

Dynamics of extinction: population decline in the colonially nesting Tricolored Blackbird *Agelaius tricolor*

LIZETTE F. COOK and CATHERINE A. TOFT

Summary

Tricolored Blackbird *Agelaius tricolor* is a rapidly declining species largely endemic to California and forms larger breeding colonies than any other extant North American landbird following the extinction of Passenger Pigeon *Ectopistes migratorius*. We present information on its distribution, breeding habitat and changes in global population size using data collected since the 1930s. We also present data on reproductive success at 103 colonies between 1992 and 2003. While possibly once the most abundant bird throughout much of its range, it declined by over 50% between the 1930s and early 1990s, and by a further c. 56% between 1994 and 2000. The global population is now smaller than the historic size of some individual breeding colonies. Reproductive success was significantly higher in upland non-native vegetation (primarily Himalayan blackberry *Rubus discolor*) than in native emergent cattail *Typha* spp. and bulrush *Scirpus* spp. marshes, its likely predominant historic breeding habitat. Contemporary losses of important upland nesting substrate, combined with low reproductive success in native habitats and complete breeding failure in harvested agricultural fields, are the most likely causes of recent declines. Recovery of this species presents possible conflicts in conservation policy because successful reproduction now largely depends on invasive non-native plants and the willingness of farmers to delay harvest or to lose portions of their crops.

Introduction

Colonially nesting birds are especially vulnerable to extinction. Three of the half-dozen or so modern extinctions among bird species in North America north of Mexico were colonial or highly social breeders: Passenger Pigeon *Ectopistes migratorius*; Carolina Parakeet *Conuropsis carolinensis* and Great Auk *Pinguinus impennis*. Because a small number of colonies may include a relatively large proportion of the population, human activities can have catastrophic effects on colonial birds either directly by the taking of adults or offspring or indirectly through habitat loss. Where breeding is socially facilitated, reduced populations may ultimately be driven to extinction through Allee effects (inverse density dependence defined as a positive relationship between population density and survival and reproduction; Allee 1931, Courchamp and Clutton-Brock 1999, Stephens and Sutherland 1999). Passenger Pigeon, once the most abundant bird in North America, may have ultimately succumbed to extinction following widespread hunting and habitat loss because it could not survive at low population densities (Blockstein 2002, Bucher 1992, Stephens and Sutherland 1999, Wilcove 1999).

Tricolored Blackbird *Agelaius tricolor* form the largest breeding colonies of any North America landbird, a distinction held by Passenger Pigeon prior to its extinction in 1914. The majority of the population can still breed in colonies of tens of thousands, but the number of such colonies is now small. Colonial breeding in this species, which includes highly synchronous nesting behaviour (Orians 1961, Collier 1968), is an adaptation that is likely to confer protection from predators through predator saturation and mutual defence (Wiklund and Andersson 1994, Picman *et al.* 2002). Tricolored Blackbirds also forage communally throughout the breeding season and are likewise social during all other times of the year. These characteristics suggest that both reproduction and survival could be inversely density-dependent.

Largely endemic to California (Neff 1937, Orians 1961, DeHaven *et al.* 1975a), and once among the most abundant bird species throughout most of its range (Baird *et al.* 1874, Grinnell 1898, Neff 1937), the global population of Tricolored Blackbird declined by over 50% during the 40 years following its first co-ordinated surveys in the early 1930s (Neff 1937, DeHaven *et al.* 1975a). In the mid-1800s, one observer described how wintering flocks could “darken the sky for some distance by their masses” (Heermann 1859), a reference reminiscent of Passenger Pigeon (Wilcove 1999). Censuses in the early 1930s revealed colonies with as many as 300,000 breeding adults and a total estimated population of over 700,000 in mostly the northern portion of the species’ range (Neff 1937). These data, combined with other information on local populations in the southern portions of its range, (Collier 1968, DeHaven *et al.* 1975a), suggest numbers historically may well have exceeded 1 million. Multiple colonies of more than 100,000 adults were reported as recently as the 1960s (Orians 1961, Payne 1969), but a decade later the estimated population was reduced by over half of that found in the 1930s (DeHaven *et al.* 1975a). Tricolored Blackbird is currently classified in California as a Species of Special Concern and federally as a Migratory Bird of Management Concern, categories which identify reduced populations but do not include the legal protections afforded species listed as threatened.

Much of the breeding habitat of Tricolored Blackbird today consists of vegetation that differs from that of its original habitats. Of those colonies observed during the 1930s, c. 97% of breeding occurred in the vast deepwater emergent marshes of cattail *Typha* spp. and bulrush *Scirpus* spp. throughout California’s Central Valley (Neff 1937). The preponderance of upland nesting that is found today was not reported during this time and the vast majority of upland substrates used now consist of non-native plant species that would not have been present in the Californian landscape prior to the arrival of Europeans. Nesting over water apparently affords protection from predators in many marsh-nesting birds and is a primary criterion for nest-site selection in congeners of the Tricolored Blackbird (Red-winged Blackbird *A. phoeniceus* and Yellow-winged Blackbird *A. thilius*, Yellow-headed Blackbird *Xanthocephalus xanthocephalus*), and other passerines (Picman *et al.* 1993, 2002, Picman and Isabelle 1995, Hansson *et al.* 2000, Massoni and Rebores 2001). Although the historic range of Tricolored Blackbird has changed little since the 1930s, approximately half of all nesting is now in upland habitats. This apparent shift from wetland to upland is surely due to the loss of 96% of California wetlands over the last 150 years from 1,500,000 ha before European settlement (Kreissman 1991).

Here we document and evaluate the population decline of Tricolored Blackbird and explore possible causes using data on this species that were collected intermittently

Table 1. Proportions of colonies and individuals of Tricolored Blackbirds by nesting substrate in the 1930s, 1970s, 1994 and 2000.

Nesting substrate	1932–1934		1968–1972		1994		2000	
	% colonies	% birds	% colonies	% birds	% colonies	% birds	% colonies	% birds
Emergent marsh	94.8	92.7	69.7	^a	47.4	25.7	59.6	54.0
Himalayan blackberry	1.3	0.1	16.1	^a	31.4	20.8	20.2	11.5
Silage	0.0	0.0	0.0	^a	5.1	40.2	5.8	16.7
Other flooded plants	1.3	0.2	5.8	^a	3.8	2.9	3.8	4.1
Other upland plants	2.6	7.0	9.0	^a	12.2	10.4	10.6	13.6
Total flooded plants	96.1	93.0	73.0	^a	51.3	28.6	63.5	58.1
Total upland plants	3.9	7.0	27.1	^a	48.7	71.4	36.5	41.9
Total native plants	96.7	93.0	75.5	^a	60.9	33.3	65.4	54.5
Total non-native plants	3.3	7.0	24.5	^a	39.1	66.7	34.6	45.5

Data from 1932–1934 are from Neff (1937), Sacramento Valley and northern San Joaquin Valley. Data from 1968–1972 are from DeHaven *et al.* (1975a), statewide. Data from 1994 and 2000 are from Hamilton *et al.* (1995), Hamilton (2000) and Cook (unpubl. data). When nesting substrate vegetation was mixed, the predominant vegetation was used to categorize the nesting substrate. Percentage of colonies and birds are for all colonies located throughout the breeding season and may represent colonies and birds counted more than once (see text).

^aData not available.

over the past 70 years. We hypothesized that if nest-site selection was predator-driven, then reproductive success should be higher in emergent marshes than in upland substrate as has been shown for other marsh-nesting birds. If true, then scarcity of available nest-sites in emergent marshes, and increased use of upland substrates, could explain the continuing decline of the Tricolored Blackbird population. Because wetland environments are among the most highly threatened worldwide, our results could have implications for management of other marsh-nesting birds. We also searched for evidence that Tricolored Blackbird could be subject to inverse density dependence, and, therefore, under threat of imminent extinction, by exploring the similarity of its circumstances to those surrounding the extinction of another colonially nesting bird, Passenger Pigeon.

Study area and methods

Study area

Over 90% of the Tricolored Blackbird population has historically nested in California's Central Valley, a basin 64 km wide and 644 km long running north-south, and this continues to be the case (Neff 1937, Orians 1961, DeHaven *et al.* 1975a, Heitmeyer *et al.* 1988, Beedy and Hamilton 1999). Most individuals and colonies are found in the southern portion, specifically the San Joaquin Valley, during

the first half of the breeding season (DeHaven *et al.* 1975*b*, Hamilton 1998). Later, most birds disperse and begin appearing in its northern portion, the Sacramento Valley, for additional nesting attempts (Hamilton 1998).

Large numbers of birds also bred historically in southern California (Baird *et al.* 1874, Grinnell 1898, Collier 1968). Today this region contains a much reduced population and one greatly smaller than that of the Central Valley. Birds have been observed nesting in other portions of California, at elevations as high as 1,200 m (DeHaven *et al.* 1975*a*), and locally in Baja California (Wilbur 1987, Howell and Webb 1995), Oregon (Neff 1933, 1937), and possibly Nevada and Washington (Beedy and Hamilton 1999). However, there is no evidence that colonies outside the Central Valley and southern California ever represented more than 5% of the total population and we know of no accounts after 1998 of Tricolored Blackbird breeding outside of California.

Data collection

Continuing field studies of this species have been conducted since 1991 throughout California. Data used in this study are derived from a series of reports on Tricolored Blackbird status, breeding habitat and reproductive success prepared semi-annually for the United States Fish and Wildlife Service and California Department of Fish and Game between 1992 and 2000 (Bowen *et al.* 1992, Hamilton 1993, 1997, 2000, Hamilton *et al.* 1994, Hamilton *et al.* 1999), and from L. Cook (unpubl. data).

Colonies were surveyed throughout the breeding season (March to July) and defined as any nesting group separated by more than 500 m from another such group, or by new settlements of groups of birds within the proximity of previously established colonies. Data on reproductive success were collected between 1992 and 2003 from 103 colonies ranging in size from 30 to 105,000 breeding adults. Roughly half were in emergent marshes (46%) and half in upland habitats (54%). Transects were established during the incubation period using a minimum target sample of 25 nests that already contained eggs. Colonies can be entered quickly and carefully during the incubation period without causing nest abandonment or creating trails for predators to follow, but offspring older than 8 days of age will abandon their nests if approached. On the first visit, nests were marked with plastic flagging and their contents recorded. Sample colonies were then monitored for signs of hatching by watching for parents returning to the colony with food. Because breeding is highly synchronous, hatching of marked nests often began the same day and rarely within more than a couple of days of each other.

To avoid disturbing nestlings older than 8 days, nests were re-checked in colonies shortly after hatching began to age offspring. A final record of nest contents was made 8 days after the first eggs hatched. We estimated mean reproductive success for each colony as the number of surviving nestlings per nest at that time (Beletsky 1996).

Population censuses were also conducted between 1994 and 2000 to estimate the population size and to monitor population size trends over time. More than 100 volunteer bird-watchers and personnel from the California Audubon Society, United States Fish and Wildlife Service and the California Department of Fish and Game participated. One or more observers were coordinated to census counties within the species' range to maximize the total area censused. Observers reported colony locations, estimated

colony sizes, and described nesting and foraging habitat. Censuses were limited to single weekends late in April because failed colonies may relocate to new breeding sites within a few days (Orians 1961) and because most of the population in the San Joaquin Valley relocates to the Sacramento Valley in the second half of the season (Hamilton 1998). The brief duration of the censuses was to ensure that participants counted individual birds only once.

Census effort was greatest in 1994 ($n = 37$), 1997 ($n = 34$) and 2000 ($n = 33$), calculated as the number of participants and counties surveyed. For this reason we included only data from these years in our analyses relevant to habitat use and population changes over time. Census effort and efficacy increased during the study period both because the number of participants increased from 68 in 1994 to 81 in 2000 and because participants were better informed about colony locations in each succeeding year.

Data analysis

We classified vegetative substrates used by nesting birds to evaluate patterns of habitat use in three ways (Table 1). First, we placed vegetation types into five groups: the three most commonly used substrates (emergent marsh vegetation, Himalayan blackberry and grain silage); and two less frequently used vegetation types (other flooded vegetation including native and non-native species and other upland vegetation that was not Himalayan blackberry or grain silage). We also used two classifications characterizing these vegetation types more broadly: flooded versus upland habitats, and native versus non-native plant communities.

We grouped breeding localities into geographic regions based on the physiographic distinctions between northern and southern portions of the Central Valley (Sacramento vs San Joaquin Valleys based on drainages of the two major rivers in the Central Valley) and southern California identified in the California Digital Conservation Atlas (www.legacy.ca.gov/new_atlas), and on temporal variation in use of the different regions by the majority of breeding birds (Hamilton 1998). We include a fourth region, southern Sacramento County, located in the northernmost section of the San Joaquin Valley, because relative habitat use there was distinct from other regions in the species' range.

We used a combination of MANOVA and non-parametric ANOVA (Kruskal–Wallis, Mann–Whitney) to evaluate changes in colony sizes and frequencies over time and to determine differences in reproductive success among colonies. We used parametric MANOVA where assumptions of normality and independence were met. We used non-parametric ANOVA where data were not normally distributed even after log transformation or when proportions were evaluated.

Results

Population trends

The total Tricolored Blackbird population was estimated to be 369,000 in 1994, 233,000 in 1997 and 162,000 in 2000, a decline of 56% over this period, and fewer colonies were located in 2000 ($n = 104$) than in 1994 ($n = 156$) (Figure 1). Because participation in the censuses was greatest in 2000 and the census effort was

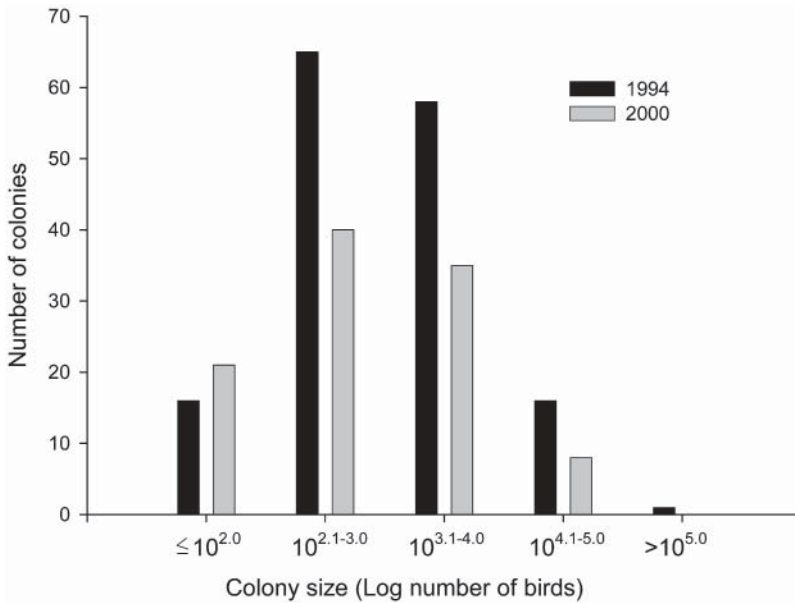


Figure 1. Size distributions of Tricolored Blackbird colonies (log number of birds) in 1994 and 2000.

increasingly informed each year about the birds' locations (Methods), this estimate of population decline may be conservative. With the declining global population size, colonies were smaller, on average, in 2000 than in 1994 (Figure 1; MANOVA full model, log colony size vs year, region, and nesting substrate: $F_{10,345} = 12.79$, $P < 0.001$; year effect: $F_{2,345} = 4.42$, $P = 0.013$).

The greatest changes to a regional population were in southern Sacramento County, where the number of located breeding birds declined by 95% between 1994 and 2002 (Figure 2). During this time, the proportion of birds using the Sacramento Valley increased in 2000 over that in 1994 (36% and 23% respectively). The proportion of the population nesting in the remainder of the San Joaquin Valley in 1994 and 2000 was relatively unchanged (53% and 51% respectively). Mean colony size varied among regions (Figure 3A). On average, colonies in the Central Valley (Sacramento and San Joaquin Valleys inclusive) were an order of magnitude larger than those elsewhere (MANOVA above; region effect: $F_{4,345} = 14.44$, $P < 0.001$).

Nesting substrates

Nesting was predominantly in flooded vegetation or in vegetation that was armoured in some way by spines, thorns, urticating structures, or other means of protection, whether these plants were flooded or not (Table 1). The most commonly used nesting substrates were cattail and bulrush in deep-water emergent marshes and Himalayan blackberry and grain silage crops in uplands. Himalayan blackberry substrates used were almost entirely those that occurred in open spaces surrounded by grasslands including rangeland. Tricolored Blackbirds also colonized pure stands of weeds including prickly lettuce *Lactuca serriola* and thistles *Cirsium* spp. in fallow agricultural

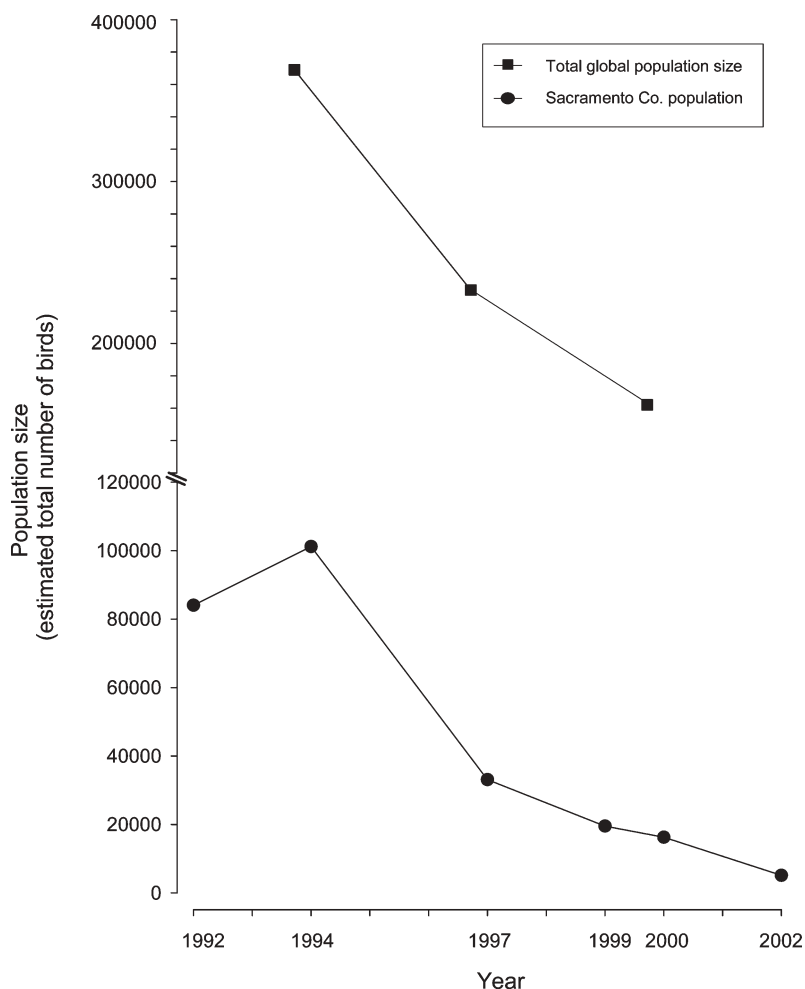


Figure 2. Population decline of the global Tricolored Blackbird population and of the population in Sacramento County between 1992 and 2002. The upper curve is vertically compressed relative to the lower curve because of the magnitude of population size differences.

fields. Overall, 91% of breeding individuals and 96% of colonies located in flooded habitats nested in native vegetation and 93% of breeding adults and 76% of colonies located in upland substrates nested in non-native vegetation.

The proportion of birds nesting in flooded habitats, and in particular native emergent marshes, decreased precipitously between the 1930s and 1990s. Concomitantly, nesting increased in upland substrates dominated by non-native plants. Some reversal of this trend occurred between 1994 and 2000, with increased proportions of birds using native emergent marshes and grain silage. Use of Himalayan blackberry, in particular, declined between 1994 and 2000, resulting in an overall decrease in the proportions of adults nesting in non-native substrates and an increase in the proportion of the population nesting in emergent marshes in the smaller 2000 population.

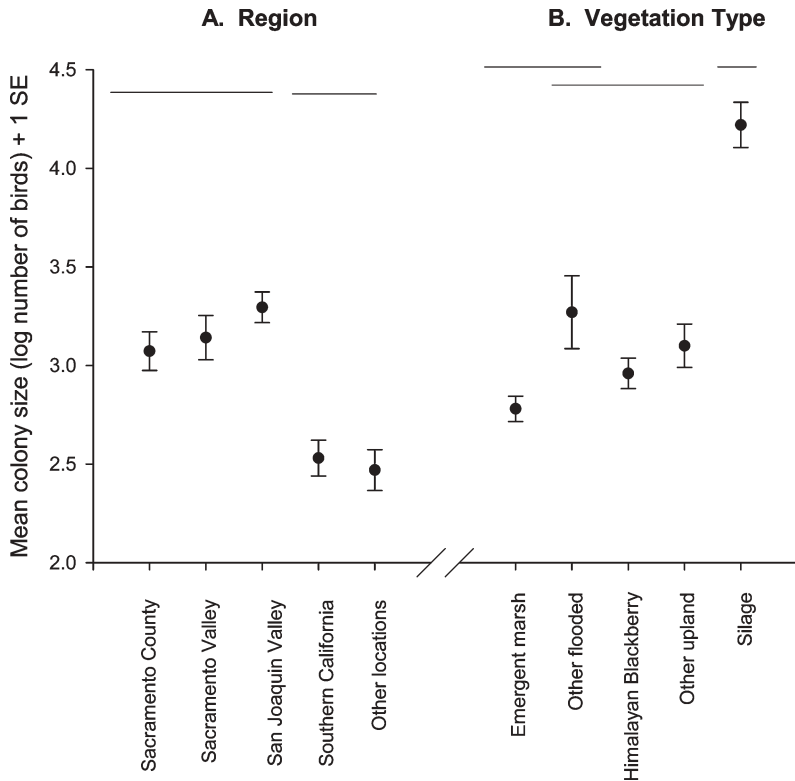


Figure 3. Mean colony size (log number of birds) by (A) region and (B) vegetation type. Lines connect means that are not significantly different (Tukey multiple means comparison).

Habitat use varied among regions (Table 2). In the Sacramento Valley, most nests were in native emergent marshes. In the San Joaquin Valley most nests were in upland non-native vegetation. Proportionately more colonies in southern Sacramento County settled in Himalayan blackberry than in other regions. In the lower San Joaquin Valley, a substantial proportion of birds nested in grain silage crops that were located near dairies. At these sites, adults forage largely on the abundant feedlot grain provided to cattle before switching to insects in nearby fields (often alfalfa) to feed their young. Birds using silage represented 5% of all located colonies among regions and 30% of all nests, but up to 50% of the total population of birds in recent years. Colonies nesting in grain silage were significantly larger than those in either flooded or other upland vegetation, primarily Himalayan blackberry (Figure 3B). Some of the largest colonies located were in native emergent marshes; however, colonies nesting in this substrate were smaller on average than those nesting in other flooded vegetation and all types of upland vegetation (MANOVA above; nesting substrate effect: $F_{4,345} = 11.35$, $P < 0.001$).

Reproductive success

Mean number of fledglings per nest varied among nesting substrates (Table 3). Nests in non-native vegetation fledged significantly more offspring than those in native

Table 2. Numbers of Tricolored Blackbird colonies and proportions of colonies and individuals nesting by substrate during the years 1994, 1997 and 2000 combined among identified regions in California.

	Emergent marsh			Himalayan blackberry			Silage			Other flooded vegetation			Other protective vegetation		
	No. of colonies	% colonies	% birds	No. of colonies	% colonies	% birds	No. of colonies	% colonies	% birds	No. of colonies	% colonies	% birds	No. of colonies	% colonies	% birds
San Joaquin Valley	52	15.0	12.6	14	4.0	2.3	17	4.9	29.6	7	2.0	3.4	16	4.6	5.2
Sacramento Valley	40	11.6	20.8	18	5.2	2.7	0	0	0	5	1.4	1.2	1	0.3	2.1
Sacramento County	7	2.2	1.6	48	13.9	9.5	0	0	0	0	0	0	0	0	0
Southern California	59	17.0	5.4	2	0.6	0.1	0	0	0	2	0.6	0.1	8	2.3	1.1
Other	30	8.7	1.2	5	1.4	0.4	0	0	0	3	0.9	0.3	12	3.5	0.6

Table 3. Mean reproductive success (number of chicks per nest at 8 days after first egg hatched) of colonies by substrate and study region from 1992 to 2003

	No. of chicks per nest		
	<i>n</i>	Mean	SE
Nesting substrate			
Emergent marsh	40	0.5	0.09
Himalayan blackberry	23	2.0	0.16
Silage	26	0.2	0.08
Silage ^a	4	1.0	0.26
Other flooded plants	6	1.2	0.51
Other upland plants ^a	7	1.2	0.37
Total native plants	46	0.6	0.11
Total non-native plants ^a	34	1.7	0.15
Region			
San Joaquin Valley	45	0.6	0.12
San Joaquin Valley ^a	22	1.1	0.17
Sacramento Valley	32	0.3	0.09
Sacramento County	24	1.8	0.19
Southern California	3	0.9	0.76
All colonies	103	0.8	0.09

^aExcluding colonies that failed entirely when crops were harvested.

habitats ($U_{78} = 258.50$, $P < 0.001$). Of colonies where one or more offspring fledged per nest on average, 70% ($n = 26/37$) nested in non-native substrates. Of colonies where mean number of fledglings per nest was 0.5 or lower (excluding colonies lost to harvest operations) 94% ($n = 30/32$) were in native vegetation. Approximately 40% ($n = 16/40$) of all native emergent marsh-nesting colonies failed completely, compared with 6% ($n = 2/34$) of colonies in non-native vegetation not destroyed by harvesting. Colonies in grain silage failed entirely unless intervention protected them from harvest operations.

When we removed colonies destroyed by harvest from the analysis, mean number of fledglings per nest was significantly higher in grain silage than in emergent marshes ($U_{42} = 33.50$, $P = 0.05$) but still significantly lower than in Himalayan blackberry ($U_{25} = 80.50$, $P = 0.018$). Within colonies where reproduction did not fail entirely, the proportion of nests failing to produce any young was significantly higher in native emergent marshes (80.0%) than in the non-native substrates (Himalayan blackberry, 19.7%, and silage 40.3% respectively; $H_{2,51} = 26.336$, $P < 0.001$). Thus, by various measures reproductive success was significantly lower in native emergent marshes than in upland non-native vegetation of various kinds.

Number of fledglings per nest was significantly higher in southern Sacramento County than in other regions ($U_{101} = 252.000$, $P < 0.001$). This result reflected the greater use of Himalayan blackberry in that region compared with other regions, combined with the higher reproductive success in Himalayan blackberry on average. When colonies lost to crop-harvesting were excluded from the analysis, more offspring were fledged per nest in the San Joaquin than in the Sacramento Valley ($U_{52} = 568.00$, $P < 0.001$). This result reflected the proportionately lower use of emergent marshes in the San Joaquin Valley than the Sacramento Valley and the greater reproductive success in upland substrates compared with emergent marshes.

Colonies that experienced total failure in reproduction were slightly smaller on average than those in which some young were fledged, excluding the silage colonies destroyed during harvest (mean log number of birds 3.22 and 3.61 respectively; $F_{1,80} = 4.26$, $P = 0.043$). However, mean number of young fledged per nest did not differ significantly between small and large colonies (cut point log size = 3.5 or about 3,000 birds; $F_{1,80} = 0.44$, $P = 0.51$).

Discussion

Causes of population decline

Native wetland habitat losses in the later nineteenth and early twentieth centuries, and several other causes, may have originally reduced the Tricolored Blackbird population from that prior to European arrival and the first coordinated effort to estimate the species' abundance (Neff 1937). Market hunting was a major source of mortality between the later nineteenth and early twentieth century (Neff 1937). This period was shortly followed by large-scale poisoning efforts to control crop depredation during the 1930s (Neff 1942). Since c.1930, when Tricolored Blackbird was identified as an agricultural pest, subsequent population data (Orians 1961, DeHaven *et al.* 1975a, Hamilton 2000) have shown a continuing decline throughout its range. The estimated global population by the year 2000 was at an all-time low of no more than 200,000 birds, or c. 20% of its estimated historic size and smaller than some of the single, large colonies reported earlier (Neff 1937).

The causes for decline, as revealed by this and previous studies, are straightforward and suggest urgent concern for the continuing trajectory of this species' population size. Although Tricolored Blackbird is still found throughout its historic range, loss of suitable nesting habitat statewide because of changes in land-use throughout the past century (Kreissman 1991) continues to cause widespread failure of breeding.

The first adverse change in land-use was the drainage and conversion of 96% or more of California's wetlands, Tricolored Blackbird's likely primary native nesting habitat in the past 150 years (Kreissman 1991). The loss of native wetlands alone, however, has not contributed to the recent precipitous decline. Tricolored Blackbirds have been adaptable in their choice of nesting substrates. In particular, they can reproduce successfully in upland environments, primarily in the introduced Himalayan blackberry, but also in other patches of largely non-native armoured plants, which deter predation on nests, and grain crops at large dairy operations where feedlots provide abundant feed and the crops themselves provide some deterrence of predators. The availability of some of these upland nest-sites, particularly Himalayan blackberry patches where these occurred in open rangelands, between the 1970s and mid-1990s may have helped delay the kind of precipitous decline observed between 1994 and 2000.

With a rapidly growing human population in California's Central Valley in the past 20 years has come more intense land-use, with removal of Himalayan blackberry patches, conversion or degradation of former rangeland, and highly managed harvest of grain silage for dairies that run on a narrow economic margin. A portion of the decline in the Tricolored Blackbird population during the 1990s was probably a result of its near extirpation from southern Sacramento County, where extensive Himalayan

blackberry patches and rangeland once supported a large and highly successful breeding population (Cook 1996). This region served, as early as 1994, as the single largest source location for fledgling production. In recent years, pressure from the human population, including conversion of rangelands to vineyards, has been particularly intense there, resulting in the loss of the largest colony-sites and approximately two-thirds of all known breeding locations in the region. Ultimate causes have included one or both of direct destruction of Himalayan blackberry patches themselves and permanent changes in land-use that reduce or degrade the suitability of the available surrounding foraging habitat. Substantially reduced breeding in southern Sacramento County most likely explains the more recent increasing trend toward nesting again in emergent marshes, especially in the nearby Sacramento Valley, where reproductive success is lowest on average.

Evidence from studies of marsh-nesting passerines implicates predation as the most common cause of partial and entire nest failure in native wetlands (Picman *et al.* 1993, 2002, Picman and Isabelle 1995, Massoni and Reboresda 2001). Nesting over water provides some protection from predators (Picman *et al.* 1993). However, the reduction of native wetlands to less than 4% of their original extent has probably concentrated predator populations in the remaining wetlands more than was true historically. In this study, a larger proportion of colonies in native wetlands than in upland substrates suffered complete reproductive failure attributable primarily to predation. In particular, some of the largest breeding colonies in wetlands, such as those in the Sacramento Valley, failed completely despite a weak trend in this study for larger breeding colonies to be less likely to fail completely, and the fact that colonial nesting is considered an adaptation against predation through the efficacy of mutual defence (Picman *et al.* 2002). In earlier studies, colony settlement was reported to be sporadic and unpredictable (Neff 1937, Orians 1961) and banded nestlings were only somewhat philopatric (DeHaven *et al.* 1975b). More recent data, however, indicate repeated settlement of many sites despite poor breeding outcomes (this study). In addition, the recent losses of known breeding sites are concomitant with the decline in local breeding populations despite an abundance of what appear to be other suitable sites which do not become used. This trend toward apparent increased philopatry probably reflects the now vastly limited availability of suitable nesting habitat.

In contrast to breeding in native wetlands, breeding in upland vegetation was far more successful by every measure: complete failure of breeding colonies was less likely and number of fledglings per nest was higher in upland vegetation (primarily Himalayan blackberry but also dense patches of non-native bull, milk and Canada thistles *Cirsium* spp., native nettles *Urtica* spp. and other spiny weed patches) than in native wetlands, a pattern reported in other studies of marsh-nesting passerines (Jobin and Picman 2002). Well-developed Himalayan blackberry patches also support highest nest densities: two or three nests per square metre are not uncommon, whereas these densities are relatively rare in native emergent marshes and other substrates. Native blackberries *Rubus* spp. do not provide adequate alternative nest-sites and are rarely used even when they co-occur with Himalayan blackberry. This is probably because patches of native blackberry species do not develop the density, armouring and height characteristics of Himalayan blackberry.

Although reproduction in non-native, upland vegetation that is not agricultural (primarily Himalayan blackberry) was more successful than that in grain silage, colonies in grain silage were an order of magnitude larger than those in any other upland nesting substrate. In the few instances in which the nests were not destroyed by

harvest, the number of fledglings per nest was higher in grain silage than in native emergent marshes. Thus the contribution to population recruitment of colonies nesting in grain silage could be considerable and could potentially play a large role in stabilizing the population.

Patterns of reproductive success in the different nesting substrates suggest that a significant proportion of the breeding population now occurs in population sinks (Pulliam 1988). In this study, catastrophic losses of an entire colony's breeding attempt were frequent and occurred in all years in all commonly used substrates except Himalayan blackberry. Importantly, both native emergent marshes and plants associated with agricultural harvest operations appear to be critical population sinks for Tricolored Blackbird because they are so attractive to the birds for nesting and because complete, colony-wide failure of breeding is so frequent in these nesting substrates. As recently as 2003, approximately 80,000 (half of the last known breeding population) nested in two grain silage fields where 80% of the nesting effort was lost to harvest operations (L. Cook unpubl. data). The recent losses of favourable nesting habitat, combined with the steady state of colony failure in emergent marshes and destruction in grain silage fields, leaves little prospect that the population has remained stable or increased since the last census in 2000. Although re-nesting in other, more productive habitats could in principle compensate for reproductive failures in these putative habitat sinks, the continuing losses of productive habitats together with the continuing decline of the global population of Tricolored Blackbird argues otherwise.

Allee effect and reversing population decline

Like Passenger Pigeons, Tricolored Blackbirds breed colonially and are now adapted to the patchy distribution of a habitat that was widespread before European immigration to North America. The extinction of Passenger Pigeon has been attributed to a combination of highly social and nomadic breeding, the fragmentation of the mast forests that provided abundant forage, and intense commercial hunting (Blockstein 2002, Bucher 1992, Stephans and Southerland 1999, Wilcove 1999). Together these factors pushed the population past a lower threshold of inverse density dependence (the Allee effect) and on to the alternative stable state of global extinction (Stephans and Southerland 1999). Importantly, Passenger Pigeon was once the most abundant bird species in North America, with flocks reported to darken the skies for hours (Wilcove 1999), similar to descriptions of flocks of Tricolored Blackbird in California's Central Valley in the mid-1800s (Heermann 1859).

Because local populations of Tricolored Blackbird are still found in dense breeding colonies, they can leave a false impression of abundance upon casual observers. The long-term population trends and patterns in reproduction reported in this study reveal that Tricolored Blackbird possesses most of the traits that ultimately led to the extinction of Passenger Pigeon in the same ecological circumstances. These factors include the loss of vast areas of native wetland along with the increasing loss of upland, non-native vegetation favourable for nesting, the trend of decreasing colony size in a highly social breeder, a habit of itinerant breeding (Hamilton 1998), and wholesale mowing down of the largest breeding colonies in agricultural harvest.

We interpret our results to provide clear evidence that extinction is imminent for Tricolored Blackbird if current land-use trends continue, as they certainly will, and if

measures are not implemented immediately to protect breeding colonies in non-native nesting substrates. Overall the current decline of the population is strongly correlated with its persistent use and re-use of attractive habitats where reproduction often fails, combined with continuing losses of productive nesting substrates of all kinds. Introduced plants considered noxious weeds and undesirable in the landscape, now the best nesting habitat for Tricolored Blackbirds, are being lost not only to routine agricultural practices and land conversion but also to removal by the well-meaning conservation community. Although Tricolored Blackbird is considered by the state and federal government as a species of some concern, and is included in various mitigation and conservation management plans, the relationship between its breeding habitat and reproductive success, and other requirements such as suitable and sufficient nearby foraging habitat, have not been adequately addressed. The protection of native emergent marshes is not the solution to reverse the declining population because this habitat provides attractive population sinks. Under current protections, Tricolored Blackbird may therefore be falling through the policy "cracks", because it is not targeted directly as an officially endangered species and protecting its native breeding habitat under current environmental policy is not sufficient to reverse the declining population.

Surely the legacy of Passenger Pigeon should be our understanding of how such extinctions can occur rapidly in extremely abundant organisms because of non-linear population dynamics and thresholds caused by inverse density dependence. Failure to address the impact of habitat and human activities on reproductive success of Tricolored Blackbird may again lead to the extinction of a once-abundant bird. We predict that the Tricolored Blackbird population will decline below an extinction threshold within a decade if measures are not taken immediately to protect Himalayan blackberry, portions of grain silage fields settled by breeding colonies, and other upland habitats that provide for suitable nesting and foraging.

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LIZETTE F. COOK

California Department of Water Resources, Division of Environmental Services, 3251 S. Street, Sacramento, CA 95816-7017, U.S.A. (e-mail: lcook@water.ca.gov)

CATHERINE A. TOFT

Section of Evolution and Ecology, University of California, Davis, CA 95616-8755, U.S.A.

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