Notes

Bioacoustic Monitoring Reveals Details of Tricolored Blackbird Breeding Phenology

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Abstract

Bioacoustic monitoring has been used to study behaviors of organisms from insects to whales. Studies using multiple vocalizations of a single species have the potential to determine detailed phenology, but to date they are rare. We tested whether bioacoustic monitoring of multiple gender- and age-specific vocalizations of the imperiled tricolored blackbird *Agelaius tricolor* could provide detailed information on reproductive phenology and breeding success. Using inexpensive cell phones and free software applications, we collected audio recordings of tricolored blackbird colonies during their breeding season. Adding solar panels enabled the stations to run autonomously, and use of cellular data enabled remote uploading of recordings. Analysis of the presence or absence of three vocalizations—male song, female song, and nestling call—provided a rich and detailed description of the breeding phenology including the dates for courtship; onset of nest building, incubation, and nestling hatching; and fledgling departure from nesting colonies. The resulting detail was more granular and accurate than comparable data from field monitoring, although field monitoring provides data such as abundance counts that bioacoustic monitoring does not. This information has a wide range of applications to research and conservation, from enabling more accurate abundance estimates, to assessing colony success or failure with fewer visits, to providing stronger guidance for when a colony must be protected from disruption.

Keywords: tricolored; blackbird; bioacoustics; phenology

Received: October 4, 2019; Accepted: April 9, 2020; Published Online Early: April 2020; Published: December 2020

Citation: Schackwitz W, Airola DA, Greene A, Schackwitz M, Woodruff J. 2020. Bioacoustic monitoring reveals details of tricolored blackbird breeding phenology. *Journal of Fish and Wildlife Management* 11(2):518-530; e1944-687X. https://doi.org/10.3996/102019-JFWM-083

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Introduction

The range of the tricolored blackbird *Agelaius tricolor* (Figure 1) is limited, with more than 99% of the population occurring in California, and it is listed as Threatened under California's Endangered Species Act (Beedy et al. 2020). Recent statewide surveys and analyses of eBird records, an electronic repository of crowd-sourced bird observations, showed an alarming decline of approximately 40% from 2008 to 2016 (Meese 2014; Robinson et al. 2018; Meehan et al. 2019). The species has low fecundity, averaging fewer than two fledglings per nesting attempt (Meese 2013; Holyoak et al. 2014; Airola et al. 2015), making recovery challenging. The survey in 2017 showed a 22% increase in abundance, which may reflect an actual population increase or improvement in survey coverage, or both (Meese 2017; Clipperton 2018). Further analysis and better tools are necessary to understand the actual status of the species.

Several aspects of tricolored blackbird breeding biology create challenges in assessing reproductive success. Tricolored blackbirds nest colonially (Figures 2A and 2B), with some colonies historically reaching more than 100,000 birds and current colonies supporting tens of thousands of individuals (Clipperton 2018; Beedy et al. 2020). Nesting often occurs at inaccessible locations (e.g., in spiny vegetation, over water, or on private lands), precluding efficient monitoring (Airola et al. 2015). When they are accessible, they are monitored at a distance to avoid disturbance that could result in colony abandonment (Beedy et al. 2020). Therefore, assessment of success is often done from distant and infrequent visits and is evaluated at the colony level based on the presence (successful) or absence (failed) of fledglings (Airola et al. 2015), rather than on counting the actual number of fledged young.

Only a small subset of colonies is monitored, resulting in an incomplete picture of breeding success of the species. Evaluating tricolored blackbird breeding success is done through labor-intensive field visits by dedicated researchers and trained volunteers. The number of colonies vastly outnumbers the field monitors, so visits occur at most a few times during the breeding season (Meese 2010; Wilson et al. 2016). Individual tricolored blackbirds breed more than once per year, and individual colony sites sometimes support multiple "pulses" of nesting (Hamilton 1998; Airola et al. 2018; Beedy et al. 2020), but some of these additional pulses go undetected due to the infrequent visits. Under these limitations, assessment of breeding phenology, colony size, and reproductive success may be imprecise (Airola et al. 2015, 2018).

Infrequent field visits miss key data needed for precise understanding of the phenology of a colony. Information researchers need includes 1) dates birds arrived at colony sites; 2) whether a group that arrived at a colony site remained and nested, or whether it abandoned before nesting; 3) starting and ending dates of nest building, incubation, hatching, and fledging; 4) whether nesting efforts succeeded or failed; 5) the number of breeding individuals; 6) the number of young fledged per nesting attempt; and 7) whether multiple nesting attempts occurred at a colony site. Getting precise information requires that data be collected on the colony daily, but as frequent field visits are impractical, a new tool that could collect data every day is needed. Bioacoustic monitoring is a potential candidate.

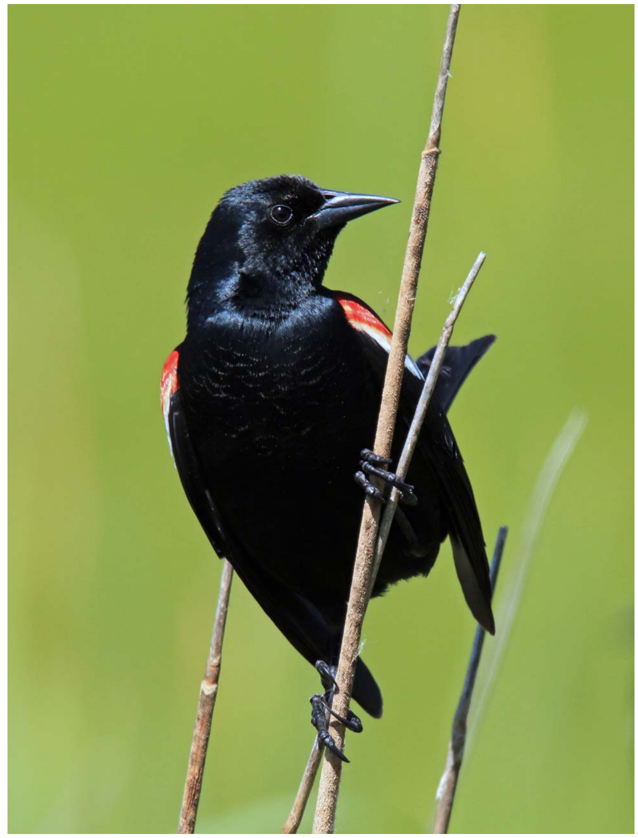

Figure 1. Male tricolored blackbird *Agelaius tricolor*, Rush Ranch colony, Solano County, California (38.208, −122.014), 4 April 2017. Male tricolored blackbirds can be distinguished from red-winged blackbirds *Agelaius phoeniceus* by shiny plumage, sharper bill, white median coverts, and vocalizations. Image used with permission from photographer Tom Muehleisen.

Bioacoustic monitoring is widely used to determine the presence of a variety of taxa, including birds (Campos-Cerqueira et al. 2017), bats (Jennings et al. 2008), amphibians (Ospina et al. 2013), insects (Aide et al. 2017), and marine mammals (Širović et al. 2009). Compared with intermittent and time-bound field visits, bioacoustic monitoring can collect data continuously over an extended period from multiple locations. It also permanently records the raw data from the field, allowing for future reanalysis of the recordings as well as independent analysis by other researchers. Most applications focus on a single vocalization to assess phenology for a single species, and studies focusing on multiple vocalizations are rare (Lynch et al. 2013; McDonald et al. 2017).

Tricolored blackbirds have behaviors that make them potential candidates for monitoring using bioacoustic analysis. They produce an array of gender- and age-specific vocalizations associated with various breeding

Figure 2. Colonial nesting of tricolored blackbirds at the Rush Ranch colony, Solano County, California (38.208, –122.014). (**A**) Female tricolored blackbirds *Agelaius tricolor* exhibiting social behavior, 2 June 2017. Image used with permission from photographer Tom Muehleisen. (**B**) Two tricolored blackbird nests after the colony had departed for the season, 5 July 2017. Tricolored blackbirds nest in dense colonies with females constructing nests as close as 13 cm apart (Beedy et al. 2020). Image used with permission from photographer Wendy Schackwitz.

stages and behaviors (Figure 3; Collier 1968; Orians and Christman 1968; Beedy et al. 2020). In addition, colonies usually exhibit synchronous nesting and breeding (Orians 1961; Collier 1968). In synchronous colonies, these vocalizations can be used as indicators of the colony's breeding stage. For example, changes in the frequency of male song (Figure 3; Video S1, *Supplemental Material*) signal onset of settling (sudden increase in frequency) and onset of incubation (sudden decrease in frequency). Females sing (Figure 3; Video S1) during nest building and continue until eggs hatch (Orians and Christman 1968), indicating colony-wide nest-building and incubation activities, whereas colony-wide hatching is marked by the presence of nestling or fledgling begging calls (Figure 3; Video S1). Thus, analysis of these vocalizations could determine the breeding stage of a colony.

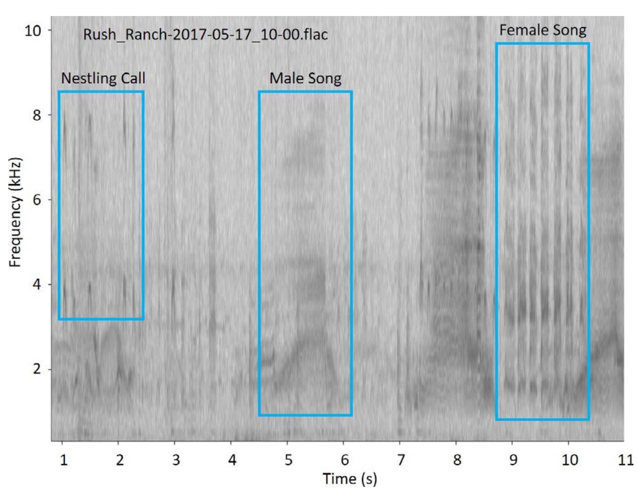

Figure 3. Sonogram of three tricolored blackbird *Agelaius tricolor* vocalizations: nestling begging calls, female song, and male song. Recording was made at Rush Ranch colony, Solano County, California (38.208, –122.014), 17 May 2017 at 1000 hours. See Video S1 (*Supplemental Material*) for sound and animation of the sonogram.

Our goal was to develop a bioacoustic monitoring tool for tricolored blackbirds that could overcome the challenges of the current approach. Ideally, this tool determines the exact dates of the onset and cessation of breeding stages including nest building, incubation, hatching, and fledging; operates with no human intervention; and provides results in nearly real time to a remote operator. This richer information enhances our understanding of breeding phenology of tricolored blackbirds by allowing researchers to monitor more colonies with higher confidence and less effort.

Study Area

We conducted bioacoustic monitoring at four tricolored blackbird colonies: Rush Ranch, Markham Ravine, Iron Point, and Red Wing Ranch. The Rush Ranch colony site is located on the Rush Ranch Preserve, adjacent to the Suisun Marsh in Solano County, California (38.208, –122.014) at 9-m elevation. The colony nested in a 0.9-ha, stream-fed pond containing cattails *Typha* spp. and bulrushes *Schoenoplectus* spp., together covering approximately 60% of the pond (Figure 4A). Grassland, which is grazed by cattle, surrounds the site.

The Markham Ravine colony site is located on Markham Ravine Creek near South Brewer and Nicolaus roads in western Placer County, California (38.889,

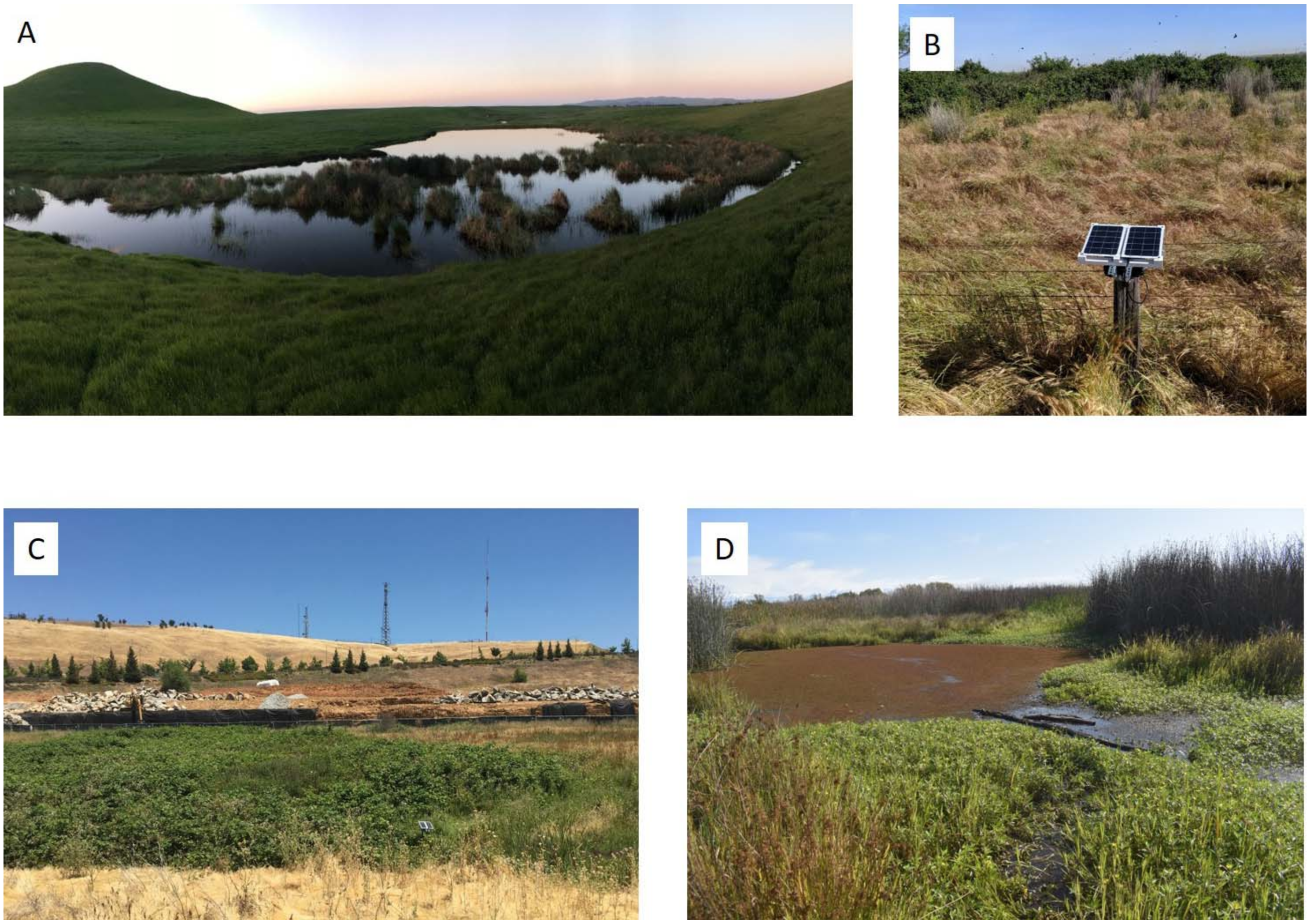

Figure 4. Photos of study areas. (**A**) Rush Ranch colony, Solano County, California (38.208, –122.014). Monitoring occurred from 2 March to 26 July 2017 and from 20 February to 25 June 2018. Image used with permission from photographer Wendy Schackwitz. (**B**) Markham Ravine colony, Placer County, California (38.889, –121.468). Monitoring occurred from 26 June 2018 to 20 July 2018. Image used with permission from photographer Wendy Schackwitz. (**C**) Iron Point colony, Sacramento County, California (38.647, –121.104). Monitoring occurred from 22 April to 10 May 2018. Note construction activities in the image's background. Image used with permission from photographer Wendy Schackwitz. (**D**) Red Wing Ranch colony, Placer County, California (38.963, –121.346**)**. Monitoring occurred from 4 May to 30 May 2018. Image used with permission from Westervelt Ecological Services.

–121.468) at 19-m elevation. The nesting colony used several patches of Himalayan blackberry *Rubus armeniacus*, totaling approximately 0.6 ha, along Markham Ravine Creek (Figure 4B). The site was surrounded by cultivated rice fields, open grassland, and a former irrigated hayfield that was under active construction as a wetland mitigation site during 2018. Construction halted around the colony during the breeding period.

The Iron Point colony site is adjacent to Iron Point Road within the city of Folsom, Sacramento County, California (38.647, –121.104) at 172-m elevation. Tricolored blackbirds nested in a 0.2-ha patch of Himalayan blackberry in a small area designated as open space surrounded by roadways, commercial stores, parking lots, and a housing development (Figure 4C). Commercial and residential construction occurred within 80 m of the nesting site in 2018, and construction activities continued during the breeding period.

The Red Wing Ranch colony site is on the Red Wing Ranch, adjacent to Nader Road and Yankee Slough in Placer County, California (38.963, –121.346) at 33-m elevation. The nesting colony was in a 10-m-wide section of the stream that supported a dense 0.9-ha patch of cattails and bulrushes (Figure 4D). Annual grassland, grazed by cattle, surrounds the site.

Methods

During 2017, we tested the ability of bioacoustic monitoring to determine breeding stages of tricolored blackbirds at the Rush Ranch colony. We collected and analyzed audio recordings of the colony and compared the results with those of field surveys and the documented timing of breeding behaviors (Beedy et al. 2020). We typically conducted field surveys twice per week during the breeding season, resulting in 40 visits from 7 March to 24 July. To evaluate the breeding stage of the colony, we noted behaviors including males singing (indicating colony presence), females carrying nesting material (nesting stage), adults carrying food (nestling stage), and

Figure 5. Bioacoustic monitoring station. (**A**) The Automated Remote Biodiversity Monitoring Network (ARBIMON) audio recorder (Aide et al. 2013) consisted of an LGMS323 cellphone (LG Electronics) running the ARBIMON Touch audio recording software application (Sieve Analytics), enclosed in a waterproof case (Otterbox), with an external microphone attached (Monoprice). Image used with permission from Sieve Analytics. (**B**) Station design for 2017 data collection that was placed at the Rush Ranch colony, Solano County, California (38.208, −122.014). Image used with permission from Wendy Schackwitz. (**C**) Station design for 2018 data collection including solar panel (sCharger-14; Suntactics) that provided power to the ARBIMON audio recorder. Image used with permission from Wendy Schackwitz.

whether the colony was quiet (incubating stage), as well as the presence of fledged young (fledgling stage).

We made audio recordings of the colony by using a custom-designed bioacoustic monitoring station. Our initial station included an audio recorder (LGMS323 cellphone; LG Electronics, Seoul, South Korea) that ran the Automated Remote Biodiversity Monitoring Network (ARBIMON) Touch audio recording software application (Sieve Analytics, San Juan, Puerto Rico), enclosed in a waterproof case (Otterbox, Fort Collins, CO), with an external microphone (Monoprice, Rancho Cucamonga, CA; Aide et al. 2013). We attached the recorder to a metal T-post with an elastic cord and installed it near the edge of the Rush Ranch colony (Figures 5A and 5B). We recorded 1 min of audio every 20 min from 2 March to 25 July, totaling 72 min/d and more than 8,000 min over the 16-wk breeding season. The battery life of the unit was approximately 2 wk, so we periodically exchanged the recorder.

We uploaded audio files to ARBIMON II, a data storage and analytic software service (Sieve Analytics) for quality assessment and analysis. We removed recordings that were unusable because of microphone failures, excessive wind, or anthropogenic sounds. In addition, we excluded days with fewer than five usable recordings from analysis to avoid false negatives.

Because the colony is extremely noisy during the settling phase (Figure 6A; Video S2, *Supplemental Material*) and then suddenly becomes quiet during the incubation phase (Figure 6B; Video S3, *Supplemental Material*), we analyzed the soundscape of the 2017 Rush Ranch colony to determine whether this simple bulk analysis could detect presence of birds and determine periods of incubation. A soundscape is the full record of

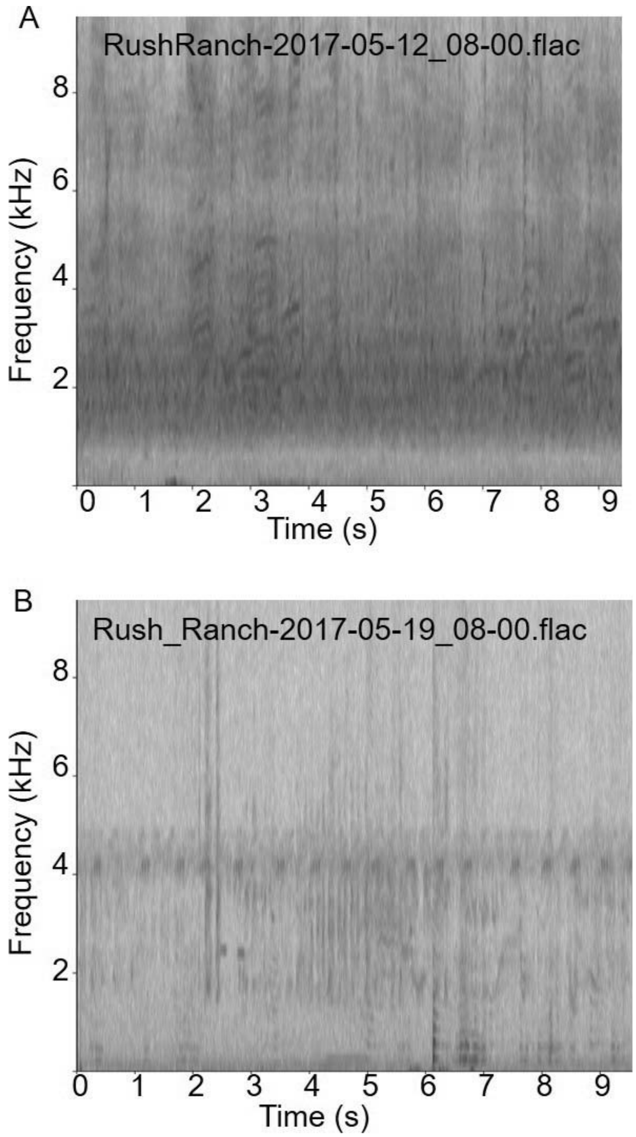

Figure 6. (**A**) Sonogram of tricolored blackbird *Agelaius tricolor* Rush Ranch colony, Solano County, California (38.208, –122.014) during the settling phase at 0800 hours on 12 May 2017. See Video S2 (*Supplemental Material*) for sound and animation of the sonogram. (**B**) Sonogram of tricolored blackbird Rush Ranch colony, Solano County, California (38.208, –122.014) during incubation phase at 0800 hours on 19 May 2017. See Video S3 (*Supplemental Material*) for sound and animation of the sonogram.

physical, biological, and anthropogenic sounds from a location (Southworth 1967; Schafer 1977). Using all 4,027 usable recordings made from 0700 to 1900 hours, we produced a graph of the daily soundscapes from 3 March to 24 July by using the analysis tools in ARBIMON II (Aide et al. 2013). Settings for the soundscape analysis were as follows: Aggregation = Day of the Year, Bin Size = 21 Hz, Visualization Scale = Normalized, Peak Amplitude Filtering = 0.1, and Absolute.

Next, we analyzed vocalizations to determine whether we could obtain a detailed understanding of the breeding stage of the colony. We selected 13 recordings per day that fell on the hour from 0700 to 1900 hours. If recording failures occurred at those times, we selected the closest recording during that hour when available, resulting in 1,601 recordings over 144 d (Data A1, *Archived Material*). For each recording, we documented the presence or absence of three tricolored blackbird vocalizations: male song, female song, and nestling or fledgling begging (Data A2, *Archived Material*). We determined vocalization types by comparing sounds we noted during field visits and previous descriptions (Collier 1968; Orians and Christman 1968; Beedy et al. 2020). We then calculated the percentage of the recordings that contained each vocalization type for each day of the nesting season (Data A2). We compared dates of vocalizations in the recordings with the reported durations of nesting stages, settling (12–17 d), nest building (4 d), incubating (11–14 d), nestling occurrence (11–14 d), and fledgling occurrence at the colony (4–8 d) to assess success of nesting attempts and timing of failures (Beedy et al. 2020). For example, if nestling calls continued throughout and beyond the nestling stage, we presumed that fledging was successful. Because the height of vegetation surrounding the colony impacts when fledglings leave, we predicted fledgling departure dates would be 15–22 d after we heard the first nestling for colonies in tall vegetation and $\geq$25 d for colonies in short vegetation (Beedy et al. 2020).

Following our 2017 pilot study, we adjusted the protocol in 2018 to scale the technique to multiple colonies without a proportional increase in field effort. To avoid returning to the colony for battery changes and data retrieval, we added solar panels (sCharger-14; Suntactics, San Jose, CA), connecting them directly to the phones with standard USB cables (Figure 5C), and acquired data plans for the phones to upload recordings automatically to Google Drive by using the Android application Autosync (MetaCtrl, Prague, Czech Republic). We assessed the presence and quality of the recordings remotely each morning by listening to at least one recording for each monitored site, allowing prompt detection and correction of technical failures.

During the 2018 breeding season, we placed these enhanced stations at four sites: Rush Ranch, 9 February–26 June; Iron Point, 22 April–19 May; Red Wing Ranch, 4 May–4 June; and Markham Ravine, 26 June–17 July. We filtered recordings and analyzed the presence and absence of vocalizations as described for Rush Ranch in 2017 (Data A2, *Archived Material*). The number of usable recordings and number of days with recordings analyzed for each site were as follows: Rush Ranch: 1,273 recordings (Data A3, *Archived Material*), 124 days; Iron Point: 246 recordings (Data A4, *Archived Material*), 19 d; Red Wing Ranch: 312 recordings (Data A5, *Archived Material*), 27 d; and Markham Ravine: 236 recordings (Data A6, *Archived Material*), 22 d.

Results

Our 2017 audio stations collected recordings throughout the field season with a few problems, including

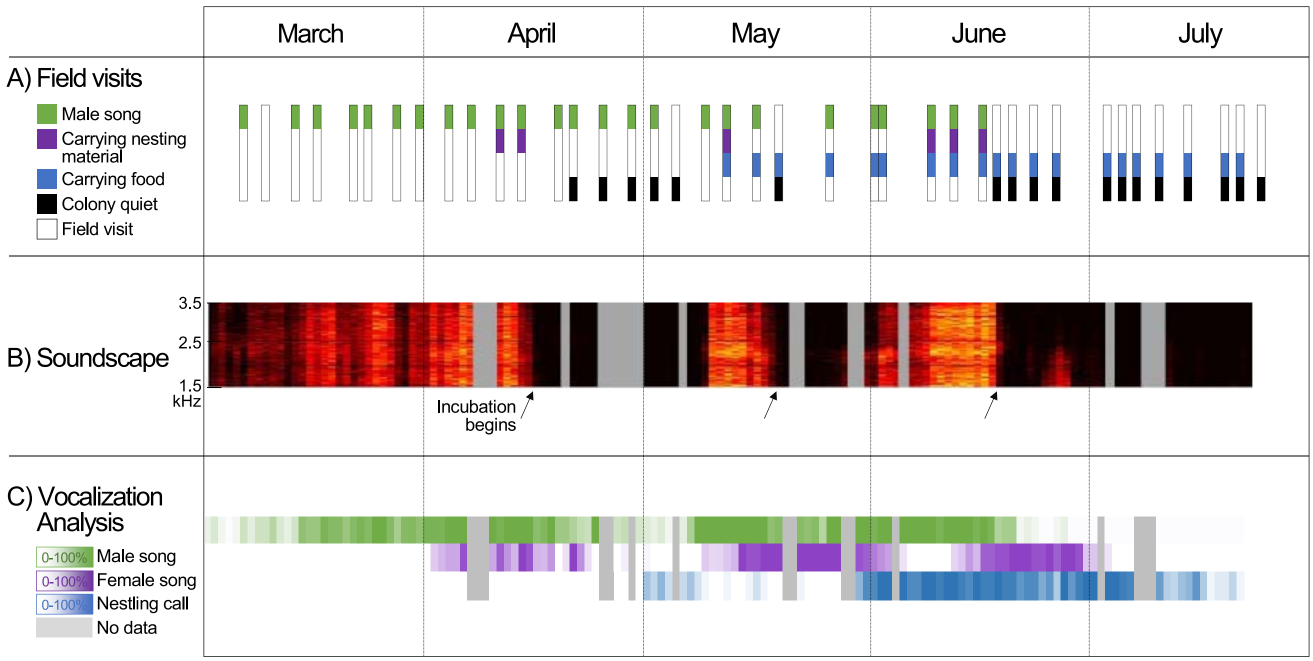

Figure 7. (**A**) Breeding activity of tricolored blackbird *Agelaius tricolor* acquired during 40 field visits to the Rush Ranch colony, Solano County, California (38.208, −122.014) in 2017. Carrying of nesting material occurred during three unique periods, suggesting three different nesting attempts. Carrying of food indicated that the first nesting attempt was successful. The extended duration of food carrying suggests that one or both of the second and third nesting attempts were successful. (**B**) Rush Ranch 2017 soundscape. Each column represents 1 d of data and runs from 3 March to 24 July. The sound volume in the marsh each day is shown on a linear color scale, with white indicating loudest sound level, red indicating moderate level, and black indicating lowest level. Missing data are indicated by gray. Even without distinguishing sound types, the sound volume alone shows the three separate incubation periods. (**C**) Abundance of three tricolored blackbird vocalizations over the breeding season (2 March–24 July, also see Data A2, *Archived Material*). Three separate female singing periods followed by an extended period of nestling calls indicate three rounds of successful fledging.

software failures, water in the microphone, loss of power, and loss of recordings due to the secure digital (SD) card filling up. The station successfully collected more than 8,000 recordings over 145 d, with a loss of 16 d. Because the station was not self-sustaining, we checked on it during each existing twice-weekly field visit.

Improvements to the monitoring stations in 2018 enabled the stations to run continuously and with fewer field visits (40 visits to Rush Ranch in 2017 vs. 7 visits in 2018). The solar panels kept the recorders charged throughout the field season, maintaining power at Rush Ranch for 124 d, Iron Point for 42 d, and Red Wing Ranch for 32 d until being retrieved. The Markham Ravine station intermittently shut off, possibly due to the phone overheating. Iron Point and Red Wing Ranch had strong cellular data coverage where data uploaded continuously for the entire length of deployment, helping to prevent data loss. For example, on 10 May 2018, we noticed that the uploaded recordings from Red Wing Ranch were silent, suggesting a problem with the microphone. Because we were monitoring the site remotely using the uploaded recordings, we promptly conducted a field visit and determined a cow had dislodged the microphone; the quick fix resulted in losing only 2 d of data, rather than the rest of the season. Unfortunately, Rush Ranch and Markham Ravine had weak data coverage, so uploads from those sites happened inconsistently, and we needed to make occasional visits to confirm the equipment was running and retrieve stored data.

Bioacoustic monitoring of age- and gender-specific vocalizations complimented field observations by providing more detailed data. The field observations of the Rush Ranch colony in 2017 provided useful data on breeding phenology and colony reproductive success but had many gaps (Figure 7A). Analysis of the recordings filled these gaps and gave precise timing of breeding behaviors (Figures 7B and 7C). Estimation of breeding phenology through analysis of vocalizations agreed with previous field studies (Beedy et al. 2020). Because the 2017 bioacoustic data aligned with our field observations and previously reported descriptions of breeding stages, we monitored the colonies in 2018 primarily through the recordings with only occasional field visits (Figures 8B–8E). Bioacoustic monitoring determined the number of nesting attempts at a single location, whether the colony abandoned or persisted each attempt, and for colonies that persisted, the date of onset and duration of incubation, the date of hatching, and whether nestlings successfully fledged.

Number of nesting attempts

Bioacoustic monitoring determined the number of nesting attempts more accurately than field visits, largely

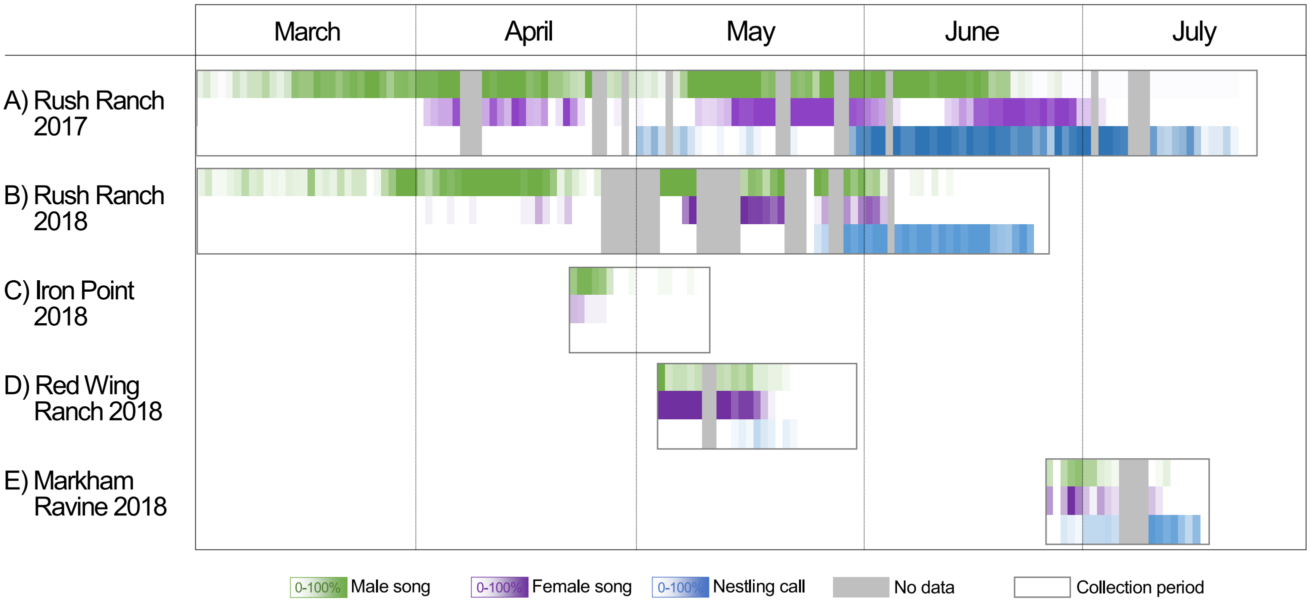

Figure 8. Abundance of three tricolored blackbird *Agelaius tricolor* vocalizations over the 2017 and 2018 breeding seasons (also see Data A2, *Supplemental Material*). (**A**) Rush Ranch, Solano County, California (38.208, −122.014), 2017: entire breeding season monitored. Three separate female singing periods followed by an extended period of nestling calls indicate three rounds of successful fledging. (**B**) Rush Ranch, 2018: entire breeding season monitored. Two separate periods of females singing with only the second period followed by nestling calls indicate one successful nesting attempt. (**C**) Iron Point, Sacramento County, California (38.647, −121.104), 2018: one short period of females singing followed by the absence of nestling calls indicates site abandoned before hatching. (**D**) Red Wing Ranch, Placer County, California (38.963, −121.346), 2018: one period of females singing followed by a brief period of nestling calls indicate abandonment after hatching. (**E**) Markham Ravine, Placer County, California (38.889, −121.468), 2018: one period of females singing followed by extended nestling calls indicate successful nesting and fledging.

because it collected data on nearly every day of the breeding season. We determined from field visits that nesting at Rush Ranch during 2017 likely had three breeding pulses, indicated by the carrying of nesting material (11–14 April, 12 May, and 9–16 May; Figure 7A), although we only observed the second pulse once, with a few females seen carrying nesting material, so our confidence that this was a true nesting attempt was low. In comparison, our analysis of the timing of female song from the recordings clearly identified three separate pulses of nesting (2–23 April, 9 May–5 June, and 12 June–3 July; Figure 7C). Similar analysis for Rush Ranch in 2018 showed two pulses (12–21 April and 7 May–3 June) and identified one pulse each at Iron Point, Red Wing Ranch, and Markham Ravine (22–26 April, 15–19 May, and 26 June–11 July; Figures 8B–8E).

Colony persistence or abandonment

Bioacoustic monitoring clarified whether a colony was abandoned or incubating. The sound and activity levels can be so low at colonies during incubation that even highly experienced researchers and tricolored blackbird monitors may be unable to determine the state of the colony (Beedy et al. 2020). Analysis of recordings from the 2017 Rush Ranch colony identified low-volume female song that occurred throughout incubation (Figure 7C) and confirmed continuous presence of the colony.

Analysis of recordings from the 2018 breeding season identified the continuous presence of the colony throughout the nesting season at Rush Ranch (Figure 8B) and throughout a breeding cycle at Markham Ravine (Figure 8E), whereas the colonies at Iron Point and Red Wing Ranch were abandoned (Figures 8C and 8D). At Iron Point, during a field visit on 22 April we found an estimated 4,500 birds with many engaged in nest building, at which time we placed a station to monitor the colony. Because this colony was already subject to significant disturbance by being adjacent to heavy construction and a busy parking lot (Figure 4B), we studied the birds during installation of the station. Although we noted the birds occasionally responding to the construction, they showed no reaction to the installation of the station. Recordings from 22 to 25 April captured both male and female songs; however, females ceased singing on 26 April and male song became nearly silent the following day (Figure 8C). The absence of nestling calls in the recordings suggests that few or no eggs successfully hatched. A visit on 1 May confirmed the colony had been abandoned during the early egg-laying period, based on examination of 11 accessible nests in the dense Himalayan blackberry nesting substrate (Airola et al. 2018). Analysis of recordings from Red Wing Ranch suggests that nest abandonment occurred just after the first nestlings hatched. The first recording containing a nestling call was on 14 May, with female song ceasing on 18 May, and the last nestling call was on 22 May (Figure 8D). Given the typical duration from hatching to fledging is 11–14 d (Payne 1969), we presumed these nestlings were abandoned and perished close to this date. We confirmed the site had been abandoned with a field visit.

Start date of incubation

Bioacoustic monitoring more precisely determined the date incubation began than did field visits. During field visits to Rush Ranch in 2017, we noted three occasions where the colony was extremely quiet (21 April–5 May, 19 May, and 18 June–24 July; Figure 7A), but as discussed above, determining whether the colony was quiet due to incubation or being in the midst of abandonment proved difficult. Later observations of carrying of food (12 May–21 July) indicated the first period of quiet (21 April–5 May) was a true incubation, and the length of time adults carried food suggested that there were likely multiple incubation periods. Bioacoustic monitoring provided a more complete picture. The soundscape showed three separate silent periods, indicating precisely when incubation began (14 April, 18 May, and 18 June; Figure 7B). In 2018, the recorder at Rush Ranch had technical failures during incubation, Iron Point was abandoned during the early egg-laying period (Airola et al. 2018), and we placed the Red Wing Ranch and Markham Ravine stations after incubation had begun, so we were unable to determine incubation dates for any sites.

Determining hatching date

Bioacoustic monitoring determined hatching dates more precisely than field visits. During field visits to Rush Ranch in 2017, we observed adults carrying food from 12 May to 21 July (Figure 7A). Although the three episodes of carrying nesting material described previously indicated three separate nesting attempts, determining whether all three led to successful hatching events was not possible. Because the first instance of carrying food occurred before the second pulse of carrying nesting material, we could confidently conclude that the first nesting attempt successfully hatched. The continuous observation of carrying of food through 25 July indicated that one or both of the second and third attempts were successful. By contrast, analysis of recordings from 2017 showed the end of female nest chatter and detected the peeping sounds of newly hatched nestlings, allowing us to estimate the first hatch dates of the three nesting pulses: 1 May, 30 May, and 29 June (Figure 7C). In 2018, the first pulse of nesting at Rush Ranch was abandoned, and the second pulse resulted in successful hatching with nestlings being detected on 25 May (Figure 8B). Iron Point abandoned before hatching occurred (Figure 8C). Eggs successfully hatched during nesting attempts at both Red Wing Ranch and Markham Ravine, with nestlings being detected on 15 May and 28 June, respectively (Figures 8D and 8E).

Determining length of incubation

Bioacoustic monitoring can more precisely determine incubation length than infrequent field visits. Because bioacoustic monitoring can determine the date incubation started and the approximate hatch date, it is possible to estimate incubation length. For Rush Ranch 2017, we estimated the length of the incubation periods for each pulse of nesting: 16, 12, and 12 d (15–30 April, 18–29 May, and 17–28 June, respectively). We were unable to calculate incubation length for the colonies in 2018 due to missing data (see above).

Assessing nestling stage and fledging success

Bioacoustic monitoring more reliably estimated nestling age and fledging success than field visits. During field visits to Rush Ranch in 2017, we did not record fledgling dates from the first nesting pulse, and we were uncertain whether this pulse successfully fledged young or whether we could not detect them because of the frantic activity of the second nesting pulse. We observed fledglings on the two subsequent nesting pulses on 23 June and 15 July. Analysis of Rush Ranch recordings from 2017 identified nestling or fledgling vocalizations over 23 d (1–22 May) during the first nesting pulse. The second and third nestling pulses overlapped for 53 d (30 May–21 July), with some fledglings from the second pulse still present when the third pulse of nestlings hatched (Figure 7C). The timing and duration of recorded vocalizations demonstrated that all three pulses of nesting successfully fledged young. Rush Ranch did not contain tall vegetation; therefore, we predicted that fledglings of each pulse would leave the area approximately 25 d after hatching. Given approximate hatch dates of 1 May, 30 May, and 29 June, we predicted that fledglings would leave the area around 26 May, 24 June, and 24 July. The first pulse of nestlings or fledglings was last heard in the audio recordings on 22 May, within a few days of our predicted date of departure. The second and third pulses overlapped, precluding determination via audio recordings of when the second pulse of fledglings left. We last heard the third pulse of nestlings or fledglings on 21 July, again within days of our predicted date of departure.

At Rush Ranch in 2018, following the failure of the first nesting pulse (shown by absence of nestling calls in the recordings), we heard nestling and fledgling calls over 32 d, indicating the second pulse was successful (25 May–25 June; Figure 8B). Given an approximate hatch date of 25 May, we predicted that fledglings would leave the area approximately 25 d after hatching, or around 20 June. We last heard vocalizations from this pulse of nestlings or fledglings on 23 June, suggesting most fledglings had left within a few days of our prediction. Nestling vocalizations for only 9 d (14–22 May) at Red Wing Ranch meant that at least some hatching occurred, but the short duration indicated abandonment and failure to fledge (Figure 8D). A field visit confirmed abandonment of the colony. Markham Ravine had nestling or fledgling vocalizations over 21 d (28

June–17 July), suggesting successful fledging before we removed the recorder (Figure 8E). Markham Ravine contained adjacent tall vegetation, so we predicted that fledglings would leave the area 4–8 d after fledging or 15–22 d after hatching. Given an approximate hatch date of 28 June, we predicted that fledglings would leave the colony around 12–19 July. We heard this pulse of nestlings or fledglings through the last day of recordings on 17 July. Field observations confirmed subsequent departure (Airola et al. 2018).

Discussion

Existing methods for monitoring tricolored blackbird colonies provide only crude estimates of colony size and activities, can be intrusive to the colony, and are expensive in human effort. Improved tools for understanding the population would enable researchers to generate more accurate assessments of the population status and assist property managers in making smarter decisions about habitat management. In this study, we used bioacoustic monitoring of three age- and gender-specific vocalizations of tricolored blackbirds to determine the breeding phenology of colonies, and we found that bioacoustic monitoring provided more accurate detail about colony activity with less impact on the colony and less effort from the researcher.

Bioacoustic monitoring provides a more complete record of activity across a breeding season compared to field visits alone, helping researchers to better understand breeding habits. Because the recordings are done continually, researchers can identify accurate dates for the onset and cessation of each breeding stage. However, obtaining a complete record of a colony requires that researchers predict where colonies will establish nesting sites before they settle or place the recorder within a few days of settling. In our study, we have only partial records from several sites because we placed the recorder after nesting activity had begun.

Bioacoustic monitoring offers a method to determine breeding stages that cannot be achieved through field visits, because field visits necessarily avoid disrupting the colony during sensitive times. For example, the low-volume female song made during nesting and incubation stages is only audible at close range, but field observations are generally conducted at a distance to avoid disturbing the colony. Because monitoring stations can be installed close to the colony when the colony is less sensitive to disturbance (i.e., settling stage), and the stations run without human intervention, we can collect detailed data about the colony when they are sensitive to disturbance without a field visit.

Furthermore, if conducted remotely using stations with cellular connections, bioacoustic monitoring can improve the efficiency and efficacy of field monitoring by identifying optimal times to conduct field efforts to count adults, monitor nests, and count fledglings. Accuracy of the estimation of the number of individuals within tricolored blackbird colonies during field observations varies substantially with nesting stage (Airola et al. 2015). Rather than visiting a colony several times to understand its breeding status, a researcher using bioacoustic monitoring from a live station can download audio recordings without leaving the office to determine when a colony is in a breeding stage optimal for counting, thereby reducing field effort and increasing confidence in the estimates. One limitation is that colonies exhibit varying levels of breeding synchrony, making determination of transition dates of the breeding stages imprecise. We are conducting research to measure synchrony in a way that could be applied to bioacoustic monitoring.

Predictions of key dates of breeding stages by using live data can help determine protection periods for colonies that are effective, but not unnecessarily restrictive, to landowners. Tricolored blackbirds nest in locations that may be disturbed by human activities, including agriculture, development, and habitat management (Arthur 2015; Meese 2016; Airola et al. 2018; Beedy et al. 2020). Agricultural operations and construction activities within or adjacent to nesting colonies have caused breeding failures (Meese 2016; Clipperton 2018). Disturbance activities that may result in injury or mortality to tricolored blackbirds are prohibited under the California Endangered Species Act, so colony establishment can substantially inconvenience landowners. Minimizing these inconveniences is particularly important because much of the species' nesting occurs on private lands that can be legally managed to reduce habitat values during nonnesting periods (Airola and Young 2015; Meese and Beedy 2015). Knowing the exact stage of a colony's breeding cycle allows prediction of when the colony will finish its breeding use of a site and thus allows improved scheduling of potentially disruptive operations. At Markham Ravine, we installed the audio recorder because the adjacent site was under construction for wetland restoration when the colony arrived and the contractor asked for assistance in determining when construction activities should be halted to avoid disturbing the colony. Remote monitoring data, combined with existing estimates of the lengths of nesting stages, allowed better prediction of when nesting would complete and improved the contractor's ability to schedule work.

The monitoring station enhancements deployed during 2018, solar panels and live uploading of data, reduced the number of visits required to monitor a colony and enabled assessment of breeding stage remotely, but they still have limitations. For example, near real-time assessment requires good cellular data coverage so applicability in remote areas is limited (e.g., two of our four colonies), and data can be lost due to technical failure of recorders. Deploying multiple audio recorders at a single site could mitigate such data loss, but until recently, the cost of these recorders was prohibitive for most researchers. Recently, however, new types of recording units have become available and prices have dramatically decreased (e.g., AudioMoth, Open Acoustical Devices, University of Southampton and Oxford University, UK; https://www.openacousticdevices.

info), enabling deployment of multiple recorders at a site. Although these new recorders do not allow remote monitoring, they are highly reliable and can collect data for an entire field season on one secure digital (SD) card and three AAA batteries, further reducing costs because solar panels are no longer needed.

Although bioacoustic monitoring saves time through fewer field visits, it still requires significant effort. Identifying the vocalizations in recordings requires a trained expert to listen to each recording, totaling approximately 20 h of listening per breeding pulse. Effort could be reduced by analyzing fewer recordings, and reanalysis of the data using fewer recordings is underway to determine whether this provides the same results. Another option could be to use machine learning to identify some vocalizations. For example, the ARBIMON II software has a machine learning component that allows an analyst to train it to detect and flag recordings with sounds of interest. This capability is in use in other species surveys (elfin woods warbler *Setophaga angelae*, Campos-Cerqueira and Aide 2016; four *Eleutherodactylus* species of coqui frogs: *coqui*, *cochranae*, *brittoni*, and *juanariveroi*; Ospina et al. 2013). Automating sound recognition for vocalizations made by a tricolored blackbird colony will be challenging because of the large number of birds singing and calling simultaneously. However, female song and nestling or fledgling begging occurs during periods when the colony is relatively quiet, so we are optimistic that we can train software to recognize them reliably. Because these sounds indicate the onset of nest building and hatching, automating identification of just these vocalizations would provide key information about breeding phenology while significantly reducing the total hours of manual analysis.

Conclusion

We demonstrated that analysis of multiple vocalizations of tricolored blackbirds can efficiently provide a richer and more detailed understanding of the timing and success of breeding events than field visits. Because audio data are collected daily, bioacoustic monitoring allowed determination of the exact dates of the onset and cessation of breeding stages including nest building, incubation, hatching, and fledging. We demonstrated the feasibility of collecting data remotely and in near real time, reducing data loss and reducing monitoring effort. Assessment of the breeding stage of a colony from the office enables decisions on when field visits to a colony are best completed, helping to optimize resources. The precise and timely understanding of breeding stage also allows for smarter management decisions. For tricolored blackbirds, this understanding can improve efforts to protect colonies and minimize disruption from disturbing activities.

Supplemental Material

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Video S1. Video of sonogram and audio of three vocalizations of tricolored blackbird *Agelaius tricolor*: nestling call, male song, and female song. Recording was made at 1640 hours on 15 May 2017 at the Rush Ranch colony, Solano County, California (38.208, −122.014).

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S1 (9.72 MB MPG).

Video S2. Video of sonogram and audio of tricolored blackbird *Agelaius tricolor* colony during settling stage. Recording was made at 0800 hours on 12 May 2017 at the Rush Ranch colony, Solano County, California (38.208, −122.014).

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S2 (13.58 MB MPG).

Video S3. Video of sonogram and audio of tricolored blackbird *Agelaius tricolor* colony during incubation stage. Recording was made at 0800 hours on 19 May 2017 at the Rush Ranch colony, Solano County, California (38.208, −122.014).

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S3 (12.76 MB MPG).

Reference S1. Clipperton N. 2018. A status review of the tricolored blackbird (*Agelaius tricolor*) in California. Report to the Fish and Game Commission. California Department of Fish and Wildlife, Sacramento, California.

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S4 (3.69 MB PDF).

Reference S2. Collier G. 1968. Annual cycle and behavioral relationships in the red-winged and tricolored blackbirds of southern California. Doctoral dissertation, Los Angeles, California: University of California.

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S5 (12.87 MB PDF).

Reference S3. Meese RJ. 2010. Detection, monitoring, and fates of tricolored blackbird colonies in 2010 in the Central Valley of California. California Department of Fish and Wildlife, Wildlife Branch, Sacramento.

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S6 (299 KB PDF).

Reference S4. Meese RJ. 2014. Results of the 2014 Tricolored Blackbird Statewide Survey. Tricolored Blackbird Portal, Information Center for the Environment, University of California, Davis.

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S7 (533 KB PDF).

Reference S5. Meese RJ. 2016. Detection, monitoring, and fates of tricolored blackbird colonies in California in 2016. California Department of Fish and Wildlife, Wildlife Branch, Sacramento.

Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S8 (291 KB PDF).

Reference S6. Meese RJ. 2017. Results of the 2017 Tricolored Blackbird Statewide Survey. Nongame Wildlife Program Report 2017–04. California Department of Fish and Wildlife, Wildlife Branch, Sacramento.

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Found at DOI: https://doi.org/10.3996/102019-JFWM-083.S10 (32.62 MB PDF).

Archived Material

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Data A1. All reviewed audio recordings used in this analysis for the Rush Ranch colony, Solano County, California (38.208, −122.014). We made recordings from 2 March to 25 July 2017. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Data A2. Data file that contains annotation of presence or absence of tricolored blackbird *Agelaius tricolor* vocalizations in recordings. We made recordings at the following locations: Rush Ranch colony, Solano County, California (38.208, −122.014) from 2 March to 25 July 2017 and from 9 February to 26 June 2018; Iron Point colony, Sacramento County, California (38.647, −121.104) from 22 April to 19 May 2018; Red Wing Ranch colony, Placer County, California (38.963, −121.346) from 4 May to 4 June 2018; and Markham Ravine colony, Placer County, California (38.889, −121.468) from 26 June to 17 July 2018. The three vocalizations that are annotated are male song, female song, and nestling or fledgling call. We used the results in columns O–Q to generate the graphs in Figures 7 and 8. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Data A3. All reviewed audio recordings used in this analysis for the 2018 Rush Ranch colony, Solano county, California (38.208, −122.014). We made recordings from 9 February to 26 June 2018. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Data A4. All reviewed audio recordings used in this analysis for the 2018 Iron Point colony, Sacramento County, California (38.647, −121.104). We made recordings from 22 April to 19 May 2018. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Data A5. All reviewed audio recordings used in this analysis for the 2018 Red Wing Ranch colony, Placer County, California (38.963, −121.346). We made recordings from 4 May to 4 June 2018. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Data A6. All reviewed audio recordings used in this analysis for the 2018 Markham Ravine colony, Placer County, California (38.889, −121.468). We made recordings from 26 June to 17 July 2018. Archived in Dryad: https://doi.org/10.5061/dryad.x0k6djhg5

Acknowledgments

Audubon California, the Solano County Fish and Wildlife Propagation Fund, Sierra Foothills Audubon and Sacramento Audubon provided funding. The Solano Land Trust provided access to the Rush Ranch colony. Westervelt Ecological Services provided access and logistical support at the Markham Ravine site. D. Ross provided field assistance at the Red Wing Ranch site. M. Aide and M. Campos-Cerqueira from Sieve Analytics provided technical support and training on the audio recorders, ARBIMON Touch, and ARBIMON II software. R. Meese provided guidance for study site selection. M. Holyoak and E. Graves provided feedback on the article. Two anonymous reviewers and the Associate Editor provided comments that improved an earlier version of this note.

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