CHRONIC LOW REPRODUCTIVE SUCCESS OF THE COLONIAL TRICOLORED BLACKBIRD FROM 2006 TO 2011

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ABSTRACT: I studied the Tricolored Blackbird (*Agelaius tricolor*) in California's Central Valley over six breeding seasons from 2006 through 2011 and documented fates of nesting attempts, reproductive success of colonies, and relative abundance of insect prey in foraging areas. I found widespread and chronic reproductive failures except in cases of relatively high insect abundance. My observations suggest that the productivity of Tricolored Blackbird colonies is food-limited and that the relatively high reproductive success at few colonies is primarily a function of unusually high abundance of insects in nearby foraging areas.

The Tricolored Blackbird (*Agelaius tricolor*) forms the largest breeding colonies of any North American songbird (Beedy and Hamilton 1999). Over 99% of the world's population occurs in California, with small numbers also in Washington, Oregon, Nevada, and Baja California (Beedy and Hamilton 1999). In California, for decades the largest colonies and the vast majority of the population have occurred in the Central Valley (Neff 1937, Beedy and Hamilton 1999, Cook and Toft 2005).

Over the 20th century, the number of Tricolored Blackbirds plummeted from habitat loss through conversion to agriculture and urbanization, market hunting, poisoning, and the birds being shot as an agricultural pest (Neff 1937, Beedy and Hamilton 1999). This decline resulted in a petition by the Center for Biological Diversity to list this blackbird under the state and federal endangered species acts (CBD 2004). Although these petitions were declined, the Tricolored Blackbird is considered a federal species of conservation concern (USFWS 2008) and a California Bird Species of Special Concern (Shuford and Gardali 2008).

Recent statewide surveys and intensive monitoring of colonies in the Central Valley have shown that its abundance has continued to decline, falling 35%, from about 400,000 to 250,000 individuals, from 2008 to 2011 (Kyle and Kelsey 2011, Meese 2011).

Large numbers formerly nested in coastal marshes in southern California (Baird 1870, Neff 1937, Unitt 2004), but workers in this region have recently documented severe population declines in this population segment (Unitt 2004, Feenstra 2009).

I report here on field work in the Central Valley over six breeding seasons, from 2006 through 2011, during which I sought to detect, monitor, and estimate the productivity of each of the Tricolored Blackbird's largest breeding colonies. Key goals were to examine the relationship between the blackbird's reproductive success and insect abundance and to use these results to inform conservation decisions intended to increase the species' numbers.

METHODS

My field work from 2006 to 2011 covered the Tricolored Blackbird's breeding season from late March through July, addressing the following topics.

Surveys of Previously Occupied Locations

I began surveys in early spring in the San Joaquin Valley, where Tricolored Blackbirds breed for the first time each season (Hamilton 1998), then moved north to the Sacramento Valley as the season progressed (Figure 1). I surveyed by car on public roads the locations of all previously occupied colonies known by or reported to me. I was especially interested in documenting those colonies where the nesting substrate is ephemeral, primarily grain fields near dairies, as these colonies were at risk from loss of nests by the harvest of triticale, a wheat (*Triticum*) × rye (*Secale*) hybrid grown for dairy cows (Beedy and Hamilton 1999, Cook and Toft 2005, pers. obs.; Figure 2).

Surveys for New Locations

I supplemented the surveys of existing colony locations with intensive searches for new ones in grain and weedy fields adjacent to dairies and in freshwater wetlands in state wildlife areas, national wildlife refuges, and accessible private duck clubs. In both the San Joaquin Valley and southern California, from the 1980s to the present, many of the largest colonies have been located adjacent to dairies (Beedy and Hamilton 1999). Therefore, to enhance colony detection, I used available GIS layers to map the locations of all dairies in the San Joaquin Valley, then transferred these locations to paper maps that I took into the field to guide survey efforts.

After birds completed their breeding efforts in the San Joaquin Valley, I used similar methods to survey for colonies in the Sacramento Valley. I surveyed locations of previously documented colonies and sites that had been reported to me by numerous collaborators (state and federal agency personnel, observers posting messages to the central_valley_birds listserv, birders) or entered into the Tricolored Blackbird Portal (http://tricolor.ice.ucdavis.edu).

Colony Monitoring

I monitored colonies from within days of the arrival of adults and the initiation of breeding until breeding ceased and the adults had departed. In most cases, I monitored colonies twice a week to assess current conditions and the colony's chronology to estimate the optimal times for making estimates of reproductive success and the size of the breeding population. Monitoring entailed making observations from the closest public road for colonies located on private property that I lacked permission to access, or from immediately adjacent roads for colonies located on public property or on private property I had permission to access.

Estimating Area Occupied

I estimated the dimensions of the available nesting substrate and the area occupied by breeding birds in one of two ways. On public or private property

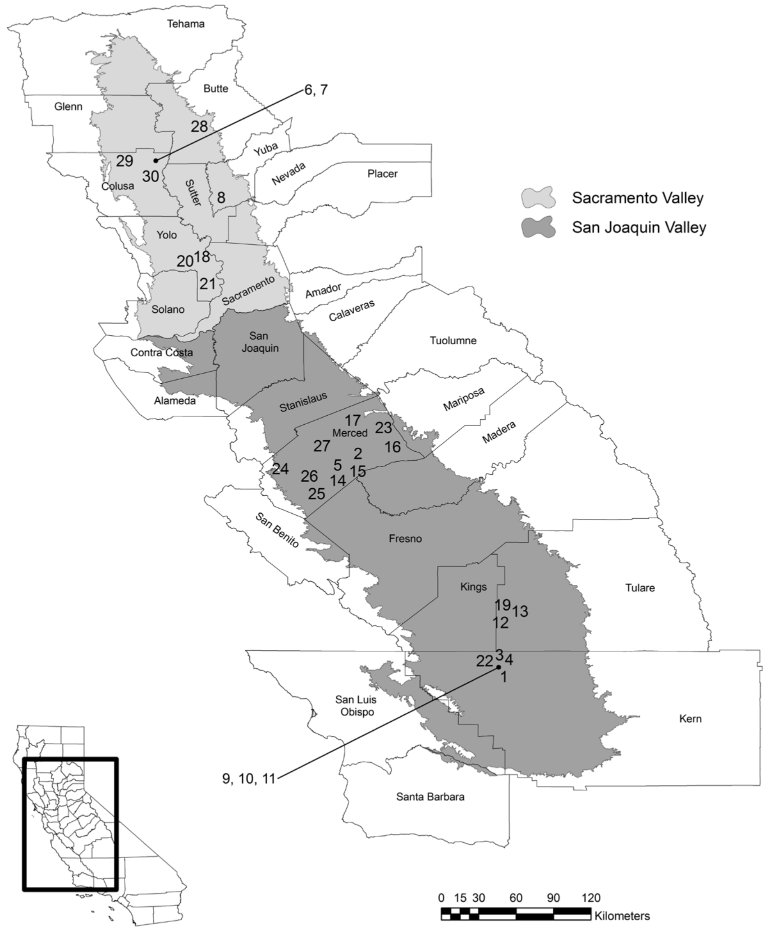

Figure 1. Locations of Central Valley Tricolored Blackbird colonies studied from 2006 to 2011. Numbers correspond to records in Table 1. Some locations were occupied in more than 1 year (see Table 1).

with access, I measured these dimensions directly with a hand-held GPS. On private property where I lacked access, I visually estimated these dimensions from a distance and sketched them in a field notebook. The area occupied by breeding Tricolored Blackbirds is reliably estimated from careful observation of the birds' behavior, as birds leave and return to nests at intervals defined by the stage of the breeding cycle. The interval is longest when females are incubating eggs, shortest when females are building nests or when both adults are feeding young. I confirmed the perimeter of the occupied area as initially outlined by the birds' behavior through subsequent monitoring. To

Figure 2. Tricolored Blackbird colony in field of triticale adjacent to a dairy in Kern County, California.

measure the size of the occupied area, I plotted both the dimensions from visual estimates and the coordinates measured by GPS into Google Earth. After birds had finished breeding, I also searched accessible but apparently unoccupied areas to confirm the absence of nests.

Estimating the Number of Breeding Birds

I estimated the number of breeding birds in a colony either visually at the time of nesting and/or by sampling nests after the breeding season. I made visual estimates of the number of breeding birds each time I monitored a colony by carefully observing it for 5–30 minutes per visit. When possible, I observed colonies from multiple vantage points to enhance detection and to increase the precision of the estimate.

At sites to which I was granted access, I re-entered colonies after the young had fledged and both young and adults had left the area and estimated nest densities by one of two methods depending on the nesting substrate. In relatively impenetrable substrates, such as some colonies established in milk thistle (*Silybum marianum*) or in Himalayan blackberry (*Rubus armeniacus*), I counted nests within samples of randomly placed 1- × 2-m sampling frames of 2-cm PVC pipe. In all other nest substrates, I counted nests within line transects 2 m wide and varying in length from 20 to 100 m. I marked the start and end points of transects by a handheld GPS unit and computed the transects' lengths by GPS or by the length-measurement tool in Google Earth.

Using the densities of nests in the sampled areas, I calculated the number of nests in the colony by multiplying the average number of nests per hectare by the number of hectares occupied by breeding birds. I assumed that on average each male breeds with two females (Beedy and Hamilton 1999) so multiplied the number of nests by 1.5 to estimate the number of breeding birds at a colony. This provided an independent estimate of the number of breeding birds for comparison with my visual estimate during monitoring.

Estimating Relative Abundance of Insects

Each time I monitored a colony I spent 15–60 minutes observing the flight lines of actively foraging birds, which typically move back and forth from the colony to foraging destinations along nearly single-file flight paths. These flight lines are conspicuous and persistent (Hoffmann 1927, Beedy and Hamilton 1999) and typically consist of several hundred to several thousand birds (pers. obs.). The distances from the colonies to foraging destinations varied from tens of meters to 9 km (Table 1).

After determining the foraging destinations, I walked or drove to the areas where the largest numbers of birds were actively foraging and, where permissible, I visually estimated the relative abundance of insects in terrestrial habitats by walking (at a pace of 1 step every 3–5 seconds) over the substrate where birds had been foraging moments before and counting the number of insects seen. I waded in rice paddies adjacent to large colonies in Yuba and Colusa counties and supplemented my visual observations by reaching into and sweeping the muddy substrate with my fingers extended in an attempt to detect aquatic insect larvae.

I subsequently categorized the number of insects observed per minute as low (1–10), moderate (11–100), or high (>100; Table 1). I estimated the relative abundance of insects 3–6 times per site within a 4-week interval while the site was occupied by breeding birds.

Estimating Reproductive Success

I estimated reproductive success, defined as the average number of young fledged per nest, either by visual estimates or by sampling. Visual estimates were derived from the number of breeding birds estimated visually during monitoring and the number of fledglings observed at the end of the breeding season. As one male breeds, on average, with two females (Beedy and Hamilton 1999), each two nests have three birds associated with them, so the product of the number of breeding birds multiplied by 2/3 provides an estimate of the number of nests constructed. The visual estimate of the number of young fledged divided by the estimate of the number of nests constructed yields an estimate of the number of young fledged per nest.

For accessible colonies, prior to the fledging of young, I estimated reproductive success by counting the contents of a random sample of nests when the average age of nestlings was 7 to 9 days and calculated reproductive success by dividing the number of young by the number of nests in the sample.

Estimating the Number of Young Produced

I estimated the number of young produced at a colony by repeated observations of young in groups ("crèches") following fledging and/or by multiplying the number nests constructed times the average reproductive success of sampled nests (see above).

At most colonies, the number of fledged birds may be counted. After fledging, the young spend a minimum of several days in groups, perching and begging conspicuously from the tops of vegetation at the colony's margins (Beedy and Hamilton 1999, pers. obs.). Typically, young begin to leave the nesting substrate to perch high in nearby shrubs or trees approximately 4 days after fledging. However, crèches remain within the colony's boundaries for up to 2 weeks or more if there are no nearby taller shrubs or trees, as is often the case in the "silage belt" of the southern San Joaquin Valley (pers. obs.).

Statistical Analyses

I used Spearman's rank correlation to test for a relationship between insect abundance and reproductive success and Pearson's product-moment correlation to test for a relationship between colony size and reproductive success. I used a Kruskal–Wallis test to evaluate potential relationships between reproductive success and breeding season, type of nesting substrate, and the location of colonies by county. I excluded Butte County from the analysis for counties as I estimated reproductive success at only one site there. Finally, I used a Mann–Whitney test to look for a difference in reproductive success between the San Joaquin and Sacramento valleys and between colonies near and distant from dairies.

RESULTS

During the 6 years of this study the Tricolored Blackbird's reproductive success across all sites and years averaged 0.62 young fledged/nest (540,000 young fledged from 870,000 nests; Table 1). Only 11% of the colonies studied (5/47) fledged an average of 1 or more young per nest.

The relative abundance of insects on foraging substrates varied greatly by site and year, from a low of zero insects per 10 minutes of searching in the case of larvae of the water scavenger beetle (Coleoptera: Hydrophilidae) or other insects in rice paddies in Colusa County in 2007 to a high of over 1000 individuals per 10 minutes of searching in the case of grasshoppers in open pasture near a colony in Merced County in 2010 (Table 1). Within a site and year, however, estimates of relative abundance of insects varied little: at any single colony, they did not differ spatially or temporally.

Insect abundance was positively correlated with reproductive success (Spearman's rank correlation coefficient $\rho = 0.737$, $P << 0.05$), and the colony with the highest reproductive success (1.44), situated in milk thistle in Merced County in 2010, was surrounded by open rangeland in which grasshoppers were extraordinarily abundant (Table 1).

Colony size was positively correlated with reproductive success ($r = 0.53$, $r^2 = 0.28$). Reproductive success did not differ by type of nesting substrate (Kruskal–Wallis $H = 6.049$, $P = 0.109$), year (Kruskal–Wallis $H = 8.8$, $P = 0.117$), or county (Kruskal–Wallis $H = 7.841$, $P = 0.165$). The presence of a dairy did not affect reproductive success (Mann–Whitney $U = 208$, $P = 0.298$), and the reproductive success of colonies in the San Joaquin and Sacramento valleys was similar (Mann–Whitney $U = 189.5$, $P = 0.41$).

DISCUSSION

The Tricolored Blackbird's reproductive success was chronically low throughout the Central Valley, in all six breeding seasons studied from 2006 to 2011, and in all types of nesting substrate. Higher reproductive success was associated with greater abundance of favored insect groups in foraging habitats surrounding colonies and was not associated with dairies.

Both terrestrial and aquatic insects varied widely in abundance. Caterpillars and grasshoppers dominated the terrestrial prey and dragonflies and larval

Table 1 Distribution, Characteristics, and Reproductive Success of Tricolored Blackbird Colonies Studied in California's Central Valley, 2006–2011

Year and site[a]	County	Nesting substrate	No. breeding birds	Foraging substrates	Distance to primary foraging destinations	Insect groups taken	No. insect samples/relative insect abundance	Reproductive success
2006								
1	Kern	Triticale	138,000	Alfalfa, alkali shrublands, dairy	<1 km	Weevils, beetles, caterpillars	3/High	1.44
2	Merced	Triticale	70,800	Pasture	1–4 km	Grasshoppers	5/Moderate	0.85
2007								
3	Kern	Cattails	20,000	Alkali shrublands, alfalfa, dairy	0.5–6 km	Weevils, beetles, caterpillars	3/Low	0.01
4	Kern	Triticale	50,000	Alkali shrublands, alfalfa, dairy	0.5–5 km	Weevils, beetles, caterpillars	3/Low	0.01
5	Merced	Milk thistle	65,460	Pasture, dairy	1–3 km	Grasshoppers, beetles	6/Low	0.14
20	Yolo	Milk thistle	35,000	Annual grasslands, alkali grasslands, fallow ricefields	0.5–5 km	Beetles, weevils, aquatic insect larvae	5/Moderate	0.91
6	Colusa	Cattails	58,800	Annual grasslands, rice	2–5 km	Beetles, weevils, aquatic insect larvae	4/Moderate	0.95
7	Colusa	Cattails	20,000	Rice, shrublands	0.5–5	Aquatic insect larvae	3/Low	0.03
8	Yuba	Cattails	23,400	Irrigated pasture, wetlands	0.5–5 km	Dragonflies, beetles, weevils	5/Moderate	0.82
2008								
3	Kern	Cattails	8000	Alkali shrublands, alfalfa, dairy	0.5–6 km	Beetles, weevils, caterpillars	3/Low	0.03
9	Kern	Triticale	60,000	Alfalfa, alkali shrublands, dairy	0.5–6 km	Beetles, weevils, caterpillars	3/High	1.1
10	Kern	Cattails	5,000	Alkali Shrublands, alfalfa, dairy	0.5–6 km	Beetles, weevils, caterpillars	3/Low	0.09

Year and site[a]	County	Nesting substrate	No. breeding birds	Foraging substrates	Distance to primary foraging destinations	Insect groups taken	No. insect samples/relative insect abundance	Reproductive success
11	Kern	Cattails	2,000	Alkali shrublands, alfalfa, Dairy	0.5–6 km	Beetles, weevils, caterpillars	3/Low	0.04
12	Tulare	Cattails	2,000	Alkali shrublands, alfalfa, dairy	1–6 km	Beetles, weevils, caterpillars	3/Low	0.5
13	Tulare	Triticale	10,000	Pasture, alkali shrublands, alfalfa, dairy	0.5–6 km	Beetles, weevils, caterpillars	3/Low	0.37
14	Merced	Milk thistle and mustard	16,500	Pasture, dairy	0.5–5 km	Beetles, weevils, grasshoppers	4/Low	0.01
15	Merced	Milk thistle and mustard	4,000	Pasture, dairy	0.5–5 km	Beetles, weevils, grasshoppers	4/Low	0.09
16	Merced	Fiddlehead and milk thistle	14,660	Pasture, dairy	0.5–5 km	Beetles, weevils, grasshoppers	5/Low	0.08
17	Merced	Himalayan blackberry	30,000	Pasture, dairy	0.5–5 km	Beetles, weevils, grasshoppers	3/Low	0.25
18	Yolo	Milk thistle	35,000	Annual grasslands, alkali grassland, fallow ricefields	0.5–5 km	Beetles, weevils, grasshoppers, aquatic insect larvae	3/Low	0.26
8	Yuba	Cattails	21,000	Irrigated pasture, rice, wetlands	0.5–8 km	Beetles, aquatic insect larvae, grasshoppers	3/Low	0.21
2009								
3	Kern	Cattails	5,000	Alkali shrublands, alfalfa, dairy	0.5–8 km	Beetles, weevils, caterpillars	3/Low	0.15
10	Kern	Cattails	1,500	Alkali shrublands, alfalfa, dairy	0.5–8 km	Beetles, weevils, caterpillars	3/Low	0.25
9	Kern	Triticale	18,000	Alkali shrublands, alfalfa, dairy	0.5–8 km	Beetles, weevils, caterpillars	3/Moderate	1.0

(*continued*)

Table 1 *(continued)*

Year and site[a]	County	Nesting substrate	No. breeding birds	Foraging substrates	Distance to primary foraging destinations	Insect groups taken	No. insect samples/relative insect abundance	Reproductive success
19	Tulare	Triticale	31,500	Alkali shrublands, dairy	0.5–8 km	Beetles, weevils, caterpillars, grasshoppers	3/Moderate	1.05
20	Yolo	Cattails	57,000	Annual grasslands, sunflowers, rice	0.5–8 km	Beetles, weevils, grasshoppers, caterpillars	6/Moderate	0.79
21	Yolo	Cattails	5,600	Annual grasslands, rice	0.5–5 km	Beetles, weevils, grasshoppers, caterpillars	6/Low	0.8
7	Colusa	Cattails	75,000	Annual grasslands, rice	1–8 km	Aquatic insect larvae, beetles, weevils, grasshoppers	4/Low	0.26
2010								
9	Kern	Triticale	66,000	Alkali shrublands, alfalfa, dairy	0.5–8 km	Beetles, weevils, caterpillars	4/Low	0.15
22	Kern	Cattails	20,000	Alkali shrublands, alfalfa, dairy	.5-8 km	Beetles, weevils, caterpillars	3/Low	0.09
3	Kern	Cattails	15,000	Alkali shrublands, alfalfa, dairy	0.5–8 km	Beetles, weevils, caterpillars	3/Low	0.1
23	Merced	Milk thistle	83,000	Pasture, dairy	0.1–3 km	Grasshoppers	6/High	1.44
24	Merced	Himalayan blackberry	25,000	Pasture, dairy	0.1–6 km	Grasshoppers, beetles, weevils	4/Moderate	0.42
14	Merced	Mustard and milk thistle	10,000	Pasture, dairy	0.5–5 km	Grasshoppers, beetles, weevils	5/Low	0.07
25	Merced	Cattails	10,000	Pasture, annual grasslands, dairy	0.5–8 km	Caterpillars, beetles, weevils	5/Low	0.45
26	Merced	Bulrush	800	Annual grasslands, pasture, dairy	0.5–5 km	Grasshoppers, beetles, weevils	5/Low	0.37

Year and site[a]	County	Nesting substrate	No. breeding birds	Foraging substrates	Distance to primary foraging destinations	Insect groups taken	No. insect samples/relative insect abundance	Reproductive success
17	Merced	Himalayan blackberry	2,000	Pasture, dairy	0.5–5 km	Grasshoppers, beetles, weevils	4/Low	0.23
27	Merced	Milk thistle	2,000	Pasture, dairy	0.1–5 km	Grasshoppers, beetles, weevils	4/Low	0.15
20	Yolo	Cattails	18,900	Annual grasslands, rice	0.1–8 km	Beetles, aquatic insect larvae, caterpillars	5/Low	0.42
21	Yolo	Cattails	2,500	Annual grasslands, rice	0.1–6 km	Aquatic insect larvae, caterpillars, beetles	5/Low	0.45
7	Colusa	Cattails	49,545	Annual grasslands, rice, wetlands	1–8 km	Aquatic insect larvae, beetles, grasshoppers	3/Low	0.25
28	Butte	Himalayan blackberry	7,000	Annual grasslands, pasture	1–8 km	Grasshoppers, beetles	3/Moderate	0.86
2011								
9	Kern	Triticale	20,000	Alkali shrublands, alfalfa, dairy	1–8 km	Beetles, weevils, caterpillars	3/Low	0.62
15	Merced	Mustard, milk thistle	40,000	Pasture, annual grasslands, dairy	1–8 km	Beetles, weevils, grasshoppers, caterpillars	5/Low	0.34
14	Merced	Milk thistle	25,000	Pasture, annual grasslands, dairy	1–5 km	Grasshoppers, beetles, weevils, caterpillars	6/Low	0.44
29	Colusa	Cattails	10,000	Annual grasslands, rice, wetlands	1–8 km	Grasshoppers, beetles, weevils	3/Low	0.09
30	Colusa	Cattails	2,500	Annual grasslands, rice, wetlands	0.5–8 km	Grasshoppers, caterpillars, beetles	4/Low	0.00

[a]See Figure 1 for locations.

water scavenger beetles dominated the aquatic insects foraging Tricolored Blackbirds chose. My attempts to estimate the relative abundance of aquatic insects were unsuccessful, as I observed no larval aquatic insects while sampling. The only aquatic insects observed in abundance were recently hatched dragonflies (giant green darners, *Anax junius*) at one site in Yuba County in 2007 and hatching caddisflies (Trichoptera) at one site in Kern County in 2009. The dragonflies hatched in mid-July, when only a single blackbird colony was known to be active, and although they were extremely abundant and easily captured, they were fed primarily to fledglings and emerged too late to result in high productivity at this colony. The caddisfly hatch was similarly dramatic but brief, lasting less than an hour, and did not appear to enhance the blackbirds' productivity. It is possible that greater overlap between the Tricolored Blackbird's breeding season and the peak of dragonfly hatching would have enhanced the blackbirds' reproductive success, but aquatic insects, as a group, did not appear to contribute to high reproductive success at any colony I studied.

Previous researchers have documented poor reproductive success of Tricolored Blackbird colonies, but mine is the first study to confirm low reproductive success at colonies throughout the Central Valley over a 6-year interval and the first to assess insect abundance at sites where breeding birds forage. The reproductive success of entire colonies can be reduced severely by both mammalian and avian predators (reviewed by Beedy and Hamilton 1999), but rates of predation are highly variable in space and time and, until recently, predators have not been known to cause sustained reproductive failures of multiple colonies across a wide geographic area. Since 2006, predation by Cattle Egrets (*Bubulcus ibis*) has caused nearly complete reproductive failures of even very large colonies in Tulare County (Meese 2012), but predation by Cattle Egrets on Tricolored Blackbird eggs and nestlings is unknown outside of Tulare County. The lack of influence of substrate type on reproductive success also suggests that predation is not responsible for the widespread and sustained reproductive failures I documented, as some substrates with thorns or stinging hairs, such as Himalayan blackberries and stinging nettles (*Urtica dioica*), appear to confer some defense against predators, while others lacking such armaments, such as cattails (*Typha latifolia*), are believed to expose nesting blackbirds to higher rates of predation (Beedy and Hamilton 1999, Cook and Toft 2005).

Beedy and Hayworth (1992) documented the reproductive failure of a colony in Merced County and found that lethal levels of selenium were likely responsible for mortality of nestlings and the failure of this colony. To my knowledge, theirs is the only study that has attributed a colony's failure to environmental contaminants, but because the potential role of environmental contaminants in reducing the blackbird's productivity has not been assessed, it deserves further study.

Food limitation is known to reduce reproductive success in many groups of birds (reviewed by Martin 1987), but my study provides evidence of food-limited reproduction that is spatially widespread and temporally persistent. The Tricolored Blackbird's reproductive success was low despite the diverse array of foods the species consumes, as documented in this and previous studies (Skorupa et al. 1980), and despite the suggestion that a diverse diet might allow the blackbird to exploit alternate food sources when a preferred food is limited by weather or other conditions (Crase and DeHaven 1977). During my study, a generalized diet did not appear to provide insurance against food-limited reproductive failures, and relatively high reproductive success was associated with exceptional abundance of a narrow range of favored insect groups (Table 1).

Reproductive success did not differ by major geographical region (San Joaquin vs. Sacramento Valley) or by county of the Central Valley. These results may affect management intended to increase the numbers of tricolors as they suggest there is no temporal or geographical basis for making conservation investments. Thus, all else being equal, efforts intended to benefit a year's first attempts at breeding in the San Joaquin Valley should be as effective as efforts intended to benefit subsequent attempts in the Sacramento Valley.

I found no effect of nesting substrate on reproductive success. This result differs from that of Cook and Toft (2005), who found that the proportion of colonies suffering complete reproductive failure was greater in native wetlands than in upland substrates. Those authors attributed the differences to rates of predation being higher in wetlands than in uplands. However, Cook and Toft (2005) did not measure insect abundance in nearby foraging areas and did not directly observe predators in blackbird colonies, so comparing my results to theirs is difficult. If rates of predation are substrate-dependent, as suggested by Cook and Toft (2005), the absence of substrate-related differences suggests that predators are not responsible for the chronically low reproductive success I documented.

The Tricolored Blackbird's low reproductive success from 2006 to 2011 may help to explain the decline in its abundance observed from 2008 to 2011, when methodologically similar statewide surveys of the species found a drop from 400,000 to 258,000 birds (Kelsey 2008, Kyle and Kelsey 2011). Although additional field work is needed to determine whether this recent decline is part of a longer-term trend, the chronically low reproductive success through the breeding season of 2011, which did not figure into the results of the 2011 statewide survey, suggests that the decline in abundance will continue.

Since the 1980s, numerous large dairies have been located in the southern San Joaquin Valley, and dairies appear to be attractive to Tricolored Blackbirds, as for decades some of the largest colonies have been established in grain fields adjacent to dairies (Beedy and Hamilton 1997; Figure 2). The grains stored to feed the dairy cattle appear to provide an *ad libitum* food source, and the large fields of triticale provide nesting substrate, as the stems of triticale plants are taller and stronger than are the stems of other grains and capable of supporting blackbird nests. Although the stored grains may provide a superabundant food supply, however, they appear to be insufficient to sustain breeding because the reproductive success of colonies adjacent to dairies is as low as that of colonies distant from dairies. To form eggs, breeding females require relatively high levels of essential amino acids and essential fatty acids, and these essential compounds are found in higher proportion in insects than they are in grains (Carey 1996, Ramsay and Houston 1998). In addition, nestling blackbirds require animal foods and do not eat plant materials for the first 9 days of life (Crase and DeHaven 1977, Skorupa et al. 1980), until they are almost ready to fledge. The dietary requirements of breeding female and nestling blackbirds may help to explain why the reproductive success of colonies adjacent to dairies is low despite the virtually unlimited availability of grains. Additional research is needed to assess the effects of a granivorous diet on clutch size, egg hatchability, rates of brood reduction (Beedy and Hamilton 1999), and nestling starvation.

The apparent attraction to and use of stored and provided grains extends beyond the breeding season and dairies in the San Joaquin Valley. Aggregations of thousands of birds are also observed around dairies and feedlots in winter, especially at dairies at Point Reyes National Seashore in Marin County, around feedlots near Birds Landing in southern Solano County, and at several sites in Merced County (pers. obs.). Given the large number of birds at sources of grain available *ad libitum*, both the breeding and winter distributions may be influenced if not determined by the sources of these grains. Across much of its range, the Tricolored Blackbird may be largely dependent on grains provided for livestock as a replacement for natural foods that have been lost to agriculture and urbanization, although my results suggest that a granivorous diet is insufficient to support the species' breeding.

The colonies I studied represent most of the largest colonies documented during this 6-year interval and represent the entire geographic range of the largest colonies of the Tricolored Blackbird (Kelsey 2008, Kyle and Kelsey 2011). Although these colonies had the greatest proportional potential to contribute to the productivity of the species, the chronic poor reproductive success of the largest colonies suggests that they may not serve as an effective core of a conservation strategy. Colonies adjacent to dairies, for decades many of the largest colonies, appear to serve as ecological traps (Dwernychuk and Boag 1972), fledging relatively few young in most years. Entire colonies are also lost when the triticale in which the birds nest is harvested during normal agricultural operations (Beedy and Hamilton 1997, Cook and Toft 2005, pers. obs.), although I included none of these harvested colonies in this analysis.

During the 6 years of my study, the Tricolored Blackbird has experienced chronic, widespread low reproductive success apparently because insects are insufficient. These results support the view expressed by DeHaven et al. (1975) that reductions in the Tricolored Blackbird's abundance from the 1930s to the 1970s were due at least partially to limitation of its food supply through loss of foraging habitat. This loss of foraging habitat may result in a decline in productivity over a period of years that is difficult to detect, but that decline may ultimately lead to the situation where, despite the availability of suitable nesting substrate, tricolors abandon colonies or decline to extinction in an area where they formerly were abundant. This mechanism is believed to be responsible for the decimation of the species in southern California (Unitt 2004, Feenstra 2009) and Baja California (Erickson et al. 2007, Erickson and de la Cueva 2008).

The relationships I describe here suggest that the Tricolored Blackbird's habit of colonial breeding and the requirements of egg-forming females and nestlings to consume insects place a great burden upon landscapes within the 9-km radius of a colony within which the birds forage (Hamilton and Meese 2006) and that food limitation, not predation, is responsible for widespread, chronic low reproductive success. These results suggest that future investments in conservation should stress nesting substrates that are free from possible destruction during harvest and are surrounded by secure, productive foraging habitats. The variety of foraging substrates Tricolored Blackbirds use suggests a degree of flexibility in choices of conservation strategies, as both agricultural (alfalfa and sunflowers) as well as native (non-irrigated pasture) foraging habitats supported colonies with relatively high reproductive output (this study and unpubl. data). Where the blackbird's productivity is a priority in agricultural settings, crops that serve as foraging substrates should not be sprayed with insecticides so as to maximize insect abundance. In regions of extensive pasturelands or grasslands where secure nesting substrates may be absent, management should stress the provision and maintenance of secure nesting substrates. As with foraging substrates, there are several options for nesting substrates, as nesting tricolors use a wide variety of native and non-native vegetation (Table 1).

The conservation of the Tricolored Blackbird will require strategic choices that take into account the species' unique needs. California's Central Valley, where for decades the majority of blackbirds have occurred (Neff 1937, Beedy and Hamilton 1997), has been transformed from its origin as a vast region of wetlands and vernal pools (Frayer et al. 1989), capable of supporting millions of birds (extrapolated from Neff 1937), to an agricultural heartland that provides much of the nation's fresh fruits, nuts, and dairy products (American Farmland Trust 1989) but which is unsuitable for foraging blackbirds. The future of the Tricolored Blackbird depends upon resources in California's Central Valley that appear in most years to be in short supply, and this future is made uncertain by competition between the needs of a colonial species and land uses that limit the range of strategic conservation choices.

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