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RESEARCH ARTICLE

Accurate prediction of olive-sided flycatcher breeding status using song rate measured with autonomous recording units

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Abstract

Autonomous recording units (ARUs) are recognized for their use in detecting vocalizing bird species to assess presence, occupancy, and density, but their potential to monitor reproductive status of individuals and reproductive rates is not well known. We investigated whether song rates derived from ARU data, when combined with the known date, can be used to predict the proportion of male songbirds in 3 breeding status classes (single, paired, and feeding young). We monitored breeding status with weekly field visits and collected daily ARU recordings at 46 olive-sided flycatcher (*Contopus cooperi*) breeding territories in northwestern Canada in 2016–2017. We tested 4 variations of a hierarchical multinomial regression model that used time of day, day of year, and song rate derived from 2-minute recordings to predict breeding status, and evaluated models using a novel, likelihood-based approach. We found the top model correctly estimated 79% of the observed proportions of birds in each breeding status across the length of the breeding season. Although date was the primary predictor of breeding status, singing rate reduced some of the uncertainty and provided more accurate estimates for a given time. A major challenge to prediction accuracy and data interpretation was accounting for bird movement and the associated impact on detection, which we partly addressed by limiting our study to individuals who were detected on at least 30% of ARU sampling days. We demonstrate that ARUs can be used to assess breeding status in a cryptic, low-density species at risk such as the olive-sided flycatcher, suggesting this method could be applied to a wider range of species to better understand demographics and population dynamics, and inform management decisions, for bird species of concern.

KEYWORDS

autonomous recording unit, Bayesian hierarchical model, *Contopus cooperi*, demography, habitat, song rate, species at risk, visual scanning

Protecting species of conservation concern is a critical aspect of maintaining biodiversity (Quayle and Ramsay 2005, Dawson et al. 2011). Knowledge of species demographics can be important for understanding causes of decline, population viability, and habitat quality (Johnson 2007) and improving management actions (Mazaris et al. 2005). Breeding success data can be particularly challenging to collect for many species because cryptic reproductive behavior has evolved to avoid predation. For example, songbird nests are often difficult to locate and there is concern that invasive methods such as nest searching may influence birds' behavior or alter nest concealment, increasing the risk of predation or abandonment (Ibáñez-Álamo et al. 2012). Because of the potential risks from directly monitoring nests to estimate breeding success, survival rates, or productivity using traditional methods (i.e., with human observers or cameras), there is a need to explore potential alternative non-invasive methods. For some territorial bird species, measures of singing rate may provide information on breeding status without the necessity of direct observation.

The primary functions of singing in male passerines during the breeding season are to defend a breeding territory and to attract and maintain mates (Collins 2004, Catchpole and Slater 2008). Singing rates of male passerines vary throughout the breeding season, often reflecting a shift in motivation and function from primarily intersexual functions, such as attraction of mates or other females for copulation, to intrasexual functions such as territory maintenance, mate guarding, and male-male competition (Lampe and Espmark 1987, Otter and Ratcliffe 1993). Specifically, males tend to sing at high rates when unpaired and lower rates following pairing (Gibbs and Wenny 1993, Staicer et al. 1996, Robbins et al. 2009), with gradual decreases in song rate as birds progress from nest building through incubating and feeding young (Hayes et al. 1986, Wright 1997, Upham-Mills et al. 2020). This variation in singing rate results in a well-known temporal variation in detectability of birds at the population level (Johnson 2008, Nichols et al. 2009). Less is known about individual variation in song rates and whether deviations from average singing rates could be used to understand aspects of avian life history. While researchers have quantified variation in singing rates of forest songbird males throughout the breeding season based on acoustic surveys (Furnas and McGrann 2018, Sólymos et al. 2018), the potential of using such data to predict breeding phenology and success has only begun to be explored (Staicer et al. 1996, Upham-Mills et al. 2020, Brooks and Nocera 2021). This could be especially valuable for species that are difficult to study by traditional methods (i.e., field observations) because they are rare, widely distributed, occupy territories difficult to access, or have cryptic reproductive behaviors.

Upham-Mills et al. (2020) developed a modeling framework to predict breeding status classes (single, paired, and feeding young) of male olive-sided flycatchers (*Contopus cooperi*) as a function of song rate, day of year, and time of day. This species has been listed as a species at risk (special concern since 2023, and previously threatened) under Canada's Species at Risk Act (Environment and Climate Change Canada 2016), so there is a strong interest in understanding the factors influencing its demographic rates to better understand the cause of population decline. Results from Upham-Mills et al. (2020) using field observations by human observers suggested that the breeding status song-rate relationship can be used to reliably monitor breeding success for this species at the individual level. However, this approach requires song rate data from focal individual males monitored throughout the breeding season, which is time consuming and costly. As such, using this approach might suffer from some of the same problems as direct nest searches, including being limited to relatively small spatio-temporal extents and potentially biased by presence of human observers (Gutzwiller et al. 1994).

Given the strong relationship between song rate and breeding status, the advancement of autonomous recording unit (ARU) technology may provide a cost-effective way to quantify the breeding status–song rate relationship over large spatial and temporal scales. Use of ARUs would enable the monitoring of breeding males of many species with limited effort from human observers (Pankratz et al. 2017, Shonfield and Bayne 2017, Yip et al. 2017). The ARUs can be preprogrammed to record for specified times and dates and simultaneously in many locations across large spatial extents. Given the need for single ARU deployment and retrieval events, this approach is less invasive than multiple visits from human observers to monitor breeding status (Darras et al. 2018). Long-term monitoring programs are increasingly using ARUs (replacing, or in combination with, traditional human-based point count surveys) to estimate population size and distribution of birds, and promote participatory science in collaboration with a wide range of stakeholders and land owners. A limited number of studies have used ARUs to quantify phenological parameters such as timing of arrival (Johnson and Bayne 2022) or peak nest initiation based on singing or calling behavior (Digby et al. 2013, Colbert et al. 2015). Brooks and Nocera (2021) identified change points in singing rate using ARUs to determine reproductive status, but to our knowledge this study did not assess the predictive ability of this approach. Thus, the ability to accurately predict breeding status of songbirds using ARU data would help address, in a cost-effective way, an important knowledge gap in our understanding of the relative influence of this demographic process in contributing to declines of many species across North America (Faaborg et al. 2010).

The goal of this study was to evaluate the ability of the breeding status–song rate models developed by Upham Mills et al. (2020) to estimate individual- and local population-level breeding status of male olive-sided flycatcher using song rate data collected from ARUs. We used song count data from ARUs collected concurrently with human observer assessments of breeding status. We developed hierarchical, multinomial regression models and tested their predictive ability using cross-validation combined with a novel, likelihood-based approach to model selection and evaluation.

STUDY AREA

We collected ARU recordings and breeding status data from territorial male olive-sided flycatchers at study sites in Alberta in 2016 and 2017, Northwest Territories in 2016, and Yukon in 2017 (Figure 1) in areas spanning approximately 120 km^2, 3,000 km^2, and 450 km^2, respectively. Our sites were selected based on previously documented areas of high olive-sided flycatcher abundance (Pardieck et al. 2016, Knaggs et al. 2020, Stehelin 2020, E. M. Bayne, University of Alberta, unpublished data). Breeding territories in Alberta and the Northwest Territories were situated in the Taiga Plains and Boreal Plains ecozones comprising bogs (dominated by black spruce [*Picea mariana*]), fens (dominated by black spruce and tamarack [*Larix laricina*]), and upland stands dominated by jack pine (*Pinus banksiana*) or a mix of jack pine and trembling aspen (*Populus tremuloides*). Many of these sites had burned in 2014 or 2015. The elevation ranges were 150–280 m in the Northwest Territories sites and 280–310 m in Alberta. In Yukon, breeding territories were found in the Taiga Cordillera ecozone comprising white spruce (*Picea glauca*)-dominated forests, with some black spruce, intermittent lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) at higher elevations (720–1,140 m). Some Yukon sites also contained varying amounts of trembling aspen and balsam poplar (*Populus balsamifera*). The mean daily

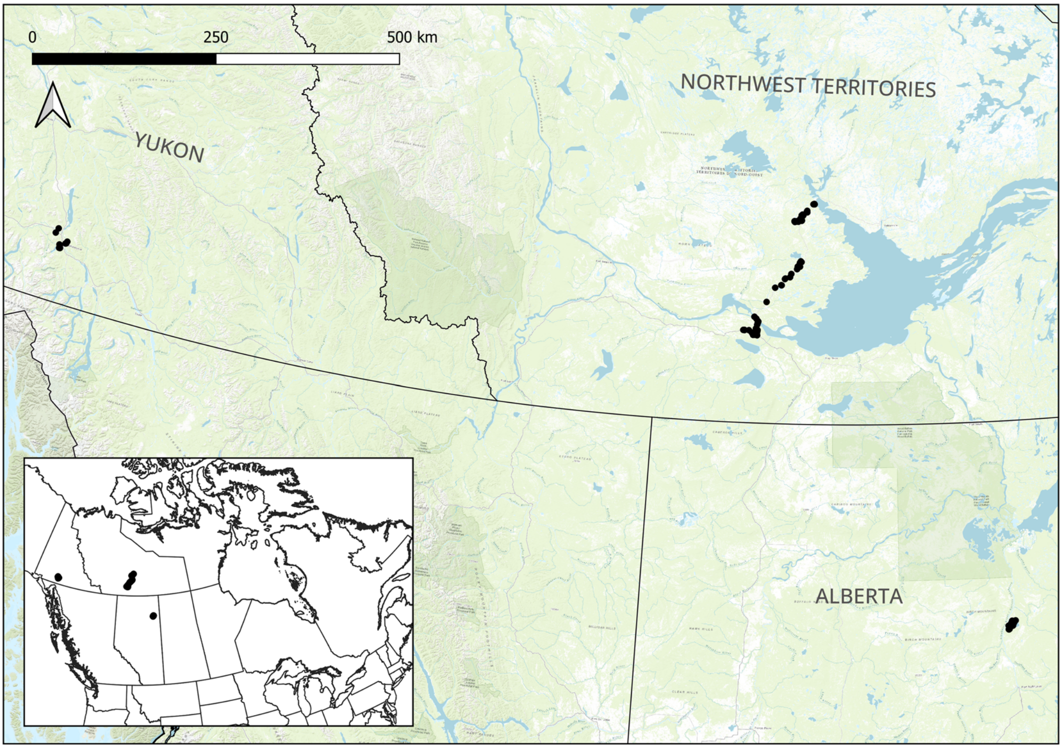

FIGURE 1 Locations (black dots) where olive-sided flycatcher territories were monitored in 2016–2017 in Yukon (*n* = 8), Northwest Territories (*n* = 18), and Alberta (*n* = 15), Canada.

temperature ranged from −22.9°C to 17.3°C and the mean daily precipitation ranged from 8.4 mm to 78.0 mm across all 3 areas (Government of Canada 2024). Primary land uses varied across study sites whereby Northwest Territory sites were relatively unaltered by anthropogenic activities other than a highway and limited non-commercial logging and Yukon sites were surrounded by urban development and recreational sites (i.e., ski and hiking trails). Alberta sites were the most impacted by anthropogenic disturbance, being situated in the Athabasca oil sands region, where large amounts of oil and gas extraction activities occur. These sites were surrounded by a network of secondary roads and cutlines.

METHODS

Sample design

We collected breeding status and ARU recording data from 46 male olive-sided flycatchers defending territories between 11 May and 10 August in 2016 and 2017. We visited each territory approximately once per week, for at least 20 minutes per visit, to confirm breeding status (i.e., single, paired, or feeding young). We confirmed breeding status from behavioral evidence, such as observing only one olive-sided flycatcher present on a given day and all past observation days (i.e., single), both members of a pair building a nest or an adult incubating (i.e., paired) or an adult carrying food (feeding young; *sensu* Upham-Mills et al. 2020). To classify breeding status between weekly in-person visits, we used average phenology periods (Altman and Sallabanks 2020). We did not include data from days when breeding status could not be determined. We collected acoustic recordings using Song Meter ARUs

(SM2+, SM3, and SM4; Wildlife Acoustics Inc., Maynard, MA, USA), which we deployed in territories after males had established a territory (i.e., a male was found singing in the same area on at least 2 separate occasions between 10 May and 8 June). We deployed 1 ARU per territory near a primary singing perch. Olive-sided flycatchers typically have 2–3 primary singing perches on a territory, where males are frequently observed singing (Wright 1997). We attached ARUs to trees with a diameter less than the width of the ARU, at a height of approximately 1.5 m. Each ARU was preprogrammed to record daily for 10–60 minutes per hour from 45 minutes before sunrise until 15 minutes after sunrise, to maximize detection probability (Wright 1997). The ARUs recorded in stereo at a sampling rate of 44.1 kHz and a 16-bit resolution. Average deployment date for all ARUs across both years was 7 June (±12 days [SD]) and recorded for an average of 68 days (±22 days).

Acoustic data processing

Our data consisted of the number of songs detected in a 2-minute interval of an audio recording. We chose this recording sample length to maximize the quantity of data available for analysis while maintaining adequate detectability and song count accuracy. Wright (1997) found marginal improvements in detectability between a 5-minute and a 3-minute listening interval, and we found little difference in mean song rate when counting songs in a 2-minute-long ARU recording versus 4-minute-long or 5-minute-long recordings (E. J. Upham-Mills, Ministry of Water, Land and Resource Stewardship, unpublished data).

We processed the ARU recordings by visually scanning spectrograms, which is an efficient (Digby et al. 2013, Cameron et al. 2020) and accurate (Ware et al. 2023) approach for processing recordings, particularly when assessing temporal patterns in call frequency (Swiston and Mennill 2009). Because of the time constraint associated with the visual scanning approach (Ware et al. 2023), we subsampled from the full dataset of recordings by randomly selecting 4,500 2-minute recordings for processing, stratified by breeding status: 1,500 recordings when an olive-sided flycatcher was confirmed as single, 1,500 when paired, and 1,500 when feeding young. We also stratified by bird to maximize the subsamples from each individual. Some birds were only in one status for the entire season, whereas others had samples from 2 or all 3 breeding status classes, resulting in an average of 32.6 song counts in single (±59.0), 32.6 in paired (±16.4) and 32.6 in feeding young (±24.6) phases. We used R software version 4.1.1 (R Core Development Team 2024) and the package seewave (Sueur et al. 2008) to create spectrograms representing 2-minute recording segments. For ease and efficiency of processing, we used a spectrogram grid approach (Figure 2). Each spectrogram in the grid had a frequency range of 1.5–5.5 kHz and used a short time Fourier transform window length of 1,000. We combined spectrograms into a JPEG file with dimensions of 33 × 20 cm and a resolution of 500 and assessed them visually on a 68-cm computer monitor.

One experienced observer scanned all recordings and counted every visible olive-sided flycatcher song. If a sound required confirmation, the observer listened to the section of recording containing the candidate song. When 2 olive-sided flycatchers were detected simultaneously in the spectrogram, the observer only counted the loudest one.

Following spectrogram processing, we calculated full-season detection rates for each bird as the number of days with at least one song detected divided by the number of sampling days. This allowed us to assess whether the male was defending a breeding territory near the ARU and whether there was adequate detection data to estimate breeding status from song rate. Five territorial males were detected at much lower rates than the rest of the sample population, with 1–4 days detected out of 13–43 days of recording data, representing full-season detection rates of 2.3–15.4% (Figure S1). The next highest detection rate was 30%, which we established as a threshold below which to remove birds from the analysis. After removal of song counts from these 5 low-detection birds, the remaining 41 birds had an average of 22.5 (±51.4), 35.6 (±13.9), and 35.2 (±23.9) song counts in single, paired, and feeding young classes, respectively.

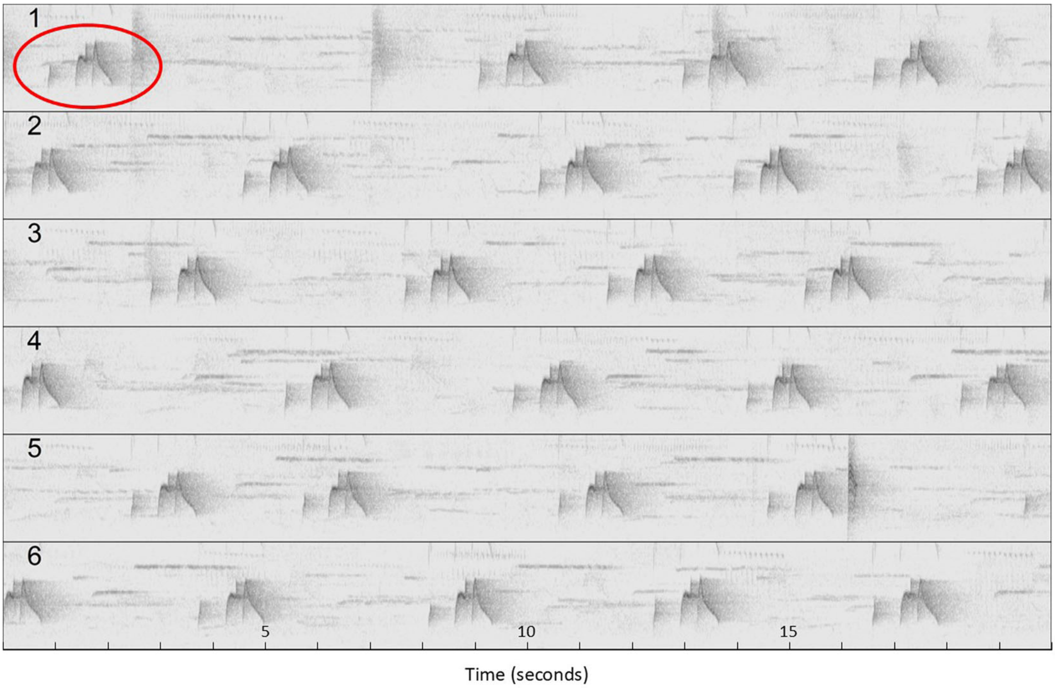

FIGURE 2 Example of a 2-minute recording represented as a single spectrogram grid of 6 consecutive 20-second panels. A single olive-sided flycatcher song is circled in red.

Statistical analysis

Hierarchical model

The sampling unit was the bird-year, defined as a given olive-sided flycatcher in a given year, where we consider each bird-year to be an independent sample despite some of the same territories being active across both sample years. The sample was the bird-day, defined as a given date for a given bird-year and this was the temporal resolution for which we estimated breeding status. For most bird-days, there were individual sub-samples, which we call surveys.

To estimate breeding status from ARU data, we adapted the hierarchical, multinomial model developed by Upham-Mills et al. (2020). The model uses date as the baseline predictor of breeding status but adjusts predictions on a given day based on singing rates. Because song rate also changes with time since sunrise, our model estimated breeding status (*BS*) as a function of ordinal day (*D*), song count (*SC*), and time relative to sunrise (*T*) following Bayes Theorem, so that

$$\Pr(BS \mid SC, D, T) \propto \Pr(SC \mid BS, T)\Pr(BS \mid D),$$

where the left-hand side probabilities (*Pr*) for each *BS*, conditional on *SC*, *D*, and *T*, are proportional to the product of 2 components on the right-hand side: the probability of a given *SC* conditional on *BS* and *T* (the behavioral component) and the probability of a given *BS* conditional on *D* (the phenological process component; Upham-Mills et al. 2020). The left-hand side is a vector of probabilities, one for each breeding status, with the constraint that the probabilities must sum to 1 (i.e., the bird must be in 1 of 3 possible breeding statuses on day *i*).

$$SC_{i,k} \sim \text{Poisson}(\lambda_{i,k}) \quad \text{and} \quad SC_{i,k} \sim \text{negative binomial}(p_{i,k}, r),$$

where $SC_{i,k}$ is the song count on bird-day i during survey k, $\lambda_{i,k}$ is the expected song count, r is the size parameter describing dispersion in the counts, and $p_{i,k} = r/(r + \lambda_{i,k})$. In both cases, we modeled the log of the expected song count as:

$$\log(\lambda_{i,k}) = \beta_{0(BS_{j(i)})} + \beta_1 T_{i,k},$$

where $\beta_{0(BS_{j(i)})}$ is the intercept specific to breeding status j (the known breeding status at bird-day i), and T is time relative to sunrise at survey k. The Poisson distribution is more commonly used with count data and can be more efficient because it uses a single parameter estimate to describe the rate (expected count) and the variability. However, the negative binomial distribution is preferable if the data are over-dispersed, meaning the variability is greater than would be described by the Poisson distribution.

In the phenological process component, breeding status was a function of ordinal day and could be one of single (S), paired (P), or feeding young (FY). We considered each bird-day combination to be an independent sample, so the phenological process component model was:

$$BS_i \sim \text{Multinomial}(p_S, p_P, p_{FY}),$$

where BS_i is the breeding status for bird-day i, and $p_S, p_P, and\ p_{FY}$ are the probabilities of each of the 3 breeding statuses. The 3 breeding status probabilities are normalized from the estimated relative probabilities for each breeding status j (where $j = S,\ P,\ or\ FY$) on bird-day i, $\delta_{j(i)}$, so that:

$$p_{j(i)} = \frac{\delta_{j(i)}}{\delta_{S(i)} + \delta_{P(i)} + \delta_{FY(i)}}$$

We considered the log relative probability of each breeding status j on bird-day i to take either a linear or quadratic form:

$$\log(\delta_{j(i)}) = \eta_{j,1} + \eta_{j,2} D_i \quad \text{or} \quad \log(\delta_{j(i)}) = \eta_{j,1} + \eta_{j,2} D_i + \eta_{j,3} D^2{}_i$$

for $j \in \{S, FY\}$, where D_i is ordinal day on bird-day i, and

$$\log(\delta_{j(i)}) = \eta_{j,1}$$

for $j = P$, where the paired status (P) is used as the reference condition and $\eta_{P,1}$ is set to 0 (Upham-Mills et al. 2020).

Model fitting and comparison

We developed 4 different versions of our model by considering all combinations of the 2 different models on the behavioral component (Poisson and negative binomial), and 2 different functional forms for the phenological process component (the linear and quadratic effects of ordinal day on breeding status). We fit the models in a Bayesian framework with R version 4.1.1 and Jags version 4.3.1 (Plummer 2003) through the JagsUI package (Kellner 2015). The Poisson model used 20,000 iterations to achieve adequate convergence according to the Rhat statistic (Brooks and Gelman 1998), with a burn-in of 15,000 and a thinning rate of 5. The negative binomial models used 50,000 iterations to achieve convergence, with a burn-in of 30,000 and a thinning rate of 5. All models used uninformative priors for the β and η values, where priors followed normal distributions with mean $\mu = 0$ and precision $\tau = 0.01$. For the negative binomial models, the prior for the size parameter was $r \sim \text{Uniform}(0,20)$.

We used 5-fold cross-validation to compare the 4 model versions using 2 separate scoring methods for comparing relative predictive accuracy of out-of-sample (OOS) data. The first method (method A) looked at survey-level predictive ability. For each saved draw of all parameters from the posterior distribution, we calculated the expected song count $\lambda_{j,i,k}$ for each of the breeding statuses j at survey k for bird-day i. We then calculated the probability of getting the observed song count for each breeding status as

$$\Pr(SC \mid BS_j, T_{i,k}),$$

where SC is the observed song count, BS_j is breeding status j, and T_{ik} is time relative to sunrise at survey k on bird-day i. Next, we multiplied these probabilities by the probability of being in each breeding status, calculated as

$$\Pr(BS_j \mid D_i),$$

where D_i is the ordinal day of bird-day i, and BS_j is the probability of being in breeding status j. These products provide the probabilities of the bird being in each breeding status on bird-day i, conditional on song count, ordinal day, and time relative to sunrise. Finally, we calculated the log likelihood of the data given the models as the probability of the observed breeding status given the estimated relative probability of being in each breeding status, and summed these across all K surveys for OOS bird-day i.

The model log-score for method A, $L_{\log(A)}$, for each cross-validation fold, based on this method, was the deviance of the observed data averaged over all draws from the posterior distribution (*sensu* Hooten and Hobbs 2015, Stevens and Conway 2019), so that:

$$L_{\log(A)} = \frac{1}{S}\sum_{s=1}^{S} -2\left(\sum_{i=1}^{I}\sum_{k=1}^{K} \log(\Pr(y_i \mid \Pr[BS_{J(i,k)}]))\right),$$

where y_i is the observed breeding status bird-day i, $\Pr[BS_{J(i,k)}]$ is the vector of expected probabilities for each breeding status ($J = [S, P, FY]$) at survey k on bird-day i estimated by the model, and s is the individual draw from the posterior distribution. We averaged the log-scores over all 5 folds from the cross-validation to get the final score for each model, and chose the model with the lowest score as the best model.

Our second method (method B) looked at population-level proportions of samples in each breeding status. To do this, we calculated the likelihood of the observed proportion of bird-days in each breeding status, given the expected proportion of bird-days in each breeding status from the model, at each draw from the posterior distribution. Because in most cases there were multiple surveys for the same bird-day, we calculated the vector of breeding status probabilities for bird-day i as the average of the probabilities for each each breeding status over all of the k surveys, so that

$$\Pr(BS_{J(i)}) = \frac{1}{K}\sum_{k=1}^{K} \Pr(BS_{J(i,k)}),$$

where $\Pr(BS_{J(i,k)})$ is the vector of probabilities of being in each breeding status at survey k on bird-day i estimated by the model. We then estimated the breeding status for bird-day i as

$$BS_i \sim \text{Multinomial}(\Pr(BS_{J(i)})).$$

To calculate the log-score of the model with this method, $L_{\log(B)}$, we used the predicted BS_i for each bird-day in the OOS data, at each iteration of the model, to calculate the predicted proportion of the OSS data in each breeding status. We used these predicted proportions as the multinomial probabilities for calculating the log-score of the observed breeding statuses given the model predictions as:

$$L_{\log(B)} = \frac{1}{S}\sum_{s=1}^{S} -2\log(\Pr(BS_{oos} \mid Prop\,[BS]_s)),$$

where $Prop\,[BS]_s$ is the vector of predicted proportions of bird-days in each breeding status at each s draw from the posterior distribution, and BS_{oos} is the observed counts in each breeding status in the OOS data. As with the survey-level evaluation, we averaged the log-scores over all k folds from the cross-validation to get the final score for each model, and chose the model with the lowest log-score as the best model.

Evaluation of predictive ability of the best model

The above scoring methods only provided relative estimates of predictive ability and thus lacked a full evaluation of the accuracy and precision of the predictions. To evaluate these metrics, we also calculated the model-predicted proportion of individuals in each breeding status at regular time intervals throughout the breeding season, and compared the estimates to the observed proportions.

To assess accuracy and precision of model-predicted breeding status, we first separated the 65-day breeding season covered by our samples into 13 5-day periods. We then estimated the accuracy and precision of model predictions of the proportion of samples in each breeding status within each period. We derived our estimates for each period from the model-predicted breeding status at each draw from the posterior distribution for each bird-day in the sample, as we did in the second log-score method above, giving us the uncertainty distribution around the estimate as our measure of precision. For each breeding status at each period, we calculated the mean and 95% Bayesian credible interval (CRI) of the predicted proportion of bird-days in that breeding status, and compared those values to the known proportion. For this assessment, we removed the first and last 5-day time intervals because the data included only a single breeding status for these intervals (only paired for the first time interval and feeding young for the final time interval).

RESULTS

We had 924 recordings from single males, 1,458 recordings from paired males, and 1,445 recordings from males in the feeding young stage, where breeding status at the time of recording was determined by cross-referencing the recording date with the phenological data collected from in-person survey observations. Our sample comprised 3,827 recordings from 41 birds, with an average of 93 (±35) 2-minute recordings per bird.

Our cross-validation showed that the linear functional form describing the effect of ordinal day on breeding status combined with the negative binomial behavioral model component had the best likelihood score (i.e., the lowest score) among the 4 models in both the survey-level and population-level assessments (Table 1). Both versions of the negative binomial model scored approximately 80% lower than the Poisson models, suggesting that there was more variability in recorded singing rate than could be explained by the Poisson model.

The behavioral component model of song rate as a function of time from sunrise showed that paired birds sang the most, followed by single individuals, and individuals feeding young sang least often (Figure 3). Song counts decreased significantly as time from sunrise increased (Figure 3).

There was strong correspondence between model-predicted proportions of the population samples in each breeding status and the observed proportions in each 5-day period (Figure 4). We found 79% of observed proportions were within the 95% CRI of model-predicted proportions. The model predicted most accurately between

TABLE 1 Results of likelihood-based model evaluation from 5-fold cross-validation of a hierarchical multinomial regression model of breeding status for olive-sided flycatchers in northwestern Canada in 2016–2017 as a function of ordinal day, singing rate (number of songs per 2-min autonomous recording unit survey), and time relative to sunrise. The 4 model types represent the error structure of the singing rate data (negative binomial or Poisson) in the behavioral component of the model, and the functional form of the relationship between day of year and breeding status (linear or quadratic) in the phenological component of the model.

	Likelihood score	
Model type	**Survey-specific**[a]	**Population**[b]
Negative-binomial	1,423	14
Negative-binomial quadratic	1,441	14
Poisson	6,826	84
Poisson quadratic	6,785	82

[a] −2 log likelihood of the data given model-predicted song count for each survey.

[b] −2 log likelihood of the data given model-predicted proportion of the population in each breeding status.

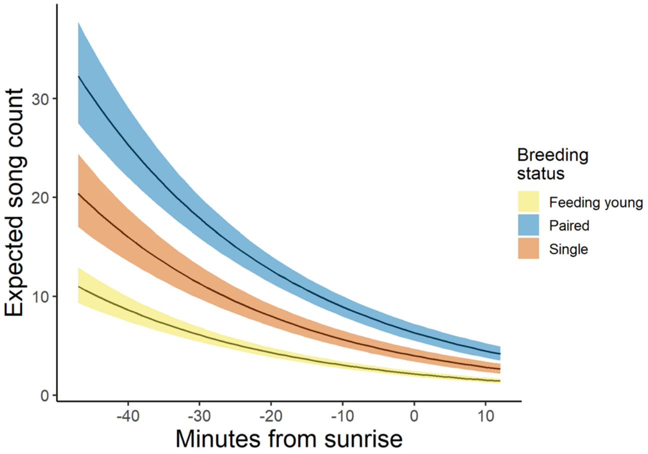

FIGURE 3 Expected song count and 95% Bayesian credible interval as a function of minutes from sunrise (where 0 = sunrise time) for olive-sided flycatchers in each of 3 possible breeding statuses based on data collected from autonomous recording units deployed in northwestern Canada in 2016 and 2017. Expected counts are estimated from a generalized linear model with negative binomial error distribution, as part of a hierarchical model of breeding status as a function of ordinal day and song rate (songs per 2 minutes).

the third and eleventh period. Prior to the third period, the model overpredicted paired and under-predicted single, while after the eleventh period, the model overpredicted feeding young and under-predicted single. There also appeared to be a lag in the model prediction of transition to the feeding young stage (eighth period; Figure 4), where many birds switched to the feeding young stage over a short amount of time, but the model predictions did not catch up until the following period (eighth and ninth period; between days 184 and 194, early July).

Plots of how estimated breeding status probabilities based on ordinal day change as a function of song count showed highly variable effects throughout the breeding season. In the early breeding season (ordinal day 165; mid-June, corresponding to period 3), model-predicted breeding status changed very little as a function of singing rate (Figure 5A). Further along in the season, when birds were beginning to switch to the feeding young stage (ordinal day 180; late June, corresponding to period 6), singing rate had a bigger effect on the estimated breeding

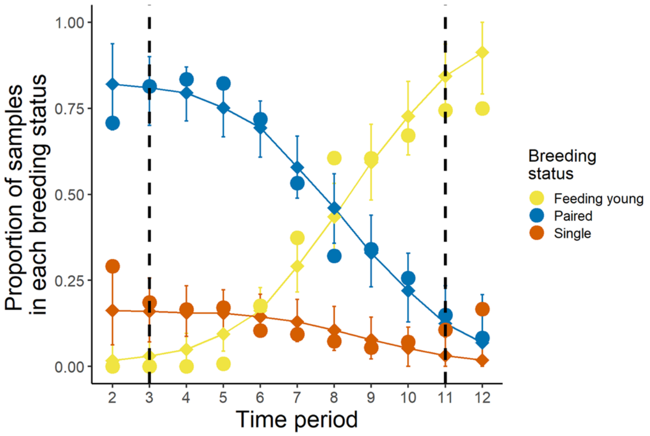

FIGURE 4 Observed (large round dots) versus predicted (small diamond dots = mean, lines = 95% Bayesian credible interval) proportions of olive-sided flycatchers (*n* = 41) in each breeding status from a Bayesian multinomial regression model using song count data from autonomous recording units deployed in northwestern Canada in 2016 and 2017. Time periods represent 5-day blocks, beginning 4 June and ending 28 July. We removed time periods 1 and 13 because data included only a single breeding status. The period between the dashed black lines represents the temporal sampling zone in which the model predictions are most accurate.

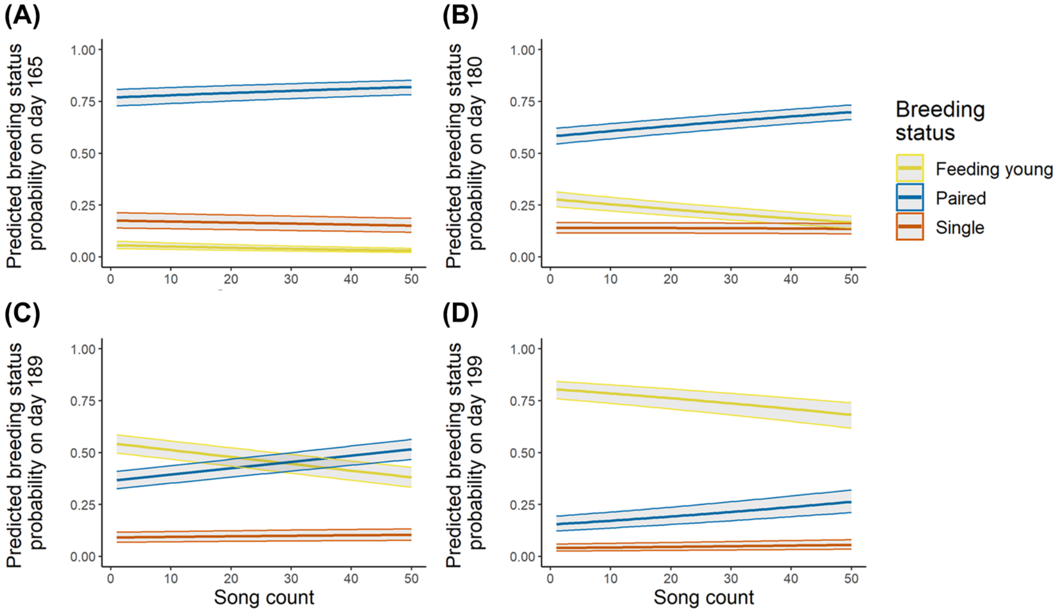

FIGURE 5 The relationship between song count and estimated breeding status probabilities of olive-sided flycatchers at 4 time periods during the breeding season in the northwest boreal region of Canada based on autonomous recording unit data collected in 2016 and 2017. Baseline breeding status probabilities are estimated as a function of ordinal day using multinomial regression. Days represent (A) the beginning of the breeding season, when most birds had recently transitioned from single to paired (where day 165 is 14 June); (B) the early mid-season, when the early breeders transitioned to the feeding young stage (29 June); (C) the middle of the season, when most paired birds transitioned to the feeding young stage (8 July); and (D) the late season, when most birds were feeding young (18 July).

status, where low song rate resulted in a higher predicted probability of being in the feeding young stage (Figure 5B). In the main transitional period (ordinal day 189, early July, corresponding to period 8), when many birds were switching to the feeding young stage, a low singing rate could change the most likely predicted breeding status from paired to feeding young (Figure 5C). Towards the end of the time when model predictions could be considered accurate (ordinal day 199; mid-July, corresponding to period 10), singing rate again had a reduced effect on predicted breeding status (Figure 5D). Thus, the model predictions were primarily driven by ordinal day, but singing rate could have a substantial effect during the middle part of the breeding season. Model-estimated probabilities of being single, and observed proportions, remained low throughout the breeding season, and song count had little effect on the estimates.

DISCUSSION

Our research demonstrates that song counts from ARUs can be used to reliably estimate breeding status rates (i.e., the proportion of the sample population in each status within a discrete period) throughout the main portion of the breeding season for the olive-sided flycatcher. The results of this research are encouraging for large-scale and cost-effective monitoring of breeding success and phenology for this and potentially other species of conservation concern. Demographic studies, particularly in remote regions such as northern Canada, can be very expensive and time consuming. The ability to deploy an ARU within a breeding territory rather than conducting intensive nest searches and behavioral observations through multiple visits can save significant resources and facilitate simultaneous monitoring of large numbers of territorial males. Demographic data derived from ARUs collected over large areas can then be used to compare breeding success across habitat characteristics, providing an index of habitat quality (Johnson 2007). This research represents an important methodological advance for demographic studies and, ultimately, to better assess habitat quality and status of forest songbirds.

The hierarchical model we developed uses date as the baseline predictor of breeding status probabilities and incorporates song counts to modify those predictions, thus accounting for spatial and temporal variability unexplained by the date (Figure 5). When fitted to data from a given number of years, the baseline predictions represent the expected (or mean) proportions of the population in each breeding status within a region in those years. Departures from those baseline probabilities estimated with song counts can then be used to explain differences in habitat quality across space, assuming no trend in the baseline probabilities through time. With enough years of data, the model can also be used to understand temporal variability in reproductive rates. The ability to estimate these parameters with a greatly reduced effort, by using ARUs in place of repeated site visits, holds promise for monitoring and conservation of at-risk species with much more efficiency than previously possible.

The mid-season period (period 8; Figure 4), when many birds were transitioning from paired to feeding young, showed the largest discrepancies between the observed and predicted proportions of samples in each breeding status. The rapid rate of change in this period was poorly captured by the model, given the linear function of date as the primary predictor. This linear function also performed poorly at the beginning and end of the season (periods 1-2 and 11-13), again showing the difficulty of capturing rapid shifts in the proportion of birds in each breeding status, such as when many birds go from single to paired within a few days. However, the observed proportions in the first and last time periods of the survey season are not necessarily representative of the true proportions in the population because smaller sample sizes (Figure S2) hampered interpretation. Although it was not well captured by the model, the baby boom in period 8 could be an interesting demographic point of interest for population monitoring. Researchers could consider using a change-point analysis (*sensu* Brooks and Nocera 2021) in combination with the hierarchical modeling approach to identify these transitions in addition to monitoring breeding status rates.

Brook and Nocera (2021) used a change point analysis to determine when significant changes in ARU-derived song rates occurred. Their study did not have corresponding empirical demographic data from field observations to validate changes in song rate with breeding status. We demonstrate that using song rate to indicate breeding status risks overestimating individuals that reach the feeding young stage, especially late in the breeding season. Low song rates in the latter stages of the breeding season can also be associated with being unpaired.

In this study, we used spectrogram visualizations to detect and count songs. Although this approach has high accuracy (Cameron et al. 2020, Ware et al. 2023), it is relatively unpopular for processing recordings compared with automated signal recognition programs (i.e., recognizers) (Knight et al. 2024, Priyadarshani et al. 2018, Gibb et al. 2019, Kahl et al. 2021). Using the visual scanning approach decreased the volume of recordings we could include in the analysis because of the time required to scan recordings compared to using a recognizer. Despite a relatively small number of recordings (<4,500 2-minute recordings) compared with the total volume of audio data collected, we detected a similar breeding status–song rate relationship as those already reported for the olive-sided flycatcher using field-based song counts (Wright 1997, Upham-Mills et al. 2020) and recognizer-assessed song counts (Brooks and Nocera 2021). Also, by using the spectrogram visualization processing approach, we found that many recordings had more than one olive-sided flycatcher within the detectable range of the ARU (Figure S3). This finding highlights the importance of detecting and accounting for the presence of conspecifics in recordings into predictive breeding status–song rate models because increased song counts could be driven by factors other than breeding status, such as a density-dependence response (Geberzahn and Aubin 2014, Stehelin and Lein 2014) or an increased proximity to recording units (Yip et al. 2017). Although we did not include presence of detectable conspecifics as a variable in our analysis, we were able to exclude non-focal olive-sided flycatcher songs from the song counts, which would be difficult to do using recognizer-processed counts without individual identification (Knight et al. 2024). We recommend the spectrogram visualization approach over recognizers for other song rate-breeding status analyses until 1) classifiers with sufficient recall (i.e., the proportion of correctly identified vocalizations of the total vocalizations) are developed, and 2) individuals can be differentiated within a single recording.

The breeding status–song rate model used in this study provides the flexibility for undetermined periods of time spent in each breeding status by assuming independence among days to predict breeding status. However, samples were not truly independent because change in breeding status of an individual bird through time typically follows a sequential pattern leading from single to paired to feeding young, with the potential to revert to a previous status in case of nest failure or adult mortality. The model could potentially be strengthened by incorporating a Markov process to include the influence of the breeding status at time $t-1$ on the breeding status at time t. However, this could potentially lead to greater overprediction of paired and feeding young, and may not function as well in the case of mid-season nest failures, as was observed in many of the olive-sided flycatchers from Yukon in 2017 (T. Stehelin, Yukon University, unpublished data). It might also be possible to include probability of nest failure as part of the model if the parameter can be reliably estimated or obtained from alternative sources and incorporated into the prior distributions. Future developments of the modeling framework could focus on testing such alternative versions.

Given differences in timing of phenology, and potentially in singing rates, across the range of this species, applying the model with parameters estimated in our study area may bias predictions if used as-is in other regions. However, field observers monitoring the breeding statuses of a large number of territorial males to re-fit the model would largely negate one of the chief advantages of using the framework. That said, it could be a reasonable initial investment to monitor a subset of territorial males in a novel study area and re-fit the model to set up a longer term ARU-based demographic monitoring program. Such programs would still be more efficient, cost-effective, and complementary to traditional field observer-based demographic studies. Re-fitting the model could include using the original parameter estimates as prior distributions to fit a model using updated data from the new study area, thus requiring much less new data. Exactly how large a sub-sample would be needed, and how informative the prior distributions should be, could be determined by researchers in advance through the use of simulation-based power analyses (Johnson et al. 2015, DiRenzo et al. 2023).

One concern with using ARU data to derive song rate and estimate breeding status is the impact of bird movement on detection rates and false counts of zero songs. Increased distance from the ARU can result in decreased detection rates when the bird is singing because of sound attenuation and other factors (Yip et al. 2020). This could be of particular concern for the olive-sided flycatcher because of their large breeding territories (Stehelin 2020). We attempted to mitigate this challenge by removing birds with low detection rates (i.e., detection threshold of 30%) to avoid erroneous song rate estimates and assumptions about territoriality, which would be an important distinction if using this model on new datasets. However, this resulted in the removal of a high proportion of unpaired males (i.e., a third of our total number of single males) from the analysis. The low detection rate in these males is likely associated with increased movement associated with their status, whereby single males either move farther distances in search of females or abandon territories after a period of unsuccessful advertising (Luepold et al. 2024). A potential solution to this issue might be to include a detectability estimate based on the average and variability in sound level measurements (Yip et al. 2020), which may also provide a proxy for territory size. An additional approach to addressing the challenge of distinguishing between movement-driven versus behavior-driven silence would be to deploy a grid of ARUs across an area of interest. Our study used one ARU placed at a popular singing post, but a larger grid of units could improve confidence in confirming territoriality at a site and the ability to monitor singing rates and distinguish between individuals (Rhinehart et al. 2020). Regardless of how researchers treat low detection rate data, we encourage potential users of this approach to collect multiple weeks of data and assess detection rate through the survey period (ideally full season) to ensure that predictions are only made on territorial males with relatively consistent detectability.

CONSERVATION IMPLICATIONS

Our study presents a proof of concept where breeding status was accurately predicted from ARU-derived song counts and dates within the breeding season. An ARU approach to monitoring breeding activity in a population is much more flexible and affordable than the field observation approach we required to collect the breeding status data in our study. For example, our study required approximately 12 visits per territory to confirm breeding status throughout the breeding season using in-person field observation and was reliant on good weather and the availability of fit and experienced field staff. However, the use of ARUs to monitor breeding status could decrease this to 2 visits with high flexibility for deployment and retrieval timing and no need for field technicians to have specialized training in bird behavior. While there is still time required for data analysis and interpretation, this step will likely be simplified and more efficient following ongoing technological advances in species recognition software. We tested the breeding status–song rate model on ARU data with olive-sided flycatchers because of their predictable singing pattern (Wright 1997), clear and consistent song, large non-overlapping breeding territories, and conservation status. However, this approach could be applicable for many other species and applied management scenarios, given there is vocalization variation associated with demographic status. Potential target species include other songbirds (Hayes et al. 1986, Gibbs and Wenny 1993, Robbins et al. 2009), owls (Herting et al. 2001), and raptors (Penteriani et al. 2002). We suggest that researchers and conservation professionals take advantage of the potential of ARUs to collect data beyond species presence and biodiversity and explore opportunities to monitor behavior, reproductive state, and breeding success through vocal patterns and variation. Such data can then be used to inform environmental assessments including breeding evidence pre-disturbance, before-after impact assessments, and restoration assessment, and inform habitat conservation area development. By efficiently monitoring demography and population dynamics of species of conservation concern, ARUs can also be used to better understand drivers of biodiversity loss, which is becoming increasingly important as global biodiversity decreases at an unprecedented rate (Brondizio et al. 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

For this observational-based study, we followed the guidelines of Fair et al. (2023) to ensure we minimized any detrimental activities. Research activities were permitted under Alberta Research Permit 56603 and Northwest Territories Wildlife Research Permit WL500435.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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