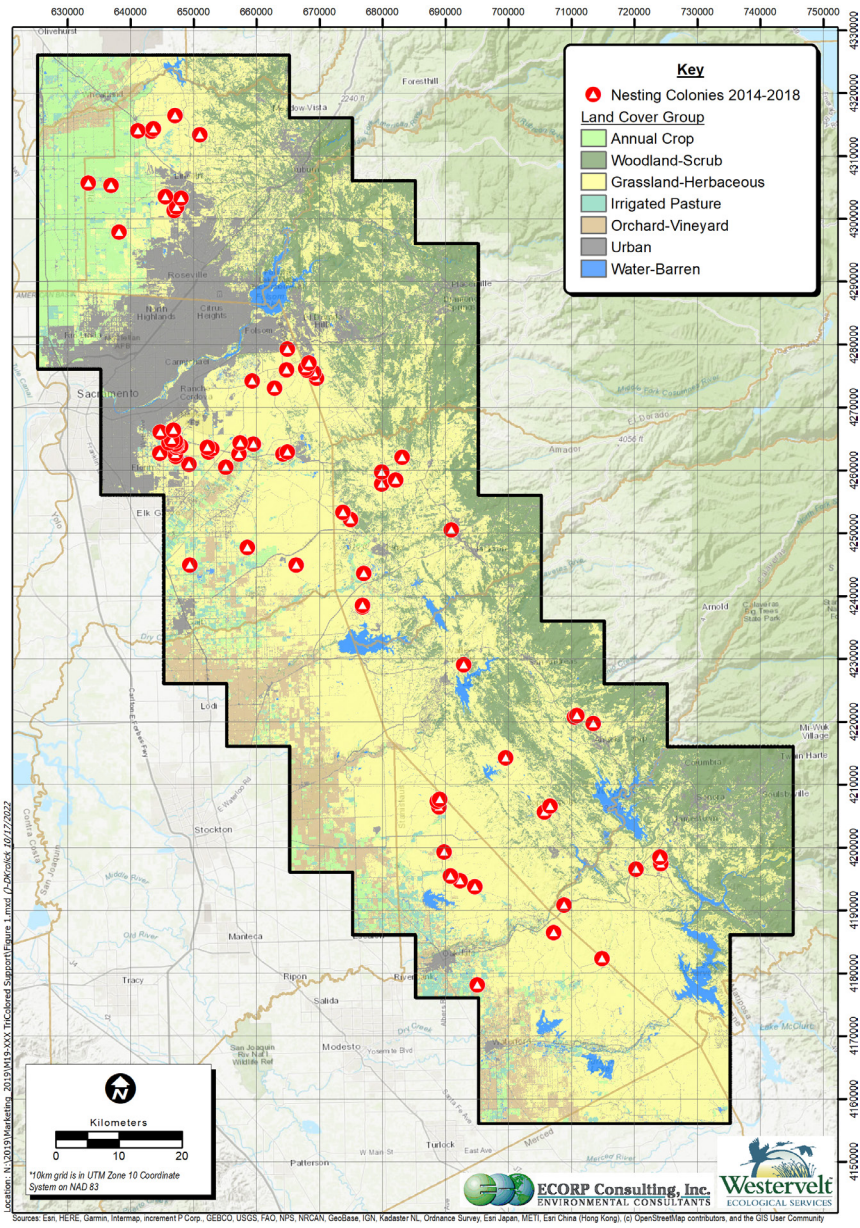

FIGURE 1. Distribution of Tricolored Blackbird nesting colonies and major land-cover types within the Central Sierra foothills study area, 2014–2018. Grid cells depicted were the same as those used in the study.

Population Survey and Abundance

The results of our population surveys have been reported by Airola et al. (2015a, b, 2016, 2018a, b; see also appendix at https://archive.westernfieldornithologists.org/archive/V54/Airola-et-al-Tricolored-Blackbird-APPENDIX-WB54-1.pdf). We repeated visual surveys at 7- to 10-day intervals over the breeding season to locate colonies, estimate numbers of breeding birds (defined as those birds at colonies that reached the egg-laying stage), and track reproductive stage and success (Airola et al. 2015b). We surveyed mainly from public roads because the multiplicity of private landowners made arranging access away from public roads impractical. Because of the high proportion of private lands in the study area, surveys included only 28–43% of the area broadly defined as suitable foraging habitat for the Tricolored Blackbird (grassland, pasture, and row crops; Airola et al. 2015b, 2016, 2018a). We believe, however, that we surveyed a higher proportion of the suitable habitat that breeding Tricolored Blackbirds actually occupied because roads gave better access to the flatter, more extensive grasslands at lower elevations than to the higher foothills (see Results).

We defined colony size at each site as the average annual number of breeding birds over the survey period. To quantify density, we applied a 10-km grid (100 km^2/cell) over the study area, defining 87 grid cells, then totaled the average annual number of breeders at all colonies within each cell. Fifty-four (62%) of the 100-km^2 grid cells were censused in at least one year from 2014 to 2018, but most were surveyed in all years (= 4.7 survey-years per site, ± 0.8 SD).

Land-Cover Mapping and Characterization

We characterized land cover primarily on the basis of 2014 data from CropScape (USDA National Agricultural Statistics Service 2014). We grouped CropScape's 70 land categories within the study area into six major land covers (Table 1) by their growth-form similarity and previously documented pattern of use by the Tricolored Blackbird (Airola et al. 2015a, Wilsey et al. 2019). CropScape does not clearly define areas of irrigated pasture, which we believed might be important as foraging habitat. Therefore, to evaluate its

Table 1 Land-Cover Types Used in the Analysis and Major Constituent Cover Types from CropScape Mapping

Land-cover type	Major constituent CropScape land categories[a]
Grassland–herbaceous	Grass/pasture, other hay/non-alfalfa, alfalfa, clover/wildflowers, herbaceous wetlands
Woodland–scrub	Evergreen forest, shrubland, deciduous forest, woody wetlands
Annual crops	Fallow/idle cropland, rice, winter wheat, oats, corn, tomatoes, triticale
Urban–road	Developed (high, medium, low density)
Orchard–vineyard	Grapes, walnuts, almonds
Water–barren	Open water, barren
Irrigated pasture	None; imported from FRAP (see Methods)

[a]Land categories by CropScape that occupied >0.1% of the study area, in descending order of extent. An additional 40 recognized categories each occupied <0.1% of the total area.

importance, we identified areas delineated as irrigated pasture in 2015 by the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP; https://frap.fire.ca.gov/mapping/gis-data/). If FRAP had identified irrigated pasture in a cell, we substituted the FRAP data for the values in the CropScape dataset.

We summarized land-cover characteristics at three scales. First, we quantified the proportions of the six land-cover types over the entire study area. Second, we summarized land cover in each of the 87 100-km^2 grid cells, to evaluate breeding density (birds/cell) in relation to land cover. Third, we quantified land cover within 5 km of each colony, selecting this radius on the basis of the reported foraging range of nesting birds (Beedy et al. 2018).

We did not quantify nesting habitat because the small patches of Himalayan blackberry (*Rubus armeniacus*) and emergent marsh vegetation (generally <1 ha; Airola 2021) in which the Tricolored Blackbird nests in this region were not mapped in CropScape.

Data Analysis

At the finest scale, we evaluated the relationship between the Tricolored Blackbird's habitat use and colony-site selection by comparing the average proportion of each land-cover type (and a combination of land-cover types) within 5 km of each colony to the proportion within the entire study area. For this we used a one-sample *t*-test, accepting statistical significance at $P < 0.05$. Land-cover types whose average proportions within 5 km of colonies were higher than their proportions in the entire study area we considered *selected*. Those cover types whose proportions were lower than expected had they been distributed randomly with respect to colony sites we considered *avoided*.

We then used a hurdle model (Potts and Elith 2006) to evaluate associations between both blackbird occurrence and abundance and the proportion of the selected land-cover types within the 100-km^2 grid cells. A hurdle model is a two-part model that specifies one process for zero counts and another for positive counts. We modeled occupancy (probability of at least one breeding pair) as following a Bernoulli distribution via a logit-link function, and abundance at occupied locations as following a Poisson distribution via a log-link function, using the function *hurdle* in the package *pscl* of the statistical programming language R (Zeileis et al. 2008). We evaluated the significance of the selected cover covariate as a predictor of occupancy and abundance on the basis of a Type I error rate of 0.1, consistent with recommendations for monitoring programs (Bart et al. 2004).

Finally, each year we recorded detrimental changes to colony sites, defined as elimination of used nesting habitat (both during and between nesting seasons) and substantial losses of suitable foraging habitat near colonies (over ~50% within 2 km).

RESULTS

Population Distribution and Density

Over the five years of our study, we found Tricolored Blackbird colonies at 79 widely distributed sites (Figure 1). Of the 54 100-km^2 grid cells we

surveyed, 28 (52%) had at least one colony in at least one year. The averaged density of the breeding population per grid cell also ranged widely, up to a maximum of 9650 breeding birds per year. Densities were highest in Sacramento and Placer counties. Many colonies were clustered around urban areas, including the cities of Lincoln and Rocklin in Placer County, Folsom and Sacramento in Sacramento County, and unincorporated areas in both counties (Figure 1).

Habitat Use and Selection

Within our study area, Tricolored Blackbird colonies were disproportionately located at elevations below 200 m (Figure 2). Land cover within 5 km of colonies was dominated by the grassland–herbaceous group; woodland–scrub, annual crops, urban–road, orchard–vineyard, and open water–barren were less extensive (Figure 3). The proportion of area covered by grassland–herbaceous was greater within 5 km of colonies than over the entire study area, suggesting its selection by nesting Tricolored Blackbirds (Figure 3; $t = 10.25$, $P < 0.0001$). The proportions of annual crops and irrigated pasture within 5 km of colonies were also greater but not significantly so. When we added cover of these two groups within 5 km of colonies to that of the grassland–herbaceous group, the proportional coverage of the three groups combined was significantly higher than over the entire study area as a whole ($t = 14.28$, $P < 0.0001$), more significantly than grassland alone (by the t-value). Conversely, the proportions of the woodland–scrub, orchard–vineyard, and water–barren groups within 5 km of colonies were significantly lower than over the study area as a whole ($t = 12.09$, 6.2, and 12.8 respectively, all $P < 0.0001$), suggesting that these types were avoided.

Relationship between Land Cover and Blackbird Occupancy and Abundance

The likelihood that Tricolored Blackbirds nested within 100-km^2 grid cells was associated with several habitat attributes. The proportion of selected

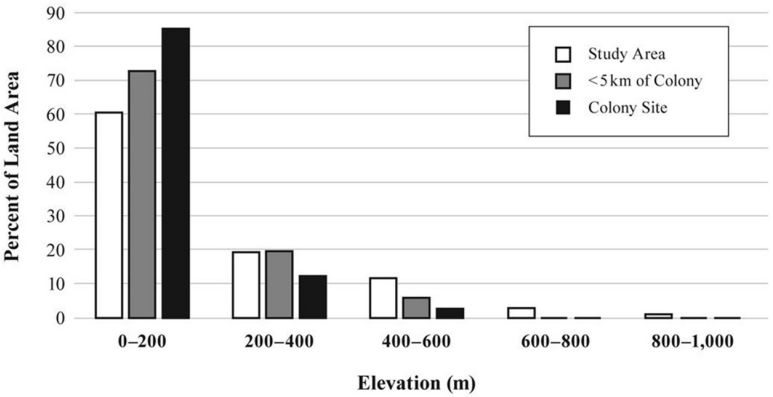

FIGURE 2. Proportions of colony sites, lands surrounding colonies, and the entire study area in various elevation zones (percent of total represented by each category).

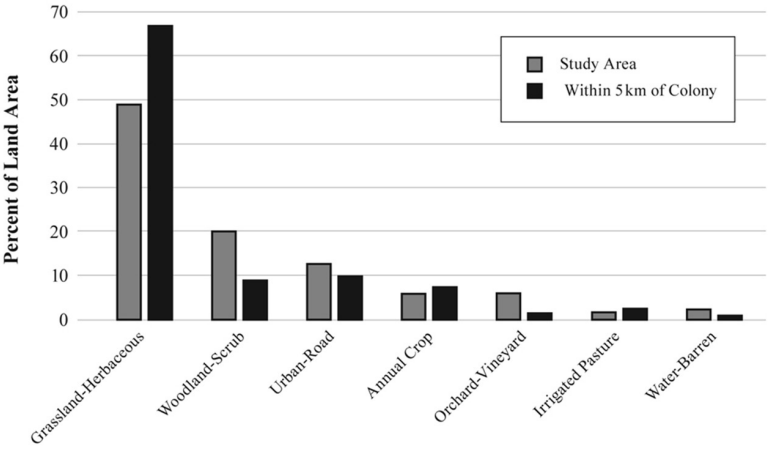

FIGURE 3. Comparison of the percent cover by land-cover type within the entire study area and within 5 km of Tricolored Blackbird nesting colonies monitored 2014–2018.

land-cover types (i.e., grassland–herbaceous, irrigated pasture, and annual crops combined) was significantly higher in occupied grid cells (= 74% ± 24 SD, n = 33) than in unoccupied cells (= 62% ± 18 SD, n = 37; t = 2.40, P = 0.01). The hurdle model shows that the proportional extent of these selected land-cover types was positively associated with both Tricolored Blackbird occupancy (P = 0.02) and abundance (P = 0.07) at surveyed locations (Table 2); however, selected land cover was a stronger predictor of occupancy than it was of abundance (Figure 4).

2014–2018 Habitat Loss and Degradation

We observed degradation of nesting habitat at nine (11%) of the 79 colonies, including one where the nesting vegetation was partially cleared during active nesting (*Sonora #3,* Stanislaus County), one cleared outside the nesting season (*Yosemite Junction,* Tuolumne County), one sprayed with herbicide

TABLE 2 Results of a Hurdle Model Showing Association of Occupancy and Abundance of the Tricolored Blackbird with the Proportion of Selected Land-Cover Types within 100-km^2 Grid Cells in the Central Sierra Foothills, 2014–2018

Model term	Estimate	Standard error	P
Occupancy			
Intercept	0.056	0.291	0.85
Selected land cover[a]	0.793	0.331	0.017
Abundance if occupied			
Intercept	7.724	0.004	<0.001
Selected land cover[a]	0.009	0.005	0.070

[a]Proportion of selected land-cover types (i.e, grassland–herbaceous, irrigated pasture, and annual crops) within 100-km^2 grid cells.

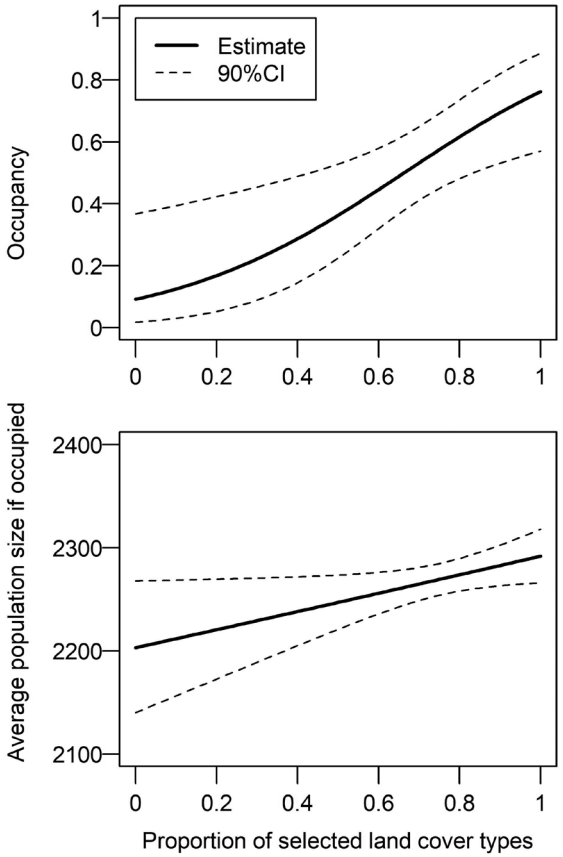

FIGURE 4. Probabilities (with confidence intervals) predicted by a hurdle model of Tricolored Blackbird occupancy and abundance (average breeding birds per year, 2014–2018) in relation to the proportional abundance of selected land-cover types (grassland–herbaceous, irrigated pasture, and annual crops combined) in 100-km^2 grid cells within the central Sierra Nevada foothills.

(*Jackson Highway Quarry,* Sacramento County), and six where cessation of irrigation killed or desiccated nesting habitat (*Elder Creek 1*, *2*, *4*, *5*, *6*, and *7,* Sacramento County; Airola et al. 2015a, b, 2016, 2018a, b).

In addition, residential and commercial development eliminated substantial areas of grassland near four (5%) colony sites where nesting habitat was not disturbed, including three in the unincorporated community of El Dorado Hills in El Dorado County (*Carson Creek Bridge*, *Farm House*, and *Tule Marsh*) and one in the city of Folsom, Sacramento County (*Iron Point Road*). These sites in El Dorado County were not used after the development of nearby grasslands in 2014. The *Iron Point Road* site was abandoned during nesting in 2018 as several hundred hectares of grassland where the birds had

foraged near the colony were developed for residential and commercial uses (Airola et al. 2018b). Tricolored Blackbirds returned and nested successfully at *Iron Point Road* in 2019 but not from 2020 to 2022 as nearby development continued.

The 13 degraded sites represented 16% of all colony sites. Prior to degradation, they supported an annual average of 11,610 breeding birds, representing 24% of the annual breeding population of 49,300 in the entire study area.

DISCUSSION

Habitat Use and Selection

In the central Sierra foothills, the Tricolored Blackbird occurs mainly in lowlands, likely because of the prevalence of grasslands at lower elevations. As elevation increases and slopes steepen, the proportional coverage of grasslands, irrigated pasture, and annual crops decreases, while that of the shrublands, woodlands, and forests that Tricolored Blackbirds avoid increases.

In a prior study of the Tricolored Blackbird's habitat use, Wilsey et al. (2019) analyzed the relationship between habitat occupancy of colonies censused during the three-day California-wide surveys conducted in April 2007, 2011, and 2014. Many of the Sierra foothills colonies are not yet active this early in the season (Airola et al. 2018a). Our analysis addressed colony locations and sizes recorded *throughout* the breeding season in this region. Nonetheless, many of our results were similar, in that Wilsey et al. (2019) found that lands within 5 km of colonies were dominated by grasslands, alfalfa, and surface water, and that lands supporting colonies had more nearby foraging habitat than did areas that lacked colonies.

Our few differences from Wilsey et al. (2019) appear to be due to different methods and conditions within our study area. For example, in the central Sierra foothills alfalfa is of limited extent, so we combined it with grasslands and wetlands into the grassland–herbaceous land-covertype, which the blackbirds selected. Wilsey et al. (2019) did not identify an association with annual crops. This may be because their larger study area, which encompassed the entire major agricultural region of California's Central Valley, is planted in a wider variety of field crops than is ours (including many crops that the blackbird rarely uses). Our finding that Tricolored Blackbirds are closely associated with grassland–herbaceous, annual crops, and irrigated pasture likely reflected these habitats' prevalence in various parts of our study area and their providing a wide range of carbohydrate (i.e., seed) and protein (invertebrate) foods in association with suitable nesting habitat, often near irrigated pastures and agricultural ditches (Airola et al. 2015a, Beedy et al. 2018).

Similarly, that Wilsey et al. (2019) found an association of colonies with water, whereas we did not, may reflect the methods by which surface water was mapped and quantified. Our mapping of water was limited mainly to large bodies, while Wilsey et al. also recognized water features at a finer scale. Water availability was certainly a factor in habitat selection in the central Sierra foothills, where Tricolored Blackbirds nest primarily in patches of Himalayan blackberries growing in wet areas and emergent marsh vegetation (Airola et al. 2018a, Airola 2021).

We also addressed water with our "irrigated pasture" cover type. Although irrigated pasture was not significantly more extensive proportionally near colonies than in the study area as a whole, it nonetheless appears to be important as Tricolored Blackbird habitat. In addition to supporting stands of Himalayan blackberry, preferred for nesting in this region (Airola 2021), irrigated pastures provide drinking water and likely produce a continuous supply of insect prey through the breeding season. Qualitatively, we often observed colonies near areas where a combination of grassland, irrigated pasture, and seed crops provided a diversity of food sources and water for adults and nestlings, but we did not analyze distance effects except within 5 km.

Habitat Loss and Degradation

The degradation of nesting habitat that we observed at nine colony sites (11% of total) and the substantial reductions of foraging habitat at four sites (5%) over the five years of this study raise serious concerns. Notably, our assessment did not include additional habitat losses from habitat conversion, such as grassland–herbaceous and annual croplands being replaced by orchards and vineyards (Cameron et al. 2014), which we observed widely during field surveys and is recognized as a long-term threat to the species (Beedy et al. 2018). Despite these losses, the breeding population we surveyed in the central Sierra foothills study region remained relatively stable (43,000–58,500) from 2014 to 2018 (Airola et al. 2018b). It is possible, however, that habitat loss may have contributed to the lack of an increase in this breeding population during this period, as the statewide population increased by 22% from 2014 to 2017 (Meese 2017). At some point, continued habitat losses without effective mitigation seem certain to lead to population decline in this region.

Conservation Guidance from Land Protection and Threats Assessment

Our results help clarify the importance of the habitats needed to sustain the Tricolored Blackbird in the central Sierra foothills. The results of the hurdle model (Table 2, Figure 4) predict the likelihood of Tricolored Blackbird nesting at the scale of 100 km^2 area on the basis of extent of land-cover types. But even where preferred habitat remains extensive, occupancy may be low; for example, where these habitats represent 67% (90% CI: 44–84%) of a 10,000-ha grid cell, the probability of the cell's supporting a nesting colony in at least one of four years is only 50%.

Our findings lead to recommendations for habitat management. For example, adult Tricolored Blackbirds are strongly attracted to feed in cut and curing oat hay (Airola et al. 2015a), presumably because it provides a concentrated source of carbohydrates like the grains on which the species feeds heavily at dairies and poultry farms in other parts of its range (Beedy et al. 2018). Therefore, fields of seed crops such as rice, oats, and winter wheat should be considered in selecting the Tricolored Blackbird's conservation lands or small amounts of these crops could be planted to diversify foraging opportunities and increase habitat value.

The analysis of land cover around colonies may be useful in identifying the quality of habitat inaccessible for surveys. Unsurveyed areas with water and suitable nesting habitat that support high proportions of grassland (e.g.,

>60%), and small amounts (5–10%) of seed crops and irrigated pasture should be priorities for future surveys.

Our study did not address vegetation constituting nesting habitat. Patches of Himalayan blackberry, the predominant nesting substrate in the study area (Airola et al. 2016), averaged only 0.24 ha (±0.22 SD; Airola 2021), smaller than the minimum units mapped in CropScape. Variations in the type, amount, quality, and stability of nesting habitat affect Tricolored Blackbird occupancy, density, and nesting success (Airola et al. 2016). Therefore, our lack of information on the condition of nesting habitat may have contributed to the variation in occupancy rates and densities we observed. Mapping suitable nesting habitat is essential to a full understanding of factors affecting these variables. This information also could be used, for example, to identify areas with high-quality foraging habitat that lack suitable nesting habitat. Creating nesting habitat in such places should be a high priority.

Most conservation efforts for the Tricolored Blackbird have been focused on eliminating the large-scale destruction of nesting colonies on farms in the lower San Joaquin Valley (see Arthur 2014), which has been largely successful (Clipperton 2018, Castañeda et al. 2023). The conversion of grasslands and annual crops to vineyards and orchards is also a concern (Meese 2014, Beedy et al. 2018), and we documented strong avoidance of these crops. But as yet this concern has led to little or no action (Clipperton 2018).

Neither have the effects of neonicotinoids and other insecticides on insect populations been addressed, though these may impair the reproduction of not only the Tricolored Blackbird (Meese 2013, Clipperton 2018) but other insectivorous species in the Central Valley (Airola 2020).

Although development and mining are localized, in the central Sierra foothills they pose the greatest threat in Sacramento and Placer counties, where the Tricolored Blackbird population is largest (Airola et al. 2018b). Habitat-conservation plans for these two counties (Sacramento County 2018, Placer County 2020) were prepared without recent data on the locations of Tricolored Blackbird colonies or consideration of the habitat needs we have identified. In light of this new information, the measures for conservation of Tricolored Blackbird habitat in these plans warrant reevaluation, as required under the plans' provisions for adaptive management.

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