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*RESEARCH ARTICLE*

# Nest survival of Tricolored Blackbirds in California's Central Valley

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## ABSTRACT

The Tricolored Blackbird (*Agelaius tricolor*), almost entirely restricted to California, USA, has recently been proposed for listing under the U.S. Endangered Species Act. Tricolored Blackbirds historically nested in wetlands, but a large proportion of the population now nests in agricultural grain fields where the crop is ready to harvest before the young have fledged. Since 1991, federal agencies have paid farmers to delay harvesting in an effort to increase nesting productivity. However, the relative nesting success of Tricolored Blackbirds breeding in agricultural fields versus wetlands is unknown. Our objectives were to estimate daily survival rate (DSR) of nests, identify habitat covariates that influence nest survival, and estimate the number of young produced per nest. During 2011–2012, we monitored 1,323 Tricolored Blackbird nests in 12 colonies using small temperature data loggers. We modeled DSR using Program RMark with combinations of the following variables: site, habitat type, nest initiation date, nest height, water depth, nest density, colony population size, year, and the proportion of nearby nests that failed. Nest survival varied greatly (range: 0.024–0.719) but was not explained by habitat type. Nest height and nest density were positively associated with DSR. DSR was lowest midway through the breeding season and declined with colony population size. Number of young produced per nest varied by site, was lowest in intermediate-sized colonies of 1,000–5,000 birds, and was highest in 2011. DSR and number of young fledged per nest were similar in agricultural fields and in wetlands. Our results suggest that Tricolored Blackbirds benefit from policies that allow them to complete their nesting cycle in agricultural fields.

*Keywords: Agelaius tricolor*, iButton, nest survival, *Plegadis chihi*

### Supervivencia del nido de *Agelaius tricolor* en el Valle Central de California

## RESUMEN

La especie *Agelaius tricolor*, restringida casi totalmente a California, USA, ha sido propuesta recientemente para ser incluida en la Lista de Especies en Peligro de EEUU. *A. tricolor* anidó históricamente en humedales, pero una gran proporción de la población ahora anida en campos de agricultura de granos que están listos para ser cosechados antes de que el polluelo haya emplumado. Desde 1991, las agencias federales han pagado a los agricultores para retrasar la cosecha como un intento de aumentar la productividad del nido. Sin embrago, se desconoce el éxito relativo de los nidos de los individuos de *A. tricolor* que crían en los campos de cultivo versus en los humedales. Nuestros objetivos fueron estimar la tasa de supervivencia diaria (TSD) de los nidos, identificar las covariables del hábitat que influencian la supervivencia del nido y estimar el número de polluelos producidos por nido. Durante 2011–2012, monitoreamos 1,323 nidos de *A. tricolor* en 12 colonias usando pequeños registradores de datos de temperatura. Modelamos la TSD usando el programa RMark en combinación con las siguientes variables: sitio, tipo de hábitat, fecha de inicio del nido, altura del nido, profundidad del agua, densidad de nidos, tamaño poblacional de la colonia, año y proporción de nidos cercanos que fracasaron. La supervivencia de los nidos varió enormemente (rango 0.024 a 0.719), pero no fue explicada por el tipo de hábitat. La altura del nido y la densidad de nidos estuvieron asociadas positivamente con la TSD. La TSD más baja se registró a mediados de la estación reproductiva y disminuyó con el tamaño poblacional de la colonia. El número de polluelos producidos por nido varío en cada sitio, fue más bajo en las colonias de tamaño intermedio de 1,000–5,000 aves y fue más alto en 2011. Las tasas de supervivencia diaria del nido y el número de polluelos emplumados por nido fueron similares en los campos de agricultura y en los humedales. Nuestros resultados sugieren que los individuos de *A. tricolor* se benefician de las políticas que permiten que puedan completar su ciclo de anidación en los campos de agricultura.

*Palabras clave: Agelaius tricolor*, iButton, *Plegadis chihi*, supervivencia del nido

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## INTRODUCTION

The Tricolored Blackbird (*Agelaius tricolor*) is under consideration for listing as threatened or endangered by the U.S. Fish and Wildlife Service (USFWS) because of habitat loss, high levels of nest predation, the inadequacy of existing regulatory mechanisms, and dramatic and ongoing population declines (USFWS 2015). Prior to large-scale agricultural and urban development in California's Central Valley, Tricolored Blackbirds primarily nested in freshwater cattail wetlands (*Typha* spp.; Neff 1937). Between 1780 and 1980, California lost ~91% of its wetlands (Dahl 1990). Where alternatives are available, Tricolored Blackbirds nest in nontraditional habitat, such as upland agricultural fields. Continued population declines, however, suggest that nontraditional nesting habitats may not be adequate substitutes for wetlands and may therefore be population sinks (Dias 1996).

Tricolored Blackbirds form the largest breeding colonies of any North American passerine (Beedy and Hamilton 1999). The largest colonies are found in California's Central Valley, but breeding also occurs in southern California and the California foothill region. Less than 1% of the total population breeds in Oregon, Washington, Nevada, and the Mexican state of Baja California (Beedy and Hamilton 1999). Tricolored Blackbird breeding colonies tend to settle where standing water, protected nesting sites, and foraging areas are within a few kilometers of the nesting area (Beedy and Hamilton 1999). The species is very flexible in its choice of nesting sites (Neff 1937, Cook and Toft 2005) and can successfully reproduce in grain fields (Figure 1A), cattail wetlands (Figure 1B), Himalayan blackberry brambles (*Rubus discolor*), thistles (*Cirsium* and *Centaurea* spp.), and nettles (*Urtica* spp.; Beedy and Hamilton 1999, Cook and Toft 2005, Kelsey 2008, Meese 2009b). Despite flexibility in their selection of breeding habitat, surveys conducted since the 1930s have documented significant declines in the abundance of Tricolored Blackbirds throughout their range (Beedy and Hamilton 1999, Cook and Toft 2005). Additionally, 2 general trends in Tricolored Blackbird breeding ecology have become apparent: (1) The birds are forming "mega-colonies" that contain progressively larger percentages of the total population and (2) there has been a progressive increase in the number of birds nesting in nontraditional nesting substrate, primarily grain fields and Himalayan blackberry patches (Beedy and Hamilton 1999, Cook and Toft 2005, Kelsey 2008). In 2008, for example, the 2 largest nesting colonies occurred in grain fields in California's Central Valley; these 2 colonies accounted for ~55% of the global population (Kelsey 2008). As a result of these trends, large portions of the global population are at risk for complete nest failure should their nesting sites be subjected to disturbance events, such as the harvest of a silage crop.

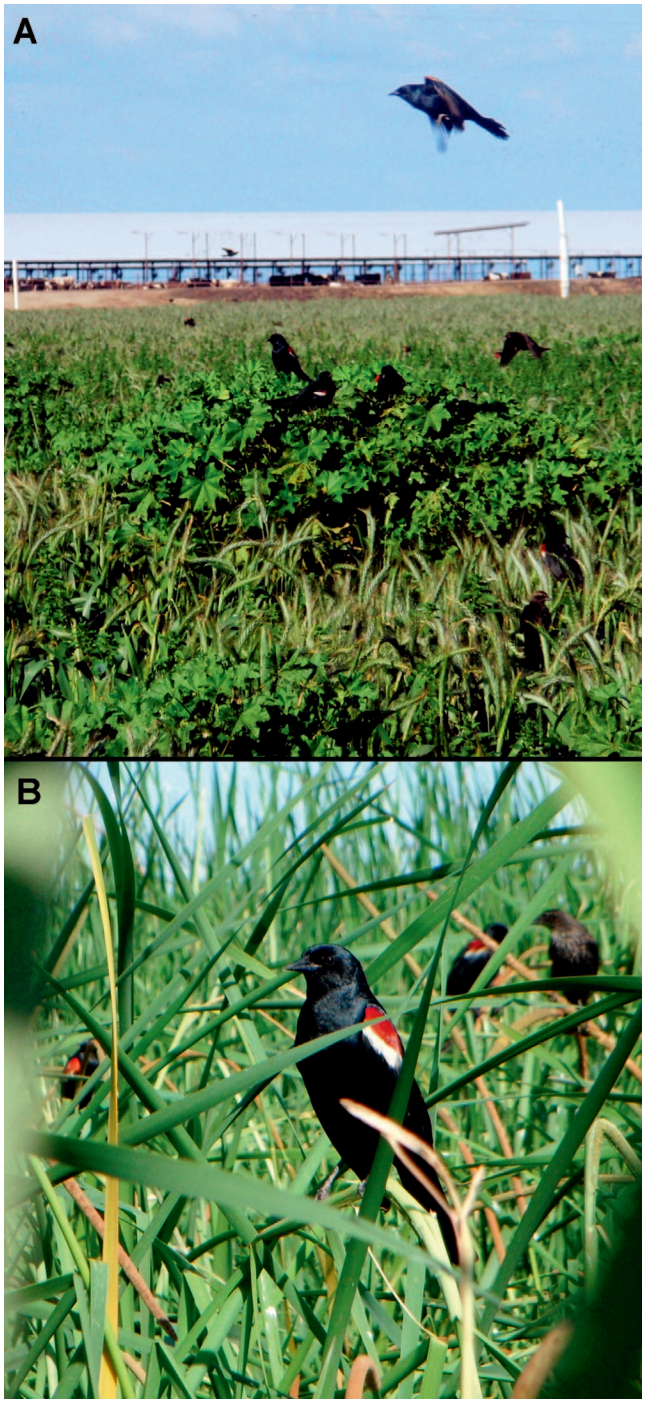


**FIGURE 1.** Tricolored Blackbird colonies in (**A**) a dairy silage field and (**B**) a wetland duck-club pond in Kern County, California, USA.

When Tricolored Blackbirds nest in grain fields, they most often settle in triticale, a wheat–rye hybrid grown to produce a fermented, high-moisture feed ("silage") for



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dairy cattle. A conflict arises because the grain crop is often ready to harvest before the young Tricolored Blackbirds have fledged (Meese 2009a). Despite federal and state protection, some farmers harvest fields containing active Tricolored Blackbird colonies. As a result, birds nesting in silage fields often experience complete reproductive failure unless farmers agree to delay harvest until the young have fledged (Cook and Toft 2005, Meese 2009a). From 2005 to 2009, the USFWS spent $331,921 to conserve 11 Tricolored Blackbird breeding colonies that cumulatively contained ~546,000 birds (Meese 2009a). The relative nesting success of birds breeding in silage fields has not been determined, however, and it is possible that Tricolored Blackbirds experience higher nest survival in native wetland vegetation than in silage fields. If this is the case, conservation efforts might be better directed toward enhancing wetland habitat (expansion of wetland habitat is unlikely due to high land and water prices) rather than protecting colonies in silage fields. A comparison of Tricolored Blackbird nest survival in silage fields vs. wetland vegetation would help managers develop an improved conservation approach for this species.

Although no study has explicitly examined daily survival rates of Tricolored Blackbird nests, the most common cause of nest failure for other wetland-nesting blackbirds is nest predation (Robertson 1972, Caccamise 1976, Picman et al. 1988, 2002, Westneat 1992, Fletcher and Koford 2004), which has been found to be influenced by 2 factors: water depth under the nest and the number of conspecifics breeding at the same site, measured as either nest density or nesting synchrony. Nest survival was positively correlated with water depth for Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) nesting in wetland environments (Robertson 1972, Picman et al. 1993, Fletcher and Koford 2004). Survival of Red-winged Blackbird and Yellow-headed Blackbird nests in cattail wetlands increased with increasing nest density, an effect that was most likely the result of mutual protection from egg predators like Marsh Wrens (*Cistothorus palustris*; Picman et al. 1988, 2002). Similarly, the probability of nest survival in Red-winged Blackbird colonies was positively associated with the number of nests initiated at a breeding site within a 5-day period (Westneat 1992).

The influences of water depth and population density on nest predation rates lead to conflicting predictions about whether Tricolored Blackbird nest survival is higher in silage fields or in wetlands. Nest survival may be higher in wetland habitat than in silage fields because of the presence of standing water in wetlands that may restrict predator access. However, because Tricolored Blackbird colonies tend to be larger in silage fields than in wetlands (Cook and Toft 2005), the effects of mutual nest protection may be more pronounced in silage fields and may lead to higher nest survival rates. The objectives of this study were to estimate nest survival rates of Tricolored Blackbirds in upland silage fields and in wetlands and to identify habitat variables that influence nest survival and number of fledglings.

## METHODS

We conducted the study in California's southern San Joaquin Valley in Kern County and southwestern Tulare County (Figure 2). Elevation of study sites ranged from 56 to 95 m. Historical average annual precipitation measured in Delano, California, was 18.36 cm (Western Regional Climate Center 2012). Pre-breeding-season (December 1–March 31) precipitation in Delano was 32.60 cm in 2011 and 7.96 cm in 2012. Land use in the study area included cattle dairies and associated silage and alfalfa crops, almond and pomegranate orchards, cultivated fields, grasslands, and urban areas. We monitored nests on Kern National Wildlife Refuge and at private duck clubs, water-district storage ponds, and private dairies within 40 km of the refuge. Nesting habitat included cattail wetlands, silage fields, stands of mesquite trees (*Prosopis* spp.), stands of salt cedar trees (*Tamarix* spp.), nettles, willows (*Salix* spp.), and other riparian vegetation. We included only cattail wetlands and silage fields in our analyses. Landowners agreed not to harvest the silage fields that we monitored until after the birds fledged. In the present study, "site" refers to the physical location where Tricolored Blackbirds nested, typically a discrete basin in a managed wetland or a silage field on a dairy. A "colony" is a spatially and temporally contiguous group of breeding birds occupying a site. Thus, a single colony could occupy a site over several months, and the size of the area occupied, as well as the population of the colony, could change over time. In addition, colonies that formed at the same site in 2011 and 2012 were considered different colonies.

The timing of nest-building in a Tricolored Blackbird colony falls along a continuum represented by 2 extremes: (1) synchrony, in which all nests are built and all eggs laid within one week; or (2) asynchrony, in which a colony grows over several weeks through the addition of new birds to the colony's periphery (Neff 1937, Orians 1961, Hamilton 1998, Beedy and Hamilton 1999). In the latter case, young may have hatched in one area of the colony while females in another area were still building nests (Neff 1937, Orians 1961). Thus, the nest-building phase may last 7–34 days or more in a single colony (Orians 1961, Hamilton 1998). For an individual female, however, an entire nesting cycle can be completed in as little as 28 days: 3 days for nest building (Orians 1961, Hamilton 1998), 3–4 days for egg laying (Hamilton 1998), 12 days for incubation (Orians 1961, Hamilton 1998, Beedy and Hamilton 1999), and a minimum of 10 days for the nestling period (Hamilton 1998).

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We conducted the study during the Tricolored Blackbird breeding season from March 10 to July 16, 2011, and from March 6 to June 28, 2012. In early March, we began monitoring potential nesting habitat for the arrival and formation of breeding colonies by making repeated visits to potential and historical nesting sites and looking for the presence of Tricolored Blackbirds. Once females and singing males were present, we requested permission to access the site and, if granted, returned every 1–3 days to determine the onset of nest building and egg laying. We identified the initiation of nest building by the presence of female Tricolored Blackbirds carrying nesting material (e.g., grasses). At least 4 days after the first females were observed carrying nesting material, we entered the colony to visually verify the initiation of egg laying. To reduce disturbance to nesting birds, after egg laying had commenced we monitored nest activity using Thermochron iButton temperature data loggers (Maxim Integrated Products, Sunnyvale, California, USA; hereafter "iButtons") placed within nests. The iButtons measured 17.35 mm (diameter) by 5.89 mm. Placing iButtons in nests at the beginning of the nesting cycle allowed us to monitor nest success without making repeated visits to the same location that could disrupt nesting colonies (Hartman and Oring 2006, Libsch et al. 2008). As soon as we detected egg laying in a colony, we deployed 25–30 iButtons $\geq$2m apart along one or more transects where active nests were present. We attempted to place the first round of iButtons in the first completed nests in each colony, prior to clutch completion. If there was evidence of additional nest building at a colony, we placed additional transects of 25–30 iButtons in the most recently established nests. Because nest initiation within a colony could last for several weeks, deploying iButtons over multiple days as the colony expanded allowed us to sample a range of nests from the middle (first nests) to the outer edges of the colony (last nests initiated) while (1) placing iButtons in nests as close to the onset of incubation as possible and (2) minimizing disturbance. We also placed at least one iButton on nesting substrate in each colony to record ambient air temperature. Nest temperature and air temperature were recorded every 20 minutes. Comparing nest temperature to ambient air temperature allowed us to determine how long each nest was active (Hartman and Oring 2006). When the oldest nestlings in a colony were 5–7 days old, we entered colonies on centrally located transects to count the number of young $\geq$5 days old in $\geq$30 nests colony$^{-1}$ in order to estimate the mean number of young produced per successful nest. Nestling Tricolored Blackbirds $\geq$9 days old will jump from the nest if disturbed (Cook and Toft 2005, K. Weintraub personal observation); thus, we conducted counts of nestlings before the oldest chicks in the colony were 9 days old.

The iButtons were sewn into pieces of brown nylon stocking prior to deployment. We attached a 30.5 cm piece of green floral wire to each nylon-wrapped iButton. After carefully removing the eggs from each nest, we used a long sewing needle to pass the wire through the bottom of the nest. We then secured the iButton by wrapping the wire around the nesting substrate and returned the eggs to the nest. The iButton sat flush in the bottom of the nest, under the eggs. We attached flagging with the iButton's individual serial number to the base of the plant to facilitate retrieval of iButtons. When deploying an iButton, we candled (Lokemoen and Koford 1996) one or more eggs in each nest and recorded the number of days that the oldest egg had been incubated. When we deployed an iButton, we recorded the day of the breeding season on which the nest was found (day 1 = first day that nest monitoring began), the Universal Transverse Mercator coordinates for the nest, nest height (cm; measured from ground level to top of the nest cup), water depth (cm) directly under the nest, and the number of active nests (i.e. nests containing eggs) within a 1 m radius. We used a 1 m radius to assess nest density because extremely dense vegetation often made locating nests difficult, and conducting detailed searches beyond 1 m would have caused unacceptable levels of disturbance to nearby nests, because Tricolored Blackbirds nest at very high densities (Neff 1937, Tyler 1907). We retrieved iButtons after the last birds in the colony fledged.

We estimated the population size of each colony every 3–4 days using a survey protocol described by Kelsey (2008). Accurately estimating the population size of Tricolored Blackbird colonies is extremely difficult (Neff 1937). Males are highly visible early in the nesting cycle, but many males leave the site or become inconspicuous during incubation, only to become more visible when feeding nestlings (Lack and Emlen 1939, Emlen 1941, Hamilton 1998, Beedy and Hamilton 1999, K. Weintraub personal observation). Because of substantial uncertainty involved in estimating the populations of Tricolored Blackbird colonies, at the end of the season we consolidated population estimates into broad categories of $<$1,000 birds, 1,000–5,000 birds, and $>$5,000 birds. The population size assigned to each nest was the size of the colony on the last day the nest was active.

After retrieving iButtons, we downloaded temperature records from each iButton and compared nest temperatures to ambient air temperatures to determine how long each nest was active. Nest temperature remained relatively constant during the incubation and nestling periods and was distinctly different from the cyclic pattern of the ambient temperature (Figure 3; Hartman and Oring 2006); thus, we were able to accurately monitor the incubation and nestling periods for each nest. In all cases, we were confidently able to (1) determine the day that incubation started (by candling or by using temperature graphs); and

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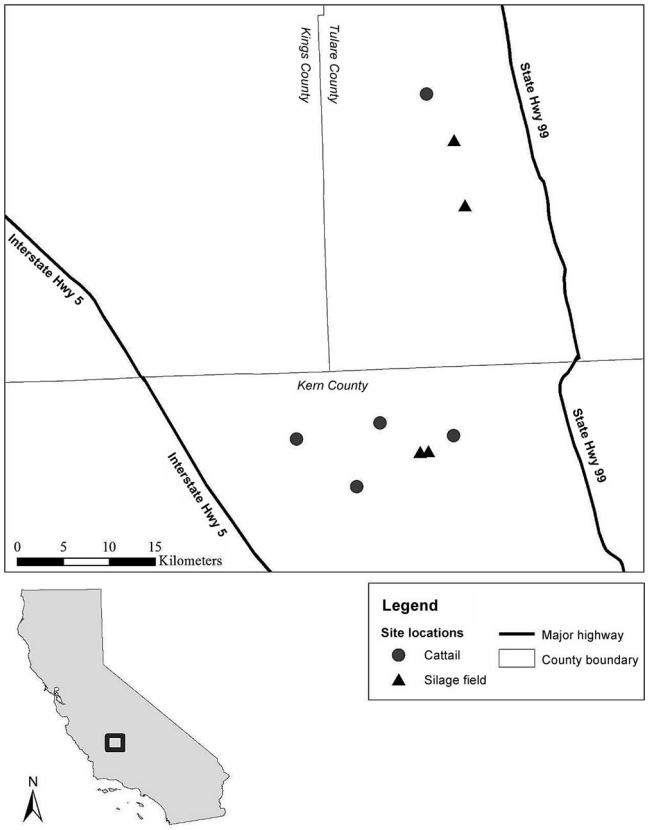


**FIGURE 2.** Tricolored Blackbird breeding sites monitored in 2011 and 2012 in the San Joaquin Valley, California, USA.

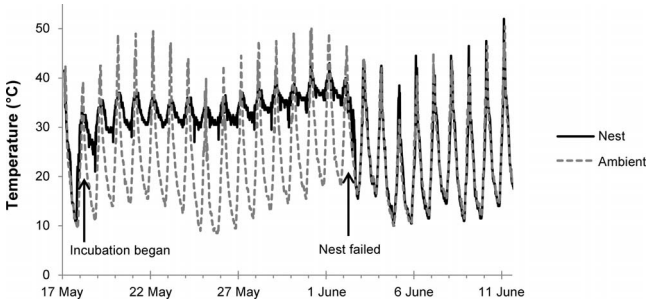


**FIGURE 3.** Tricolored Blackbird nest temperatures and ambient air temperatures recorded by iButtons in 2012 in the San Joaquin Valley, California, USA. Nest activity ceased when the 2 temperature patterns began cycling together. Incubation began on the morning of May 18, and the nest failed at 0200 hours on June 3.

(2) pinpoint nest failure to within 1 hr for all but 2 nests, and to within 4 hr for all nests. If nest temperatures and egg candling indicated that a nest was active for at least 22 days (12 days for incubation, 10 days minimum to fledge), we considered it successful.

We modeled the daily survival rate (DSR) of Tricolored Blackbird nests using known-fate models with the package RMark (Laake 2012) in R 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria) that interfaces with Program MARK (White 1999). We used 21 intervals to represent the 22-day nesting cycle, with each interval equivalent to one day. We estimated the probability of a nest surviving the 21-interval nesting period in each site as $DSR^{21}$. In a preliminary analysis conducted after the first field season, we modeled DSR as a function of nest age; because there was no change in DSR across the nesting cycle, we omitted nest age from future analyses. We modeled DSR as a function of site, habitat type, day of the season that incubation began, day of the season$^2$, nest height, water depth under the nest, nest density (number of active nests within 1 m), population size, year, and the proportion of nearby ($\leq$50 m) nests that were monitored with iButtons and failed on the last day the nest was active. To evaluate spatial dependence of nest outcome for this colonially nesting species, we included the proportion of nearby nests that failed. We evaluated relationships between independent variables using Pearson's correlation coefficient ($r$); $r < 0.70$ in all cases, so we did not remove any variables from the analysis. We used an information-theoretic approach (Burnham and Anderson 2002) to compare competing models of Tricolored Blackbird nest survival. We ran an a priori set of 576 models (256 models, including all combinations of site, season, height, year, nest density, population size, water depth, and proportion of nearby nests that failed; 128 models that included season with season$^2$ added; and 192 models with habitat substituted for site in all previous models) using all combinations of variables (Doherty et al. 2012) in order to examine the contribution of each variable to DSR. We did not include site and habitat type in the same models, and we only included season$^2$ in models that also included season. Site, habitat type, population size, and year were considered grouping variables, and the remaining variables were modeled as continuous covariates. We used Akaike's Information Criterion adjusted for small sample size ($AIC_c$) to select the best-fitting model. We summed the model weights for each variable to determine which variables were most important for predicting nest survival. We used the function "covariate.predictions" in package RMark to obtain model-averaged estimates of the DSR for each nest, then calculated the mean nest success ($DSR^{21}$) for each site. We estimated the standard error of nest success for each site using the delta method (Powell 2007).

We used model selection to determine which model best explained variation in the number of young produced per nest. We developed 24 a priori general linear models that included site, habitat type, day of the breeding season on which the count was conducted, colony population size on or near the day the count was conducted, and year. We did not include a season$^2$ term because scatterplots of the mean number of young per nest per colony plotted against



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**TABLE 1.** Daily nest survival models for Tricolored Blackbirds, ranked by Akaike's Information Criterion (AIC). Daily nest survival was estimated using known-fate models for 1,142 nests in 12 colonies in the San Joaquin Valley, California, USA, 2011–2012. The top model's $AIC_c$ score (corrected for small sample size) was 5,800.30; $\Delta AIC_c$ is the difference in $AIC_c$ score from the top model. Only models with the top 95% of the weight are shown ($w_i$ = Akaike weight, $K$ = number of parameters).

| Model [a] | $K$ | $\Delta AIC_c$ | $w_i$ | Deviance |
|---|---|---|---|---|
| S(SI + SN + $SN^2$ + HT + DN + POP + YR + PF) | 17 | 0.00 | 0.22 | 5,766.26 |
| S(SI + SN + $SN^2$ + HT + DN + POP + YR) | 16 | 0.46 | 0.17 | 5,768.73 |
| S(SI + SN + $SN^2$ + HT + WTR + DN + POP + YR + PF) | 18 | 1.25 | 0.12 | 5,765.50 |
| S(SI + SN + $SN^2$ + HT + WTR + DN + POP + YR) | 17 | 1.53 | 0.10 | 5,767.79 |
| S(SI + SN + $SN^2$ + WTR + DN + POP + YR + PF) | 17 | 2.29 | 0.07 | 5,768.56 |
| S(SI + SN + $SN^2$ + WTR + DN + POP + YR) | 16 | 2.82 | 0.05 | 5,771.09 |
| S(SI + SN + $SN^2$ + HT + DN + POP + PF) | 16 | 3.04 | 0.05 | 5,771.31 |
| S(SI + SN + $SN^2$ + HT + DN + POP) | 15 | 3.36 | 0.04 | 5,773.63 |
| S(SI + SN + $SN^2$ + DN + POP + YR + PF) | 16 | 3.76 | 0.03 | 5,772.03 |
| S(SI + SN + $SN^2$ + HT + POP + YR + PF) | 16 | 4.49 | 0.02 | 5,772.76 |
| S(SI + SN + $SN^2$ + DN + POP + YR) | 15 | 4.89 | 0.02 | 5,775.16 |
| S(SI + SN + $SN^2$ + HT + WTR + DN + POP + PF) | 17 | 5.05 | 0.02 | 5,771.31 |
| S(SI + SN + $SN^2$ + HT + POP + YR) | 15 | 5.15 | 0.02 | 5,775.43 |
| S(SI + SN + $SN^2$ + HT + WTR + DN + POP) | 16 | 5.36 | 0.01 | 5,773.63 |
| S(SI + SN + $SN^2$ + DN + POP + PF) | 15 | 5.59 | 0.01 | 5,775.86 |

[a] Variable abbreviations: site (SI), day of season (SN), day of season squared ($SN^2$), nest height from ground to top of nest cup (HT), number of active nests within 1 m (DN), population size (POP), year (YR), water depth under nest (WTR), and proportion of nearby nests (within 50 m) that failed (PF).

day of season did not suggest a quadratic relationship. We used all combinations of variables but did not include site and habitat type in the same models. We then summed the model weights for each variable. Summary statistics are presented as means ± SE; beta coefficients (β) and odds ratios are presented as estimates followed by 95% confidence intervals (CI).

## RESULTS

We monitored 1,323 Tricolored Blackbird nests in 12 colonies at 9 breeding sites during 2011 and 2012. We monitored 679 nests in 6 sites in 2011: 4 sites in cattail dominated wetlands and 2 sites in silage fields associated with a dairy. We monitored 644 nests at 6 sites in 2012: 4 sites in cattails and 2 sites in silage fields associated with dairies. Three cattail sites were monitored in both years of the study. Of the 1,323 nests monitored, we included 1,142 nests in our analyses: 570 from 2011 and 572 from 2012. We excluded nests that were never incubated (i.e. abandoned before iButton deployment or potentially abandoned in response to iButton deployment) and those in which iButtons failed to record data.

We monitored nests initiated through 91 days of the breeding season in 2011 and through 69 days in 2012. The number of active nests within 1 m of the focal nest ranged from 0 to 9 (1.0 ± 1.2). Nest height ranged from 29 to 183 cm (88.7 ± 28.5). Water depth under the nest ranged from 0 cm to 78 cm (15.0 ± 16.3). Water depth in silage fields was 0 cm. Water depth in wetland sites varied greatly: one site had no standing water; in several sites, a portion of the nests were over dry ground while other nests were over water; and at several other sites, all nests were over standing water. Population size of monitored colonies ranged from <50 to ≥50,000 birds. Mean population size of nesting colonies was higher in 2012: in 2011, 18% of nests were in colonies of >5,000 birds, vs. 66% of nests in 2012. Population size of individual colonies often decreased as the season progressed, but we observed population increases on 3 occasions. Large changes in population size occurred (1) when a nearby, occupied silage field was harvested and the birds relocated to a monitored site; and (2) when birds abandoned a site in large numbers. All of the largest, and some of the moderate-sized colonies, experienced an apparent decrease in population size as the breeding season progressed.

Model selection did not result in an obvious top model, but site, season and $season^2$, nest height, population density, year, probability of failure of nearby nests, and water depth occurred in various combinations in the top models (Table 1). DSR varied from site to site, but the variation was not explained by habitat type (Figure 4). Site occurred in all of the top models (Table 1), whereas the best model that included habitat type was 83.10 $\Delta AIC_c$ below the top model. Beta coefficients from the best-fitting model ($AIC_c$ weight = 0.22) indicated a quadratic relationship between DSR and day of breeding season (Table 2). Model-averaged DSR decreased and then increased as the breeding season progressed (Figure 5). Nest density and nest height were positively associated with DSR (Table 2); for every 1 cm increase in nest height,

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**TABLE 2.** Estimated beta coefficients (β) from the top-ranked Tricolored Blackbird daily nest survival model: S(SI + SN + $SN^2$ + HT + DN + POP + YR + PF).[a]

| Variable | β [b] | SE | 95% CI [c] |
|---|---|---|---|
| Intercept | 2.548 | 0.312 | 1.936 to 3.160 * |
| Site: Dairy3 | 1.611 | 0.260 | 1.102 to 2.120 * |
| Site: Dairy1 | 1.890 | 0.297 | 1.307 to 2.472 * |
| Site: Dairy2 | 1.525 | 0.285 | 0.967 to 2.083 * |
| Site: Cattail1 | 1.017 | 0.187 | 0.650 to 1.383 * |
| Site: Dairy4 | 2.928 | 0.303 | 2.334 to 3.522 * |
| Site: Cattail5 | −1.133 | 0.315 | −1.751 to −0.515 * |
| Site: Cattail3 | −0.063 | 0.194 | −0.443 to 0.316 |
| Site: Cattail4 | −1.733 | 0.410 | −2.536 to −0.930 * |
| Season | −0.046 | 0.012 | −0.069 to −0.023 * |
| $Season^2$ | 0.001 | 0.000 | 0.000 to 0.001 * |
| Nest height | 0.005 | 0.002 | 0.001 to 0.010 * |
| Nest density | 0.085 | 0.034 | 0.018 to 0.152 * |
| Population 1,000–5,000 | −0.342 | 0.155 | −0.645 to −0.038 * |
| Population >5,000 | −1.309 | 0.187 | −1.675 to −0.944 * |
| Year 2012 | 0.362 | 0.162 | 0.044 to 0.680 * |
| Proportion of failed nests | −0.403 | 0.251 | −0.895 to 0.090 |

[a] Abbreviations of variables are defined in Table 1.
[b] Beta coefficients for sites are in relation to the Cattail2 site. Beta estimates for population are in relation to Population <1,000.
[c] Asterisk indicates that 95% confidence interval (CI) does not overlap zero.

the odds ratio of a nest surviving one more day was 1.005 (95% CI: 1.001–1.010). For each additional nest within 1 m of the focal nest, the odds ratio of a nest surviving one more day was 1.088 (95% CI: 0.019–1.155). DSR was highest for the smallest populations, was slightly lower for populations of 1,000–5,000 birds, and was substantially lower for populations of >5,000 birds. DSR was higher in 2012 than in 2011 (Table 2). The proportion of nearby nests that failed on the last day a nest was active was negatively related to DSR, but the 95% CI overlapped zero. As the proportion of nearby nests that failed increased from 0 to 1, the odds ratio of a nest surviving one more day was 0.669 (95% CI: 0.256–1.161). Water depth had little explanatory power; it was not included in the top model, and the 95% CI of the beta coefficient for water depth overlapped zero (β = 0.005, 95% CI: –0.006 to 0.016) in the highest-ranked model (third-ranked model $\Delta AIC_c = 1.25$) in which it was included.

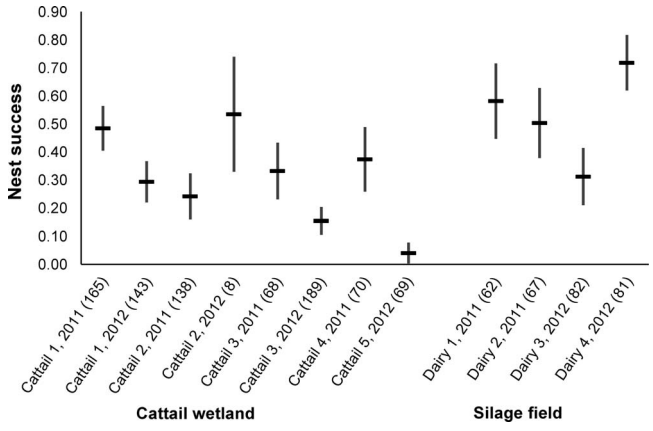


**FIGURE 4.** Nest success (the probability that a nest survived from the start of incubation to fledging) of Tricolored Blackbird colonies by site and year in the San Joaquin Valley, California, USA. Lines are model-averaged 95% confidence intervals. Colonies are grouped by habitat type: cattail wetland (*Typha* spp.) and silage field (Triticale, a wheat–rye hybrid).

**TABLE 3.** Sum of model weights for variables included in Tricolored Blackbird nest survival models.[a]

| Variable | $\sum w_i$ |
|---|---|
| Site | 1.000 |
| Population | 1.000 |
| Day of Season + $Day\ of\ Season^2$ | 1.000 |
| Nest Density | 0.931 |
| Year | 0.840 |
| Nest Height | 0.783 |
| Fate of nearby nests | 0.559 |
| Water Depth | 0.407 |
| Day of Season (alone) | 0.000 |
| Habitat | 0.000 |

[a] Because the variable pairs (1) Day of Season–Day of Season + $Day\ of\ Season^2$ and (2) Site–Habitat are not independent, variable weights should only be compared between those pairs. All other variables can be compared to each other.

Site, population size, day of season + $day\ of\ season^2$, nest density, year, and nest height were the most important variables for predicting nest survival, as indicated by summed model weights for each variable (Table 3). Model-averaged estimates of mean nest success (the probability that a nest would survive the 21-day incubation and nestling period, $DSR^{21}$) at each colony varied substantially, ranging from 0.024 ± 0.014 to 0.719 ± 0.050 (Figure 4).

The number of young produced per successful nest ranged from 1 to 3 ($n$ = 531). The number of young produced per nest was best explained by site, day of season, population size, and year. Beta coefficients indicated that the number of young produced per nest was lowest in colonies of 1,000–5,000 birds and was higher in smaller (<1,000 birds) and larger (>5,000 birds) colonies (Table 4). The number of young produced per nest was higher in 2011 than in 2012 and decreased as the breeding season progressed (Table 4). The mean number of young produced per nest per site ranged from 1.43 ± 0.63 to 2.53 ± 0.94.

We observed large-scale nest failures at 6 of the 12 colonies. White-faced Ibis (*Plegadis chihi*) were responsible for large-scale nest failure at 2 cattail sites during both years of the study. When White-faced Ibis began nesting in a site where Tricolored Blackbirds were already present,



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**TABLE 4.** Beta coefficients (β) from the top-ranked model (Site + Day of Season + Population + Year) of the number of Tricolored Blackbird young produced per nest in the San Joaquin Valley, California, USA, 2011–2012.

| Variable | β [a] | SE | 95% CI [b] |
|---|---|---|---|
| Intercept | 2.202 | 0.243 | 1.726 to 5.585 * |
| Site: Dairy3 | 0.804 | 0.210 | 0.393 to 1.573 * |
| Site: Dairy1 | 0.314 | 0.256 | −0.188 to −0.054 * |
| Site: Dairy2 | −0.232 | 0.229 | −0.680 to −1.564 * |
| Site: Cattail1 | 0.558 | 0.154 | 0.256 to 1.060 * |
| Site: Dairy 4 | 0.756 | 0.214 | 0.336 to 1.415 * |
| Site: Cattail5 | −0.166 | 0.220 | −0.598 to −1.339 * |
| Site: Cattail3 | 0.211 | 0.147 | −0.078 to 0.059 |
| Site: Cattail4 | 0.520 | 0.158 | 0.210 to 0.931 * |
| Day | −0.005 | 0.003 | −0.010 to −0.024 * |
| Year 2012 | −0.451 | 0.159 | −0.762 to −1.944 * |
| Population 1,000–5,000 | −0.414 | 0.132 | −0.673 to −1.734 * |
| Population >5,000 | −0.065 | 0.182 | −0.421 to −0.890 * |

[a] Beta coefficients for sites are in relation to the Cattail2 site. Beta estimates for population are in relation to Population <1,000.
[b] Asterisk indicates that 95% confidence interval (CI) does not overlap zero.

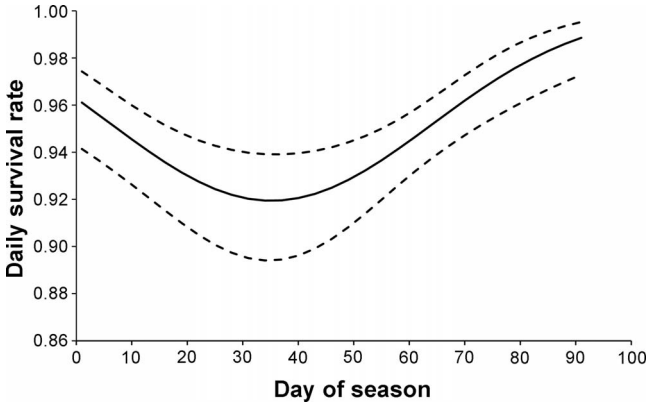


**FIGURE 5.** Relationship between Tricolored Blackbird daily nest survival and day of season in the San Joaquin Valley, California, USA.

the former ripped down or built their own nests directly on top of the latter's nests. Substrate failure also resulted in the loss of a large number of nests. Blowdown of nesting substrate occurred at 2 silage field sites. Large sections of the triticale were blown down in both fields, affecting hundreds to thousands of nests per site. In one wetland site, the cattails were senescent when the birds began nesting. Partway through the nesting cycle, cattails began to collapse in some sections of the colony. We found ~31% of monitored nests hanging sideways when we retrieved iButtons from this site. Presumably, nest contents had spilled when the cattails collapsed, resulting in nest failure. We saw evidence that nest abandonment was common. When we retrieved iButtons, we observed large numbers of abandoned nests containing full and partial clutches, as well as dead nestlings. In many of these nests, the eggs and nestlings were intact, having been neither depredated nor scavenged.

## DISCUSSION

Nest survival varied substantially among sites but was not associated with habitat type. Nesting success was similar in silage fields and in cattail wetlands, the primary nesting habitat used by Tricolored Blackbirds prior to the loss of California's native wetlands (Neff 1937). Our results suggest that silage fields can provide suitable nesting habitat for Tricolored Blackbirds and that paying farmers to delay harvest, or securing voluntary harvest delays, can increase the productivity of this species. Few studies have compared blackbird nest success between native and agricultural habitats, although grassland bird abundance and nesting success in native grasslands versus pastures has received more attention (e.g., Codesido et al. 2013, Davis et al. 2016). Red-winged Blackbird nest success was higher in wetlands than in upland hay fields in Connecticut, a difference that was attributed to differences in predator access to nests (Robertson 1972). There was no difference, however, in nest success of multiple passerine species, the most common of which was the Red-winged Blackbird, nesting in Conservation Reserve Program fields and in row-crop fields in 6 midwestern states (Best et al. 1997). Agricultural fields can provide suitable nesting habitat for some bird species, particularly blackbirds, and may expand nesting opportunities in some systems.

The large site-to-site variation in daily nest survival that we observed, coupled with the lack of consistent differences among habitats, suggests that factors other than nesting substrate—such as food availability, substrate condition, and the density, abundance, and composition of predator populations—have a large influence on nest survival. In our study area, factors such as the presence of nesting White-faced Ibis had large effects on the success of Tricolored Blackbird colonies. Additionally, the condition of cattail vegetation was not consistent across wetland sites: Old, senescent cattails collapsed under nests, whereas cattails in recently burned ponds remained vigorous throughout the breeding season. All of these factors could cause substantial site-to-site variation in nesting success and would be unrelated to habitat type.

Nest survival over the breeding season was best explained by a quadratic function first declining and then increasing as the season progressed. The same quadratic relationship has been observed in other songbird species, including Red-winged Blackbirds (Dinsmore and Dinsmore 2007, Burhans et al. 2010, Gillespie and Dinsmore 2014); it has also been observed in Willow Ptarmigan (*Lagopus lagopus*; Wilson et al. 2007) and in Semipalmated

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Plover (*Charadrius semipalmatus*), Black-bellied Plover (*Pluvialis squatarola*), Red Phalarope (*Phalaropus fulicarius*), Ruddy Turnstone (*Arenaria interpres*), and White-rumped Sandpiper (*Calidris fuscicollis*; Smith and Wilson 2010). Multiple hypotheses have been proposed to explain this pattern, including variations in weather, predation pressure, or nest density across the breeding season, but these hypotheses have received little support. Low mid-season nest survival is the opposite of what we would expect if the pattern were driven by seasonal changes in weather: In 2011 and 2012, storms in March destroyed large numbers of Tricolored Blackbird nests; weather warmed and became more stable in April and May. Thus, the most favorable weather conditions corresponded to the lowest DSRs. It is more likely that seasonal variation in DSR in our study was driven by seasonal changes in the predator community. White-faced Ibis started breeding in April, continued into May, and fledged young by mid-June. Interference from White-faced Ibis was therefore lowest at the beginning and end of the breeding season, when Tricolored Blackbird nest survival was highest.

We did not find a relationship between nest age and nest survival. Other authors have found that daily survival rates changed as nests passed through incubation and nestling phases (Grant et al. 2005, Dinsmore and Dinsmore 2007). The Tricolored Blackbird's highly colonial nature makes age effects less likely because nesting colonies are extremely conspicuous at all stages of the nesting cycle and because the close proximity of nests ($\leq$9 nests within 1 m radius) makes it easy for predators to locate individual nests at any stage in the cycle. Additionally, events like encroachment by White-faced Ibis or collapse of nesting substrate caused by high winds can occur at any time in the nesting cycle and can affect large numbers of nests.

We found that population size and nest density both affect nest survival, but that the relationships were somewhat counterintuitive: Nests in large colonies ($>$5,000 individuals) had lower survival rates, whereas areas of higher nest density within a colony experienced high nest survival. The positive relationship that we observed between nest density and daily survival is consistent with the hypothesis that, in colonially nesting species, nest predation is lower in areas with high nest density because of enhanced detection and mobbing of nest predators by adults (Shields 1984, Picman et al. 1988, Wiklund and Andersson 1994, Picman et al. 2002). Studies of the effect of colony size on nest success, however, have generally found a positive relationship (Raveling 1989, Wiklund and Andersson 1994, Barbosa et al. 1997, Hernández-Matías et al. 2003), although there are exceptions to this general pattern. Brunton (1999) found a significant positive relationship between colony size and nest loss to Black-crowned Night-Herons (*Nycticorax nycticorax*) and a negative relationship between colony size and nest loss to small mammals. Thus, the relationship is likely influenced by the ability of the prey species to repel the predator. Many of the nest losses in the large blackbird colonies we studied were caused by White-faced Ibis that nested within the colony and ripped down or built their own nests directly on top of Tricolored Blackbird nests. It is unclear whether White-faced Ibis nested preferentially within large Tricolored Blackbird colonies or if the juxtaposition was incidental.

Contrary to the results of most previous blackbird studies, we did not find a strong positive relationship between water depth and nest survival. Deeper water is thought to restrict mammalian predators' access to nests, thereby decreasing predation risk and increasing nest success (Robertson 1972, Picman et al. 1993, Fletcher and Koford 2004, van Oort et al. 2015). But some potential mammalian predators at our sites, such as rats (*Rattus* spp.), were not always deterred by water (K. Weintraub personal observation). Additionally, White-faced Ibis and Marsh Wrens, which are important nest predators in our study area, occurred in high densities over water. The negative impact of the presence of these wetland-nesting species may have countered any positive effects that Tricolored Blackbirds gained from nesting over water. This does not mean that water is not important to Tricolored Blackbird reproductive success, however. Cattails, a principal nesting substrate, germinate when standing water is present (Hotchkiss and Dozier 1949). Proper management of water depth and timing of flooding, along with maintenance activities such as burning, is essential for creating suitable nesting habitat for Tricolored Blackbirds.

Our finding that nest height and daily nest survival were positively correlated was consistent with results of a study of Red-winged Blackbird nest success in Iowa (Dinsmore and Dinsmore 2007), but Caccamise (1977) found the opposite result. Nest height, like water depth, may reduce the availability of nests to ground-based predators.

Our results suggest a negative relationship between the fate of nearby nests and nest success. We interpret these results as evidence in support of spatial dependency in nest outcome. There are many factors that could lead to spatial dependency, including area-restricted searching by predators (Tinbergen et al. 1967) and localized natural or anthropogenic events (e.g., floods, severe storms, harvesting of agricultural field; Johnson and Shaffer 1990). We observed nest failure in large portions of Tricolored Blackbird colonies as a result of White-faced Ibis nesting within colonies and, in one case, as a result of senescent nesting substrate (cattail) collapsing. We could not determine whether nest predators exhibited restricted-area search patterns, but Cattle Egrets (*Bubulcus ibis*) have been observed returning repeatedly to prey on young in Tricolored Blackbird colonies (Meese 2012), and therefore predators may also be responsible for spatial dependency

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in nest outcome. By including the fate of nearby nests in our model set, we were able to reduce the potential for confounding effects of spatial dependency on the beta coefficients of other variables in the model. Spatial dependency, however, violates the assumption that the fate of each nest is independent of other nests; therefore, our standard errors may be biased low. We felt that given the lack of information about factors affecting nest success in Tricolored Blackbirds, the advantages of examining the effects of covariates on nest outcome using model selection on individual nests outweighed the potential drawbacks associated with nonindependence.

Some of the factors influencing the average number of nestlings per nest were consistent with those influencing nesting success, but others differed. Like nesting success, the number of young per nest varied from site to site and was not associated with habitat type. Nesting success was highest in the smallest colonies (<1,000 birds), was lower for medium colonies (1,000–5,000), and was lower still in large (>5,000) colonies, whereas the average number of young produced per nest was lowest in colonies of 1,000–5,000 birds. Nesting success was higher, while the number of young per nest was lower, in 2012 compared to 2011. Variation in nesting success among colonies, however, was substantially greater (0.02–0.72) than the variation in number of young per nest (1.30–2.53); therefore, it appears that nest success exerts a greater influence on colony productivity than the number of young per nest.

Cattle Egrets did not appear to have a large impact on Tricolored Blackbird nest success in our study sites, contrary to previous reports of Cattle Egrets causing complete reproductive failure in colonies in our study area (Meese 2012). We observed Cattle Egrets preying on Tricolored Blackbird chicks on 4 occasions in a silage-field colony that we monitored in 2012, yet nest survival at this site was the highest in our study (Figure 4). We also observed Cattle Egrets preying on eggs at another silage field in our study area in 2011, but we did not obtain access to monitor that colony.

Tricolored Blackbird DSRs and numbers of young fledged per nest were similar in silage fields and in wetlands, making payments to farmers who delay harvest a viable option for increasing nesting productivity. Daily nest survival increased with nest height; therefore, managers of wetlands used by Tricolored Blackbirds should consider management practices (e.g., periodic burning and early flooding of wetlands to stimulate cattail growth) that increase the height of nesting substrate during the nesting season. The quadratic relationship between daily nest survival and day of the season suggests that nest success is highest early and late in the season; therefore, nest-protection efforts should start early in the season and continue until nesting has stopped. In addition, the high site-to-site variation in daily nest survival makes it difficult to predict the outcome of a particular colony, suggesting that all Tricolored Blackbird colonies warrant protection regardless of habitat type or population size. Our results provide evidence that White-faced Ibis can reduce Tricolored Blackbird nest success when they nest together; management approaches that discourage co-nesting should therefore be considered, but further study is warranted.

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**Author contributions:** T.L.G. and K.W. conceived the study. K.W., T.L.G., and S.J.D. developed and designed the methods. K.W. conducted the research. K.W. and T.L.G. analyzed the data and wrote the manuscript. T.L.G. contributed substantial materials, resources, and funding.

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