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Estimating abundance based on time-to-detection data

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Abstract

1. Many studies in ecology and management aim at quantifying absolute abundance based on counts at a set of surveyed sites. As time for data collection is typically limited, methods for reliable estimation of occupancy or abundance from low-cost data are desirable. Time-to-detection (TTD) models have shown promise for the estimation of occupancy. However, they remain heavily underutilized, and restricted to inference about occupancy, rather than abundance.

2. We developed a binomial N-mixture model for species-level TTD protocols that allows estimation of abundance with multiple- or single-visit data. An extension of the multi-visit version allows estimating availability per visit, given temporary emigration is random. We provide JAGS code and a new function (nmixTTD) in the R package unmarked for fitting a variety of such models.

3. Simulations showed accurate parameter estimation from single-visit species-level TTD data if individual detection probability is high (≥~0.7) and the number of visited sites is in the hundreds (≥~300). Additional visits improved the accuracy of estimates considerably. A comparison with the Royle-Nichols- and the classic binomial N-mixture-model revealed that the performance of our model is between these two, but requires data that are less expensive and less error-prone than count data required for binomial N-mixture-models. In a case study, we found similar results when analysing data with the Royle-Nichols-, the binomial N-mixture-model or the multi-visit version of our TTD model. Analysing single-visit data with our model yielded lower abundance and higher detectability estimates. Presumably these differences are due to temporary emigration, as the single-visit method estimates the abundance of individuals available at one sampling occasion, whereas the multi-visit methods refer to the superpopulation, that is, the number of individuals present over the study period.

4. Our new TTD-N-mixture model shows promise because it enables estimation of abundance, corrected for imperfect detection, for single- and multiple-visit data, based on data that are less expensive and that will be available in large quantities in the near future thanks to technical advances like autonomous recording units. The effects of unmodelled heterogeneity in detection rate and imperfect availability require further study.

1 | INTRODUCTION

The study of spatial and temporal variation in distribution and abundance underpins much of what ecologists and wildlife managers do. However, in the field neither occurrence nor abundance can be simply censused (i.e. enumerated exactly), but rather must be estimated while correcting for measurement errors like imperfect detection (Kéry & Royle, 2016: Chapter 1). Several approaches have been developed to account for imperfect detection and to obtain unbiased estimates of spatiotemporal patterns of distribution and abundance. Most of these protocols require sites being visited repeatedly (Kéry & Royle, 2016; MacKenzie et al., 2017; Royle & Dorazio, 2008; Williams et al., 2002). Distance sampling and spatial capture–recapture also account for imperfect detection. They do not require repeated measurements, but the extra information to estimate detection comes in the form of accurate distance measurements and spatial recaptures of individually recognizable animals (Buckland et al. 2001, 2004; Royle & Converse, 2014). Use of all these approaches entails a substantial increase in effort and often cost. In addition, several other formal estimation methods for single-visit data have been described (e.g. Lele et al., 2012; Peach et al., 2017; Royle et al., 2013), but they require strong parametric assumptions and may lack robustness when these assumptions are violated (Knape & Korner-Nievergelt, 2015; Phillips & Elith, 2013).

Garrard et al. (2008) developed an occupancy-based species distribution model for species-level time-to-detection (TTD) data, which is the time elapsed from the start of a survey until the first detection of any individual of a study species. Bornand et al. (2014) showed that, when analysing single-visit TTD data, detectability estimates were almost identical compared to those under a traditional occupancy model with two surveys. Thus, when TTD can be recorded, one visit per site is sufficient to separately estimate occupancy and detection probability, making this protocol logistically cheaper than designs requiring repeated measurements. However, somewhat surprisingly (to us), only a handful of papers have since used such TTD-based occupancy models (Bischof et al., 2014; Bornand et al., 2014; Ferreira et al., 2016; Garrard et al., 2013; Halstead et al., 2018; McCarthy et al., 2013). Most found this protocol to perform in a satisfactory manner, although Medina-Romero et al. (2019) and Henry et al. (2020) have shown problems related to unmodelled detection heterogeneity and low detection probability, particularly for single-visit designs. In addition, Alldredge et al. (2007) and Martin-Schwarze et al. (2017) both provide models to estimate abundance from another type of TTD data, which are more difficult to collect and also more error-prone compared to data used for our model. For their methods, TTD must be recorded for all individuals detected during a survey, while our model uses TTD only for the *first* detection of any individual of a study species. Therefore,

our model uses data we refer to as species-level TTD data, while their models require individual-level TTD data.

Here, we develop a model for estimation and modelling of abundance using species-level TTD data from single- or multiple- visit protocols. As in the binomial mixture model of Royle (2004), we can model spatial variation in abundance and detection using site-level covariates, and when there are replicated visits, also spatiotemporal variation in detection using spatiotemporal covariates. We conducted two simulation studies to assess the performance of our new model. First, we explored the relationships among model performance, sample size and true parameter values, and examine how parameter estimates improve with repeated TTD surveys. In the second simulation, we compared the accuracy of our density estimates with the binomial mixture model for replicated detection/non-detection data by Royle and Nichols (2003) and with the binomial mixture model of Royle (2004). Finally, we present a case study on forest birds in Pennsylvania, USA, where we again compare the new model with existing multi-visit estimation methods.

2 | MATERIALS AND METHODS

2.1 | Model description

We develop a model that yields estimates of abundance N (i.e. the number of available individuals present at a study site) from species-level TTD data from one or multiple visits to a collection of sites. We frame our model as a hierarchical model (Royle & Dorazio, 2008) with one submodel for the true state of a site (i.e. abundance) and a second, conditional submodel for the observations, given the true state, that is, the species-level TTD measurements.

As in other binomial mixture models (e.g. Dorazio et al., 2005; Royle, 2004; Royle et al., 2004; Royle & Nichols, 2003), we treat the latent abundance N at site s as a realization from some suitable discrete-valued distribution, such as (here) a Poisson with intensity λ_s (for other possible distributions, see mini-tutorial in the archive, Strebel et al., 2021):

$$N_s \sim \text{Poisson}(\lambda_s). \tag{1}$$

As in a Poisson GLM, the model can be extended by adding effects of covariates or random effects on a log-link scale. Thus, we can write the expected abundance on the log-scale as a linear function of the effects of $L - 1$ covariates as follows, where $X_{s,1}$ is a vector of ones coding for an intercept, while the other columns in the matrix X contain the values of continuous or indicator explanatory variables, and β_l are the coefficients of the linear model:

$$\log(\lambda_s) = \sum_{l=1}^{L} X_{s,l} \times \beta_l. \tag{2}$$

The typical parametric assumption made for TTD data is that of an exponential distribution with an expected value for the number of detection events per time unit, the detection rate r, where $1/r$ is the expected time to first detection. Key to our new model is a modification of this parametric assumption. To move from the modelling of occupancy (Garrard et al., 2008) to the modelling of abundance, the expected value for the number of detection events per time unit has to be expressed as the product $r \times N$ (this assumes independent detection of the N individuals at a site). Thus, the observed species-level time-to-detection ttd_{sj} at site s on visit $j \geq 1$, when abundance $N_s > 0$, is:

$$ttd_{sj} \mid N_s > 0 \sim \text{Exponential}(r_{sj} \times N_s). \qquad (3)$$

Note that we use r for detection rate instead of the more traditional λ to avoid confusion with the expected abundance in the Poisson model (Equations 1 and 2). Equation 3 makes two assumptions: that $N_s > 0$ and that an observer remains at a site for long enough to obtain a first detection of the study species. In reality, we do not know N_s, and N_s may be 0. Furthermore, the time spent at a site, $Tmax$, is finite. Thus, if there are zero detections during a given survey, this might be a structural zero, because a study species may not occur at the site and $N_s = 0$, or it might be a chance zero, because simply no detection occurred before the end of the survey.

Thus, we extend the model to account for both possibilities by modelling the TTD data as right-censored exponential random variables with $Tmax_{sj}$ being the survey duration of visit j at site s, and C indicating the censoring:

$$ttd_{sj} \sim \text{Exponential}(r_{sj} \times N_s)\,C(Tmax_{sj}). \qquad (4)$$

Note that when $N_s = 0$, the exponential scale will be infinite, and thus censored at $Tmax_{sj}$. Detection rate r_{sj} is indexed by site and visit, indicating that covariate models for it can be specified with site- or visit-specific covariates, typically with a log-link transformation, since this parameter is non-negative.

Often, TTD is not recorded on a truly continuous time-scale, but rather in $K + 1$ discrete time bins, where K is the number of bins, and bin $K + 1$ accommodates failures to detect the study species during the survey period. Let π_{sjk} be the probability that TTD at site s on visit j falls into bin k, where the vector of probabilities π_{sj} sums to 1. In this discrete-time case, the data generation process described in Equations 3 and 4 of the manuscript is replaced by:

$$ttdcat_{sj} \mid_s > 0 \sim \text{Categorical}(\pi_{sik}), \qquad (5)$$

with

$$\pi_{sik} = (1 - e^{-N_s \times r_{sj} \times Tmax \times (k/K)}) - (1 - e^{-N_s \times r_{sj} \times Tmax \times ((k-1)/K)}) \quad \text{when } k \leq K, \qquad (6)$$

$$\text{and} \quad \pi_{sjk} = e^{-N_s \times r_{sj} \times Tmax} \quad \text{when } k = K + 1. \qquad (7)$$

In this case, when $N_s = 0$, then $\pi_{sj(K+1)} = 1$, and thus a non-detection is a certainty.

We developed code to fit our model in JAGS (Plummer, 2003). In addition, we implemented it in the R package unmarked (Fiske & Chandler, 2011; version >1.0.1) as a new function nmixTTD for estimation with maximum likelihood. In Supporting Information 1, we describe an extension of our model that includes random temporary emigration at a site between visits. The mini-tutorial in the archive (Strebel et al., 2021) contains commented R code (R Core Team, 2019) to simulate data under the new model with different distributions for abundance and detection, including the temporary emigration model described in Supporting Information 1, and to analyse it in JAGS and in unmarked. In Supporting Information 2, we describe the marginal or integrated likelihood of the new model, which is the one maximized in unmarked.

2.2 | Simulations

We conducted two simulation studies to assess the performance of our new model under a frequentist perspective and to compare its performance with that of two related, existing binomial mixture models.

In Simulation 1, we aimed at assessing the statistical properties of the new model for single-visit data under a wide range of scenarios. Thus, we generated species-level TTD data for different values of four factors: sample size (i.e. number of sites), expected abundance, per-individual detection rate (r) and number of repeat visits. We use $Tmax = 1$ in this case so that the mean detection rates (r) can be interpreted as ratio of $Tmax$. We chose a fully factorial design in our simulation, where we varied the number of sites from 50 to 500 with increments of 50, the expected mean abundance over the values 0.5, 1, 2 and 5, and per-individual detection probability p (the chance to detect an individual before $Tmax$) over the values 0.3, 0.5, 0.7, 0.9. Under the assumption of an exponential distribution for TTD, detection rate r as a function of p is given by:

$$-\frac{\log(1-p)}{Tmax}. \qquad (8)$$

At $Tmax = 1$, the values of p chosen in our simulation translate into detection rates r between 0.36 (for $p = 0.3$) and 2.3 (for $p = 0.9$). We simulated data for sites being visited once, two or three times. For each combination of simulation parameter settings, we simulated and analysed 1,000 datasets (total of 480,000 datasets simulated and analysed) and saved the estimates of expected abundance. We visualize the results by plotting bias, and, as a measure of accuracy, the root mean squared error (RMSE) of the abundance estimates.

In Simulation 2, we compare the performance of our model with that of the model of Royle and Nichols (2003) that uses as input detection/non-detection data, and with the classical binomial mixture model of Royle (2004), which uses counts as its input. In contrast to our model, these are only identifiable when at least some sites are visited more than once (Kéry & Royle, 2016; Knape & Korner-Nievergelt, 2015: section 6.2). Thus we chose two visits throughout and varied abundance, detection (p) and the number of sites as in

Simulation 1. We simulated and analysed 1,000 triplicates of datasets for each combination of parameter settings and generated all three types of datasets (TTD, detection/non-detection and counts) from the same original data as follows:

Based on the simulated abundance per site N_s and the chosen value of detection probability p, we generated individual-level TTD data for each site and visit as draws from an exponential distribution. From these most highly resolved, individual-level TTD data (or TTD(I), with 'I' for individual), we derived all three data types by a form of summary or aggregation. First, detection/non-detection data per site and visit as the input for the Royle-Nichols model were determined to be 1 if TTD(I) ≤ Tmax for at least one individual and otherwise 0. Second, as the input for the classical binomial mixture model, we used the number of individuals per site and survey where TTD(I) ≤ Tmax. Third, as input for our model, we used the shortest time to first detection of any of the individuals that were detected per combination of site and visit. We simulated data in R (R Core Team, 2019) and analysed them with unmarked (Fiske & Chandler, 2011) using the functions occuRN (model of Royle & Nichols, 2003), pcount (binomial mixture model) and the new function nmixTTD (model described here). Code to conduct Simulations 1 and 2 under a wide range of parameter settings, and to plot the results can be found in the archive (Strebel et al., 2021).

2.3 | Case study

As an illustration of our model, we analysed data from an ongoing study that examines songbird response to forest management in the Pocono Mountains of northeast Pennsylvania, USA. Forests in this region are temperate deciduous forests, predominantly represented by the broadleaf dry-oak heath community type (Fike, 1999). We surveyed avian populations during the breeding season across four distinct forest sites ranging in size from 10.93 to 29.94 km^2. All sites contained a mosaic of forest stand age classes ranging from 0 (i.e. freshly harvested) to 120 years post-harvest. We conducted 100-m radius point counts using a species-level TTD protocol at a total of 385 unique survey locations across all sites. All survey locations were placed a minimum of 250-m apart to avoid double-counting individuals. Each site was visited two times between 15 May 2019 and 15 June 2019. Surveys were conducted by a single observer between 30 min before sunrise and 4 hr after sunrise. Technicians surveyed each site for 10 min and recorded the time to first detection for each species in 1 min bins. Subsequently, the total number of detected individuals was tallied.

To compare the results from our new model with those obtained by the existing approaches, we estimated abundance and detection probability for eight forest passerines, including rare species (i.e. observed proportion of occupied sites <25%; white-breasted nuthatch *Sitta carolinensis*, tufted titmouse *Baeolophus bicolor*, wood thrush *Hylocichla mustelina*, chipping sparrow *Spizella passerina*, golden-winged warbler *Vermivora chrysoptera*) and common species (i.e. with observed occupancy >40%;

ovenbird *Seiurus aurocapilla*, red-eyed vireo *Vireo olivaceus*, common yellowthroat *Geothlypis trichas*). While six of the eight species included were neotropical migrants, we included two resident species, as for these the number of individuals present over both visits most likely was constant, what is not essentially the case for migrants. We fitted intercept-only models in JAGS using the R package jagsUI (Kellner, 2015). For all eight species, we compared abundance estimates for (a) count-based binomial mixture models using two visits, (b) detection/non-detection-based binomial mixture (or RN) models using two visits and (c) three versions of the new TTD-based approach (the multi-visit version, and the single-visit version for each visit individually). All TTD-based versions used the discrete time bin variation of our model (Equations 5–7).
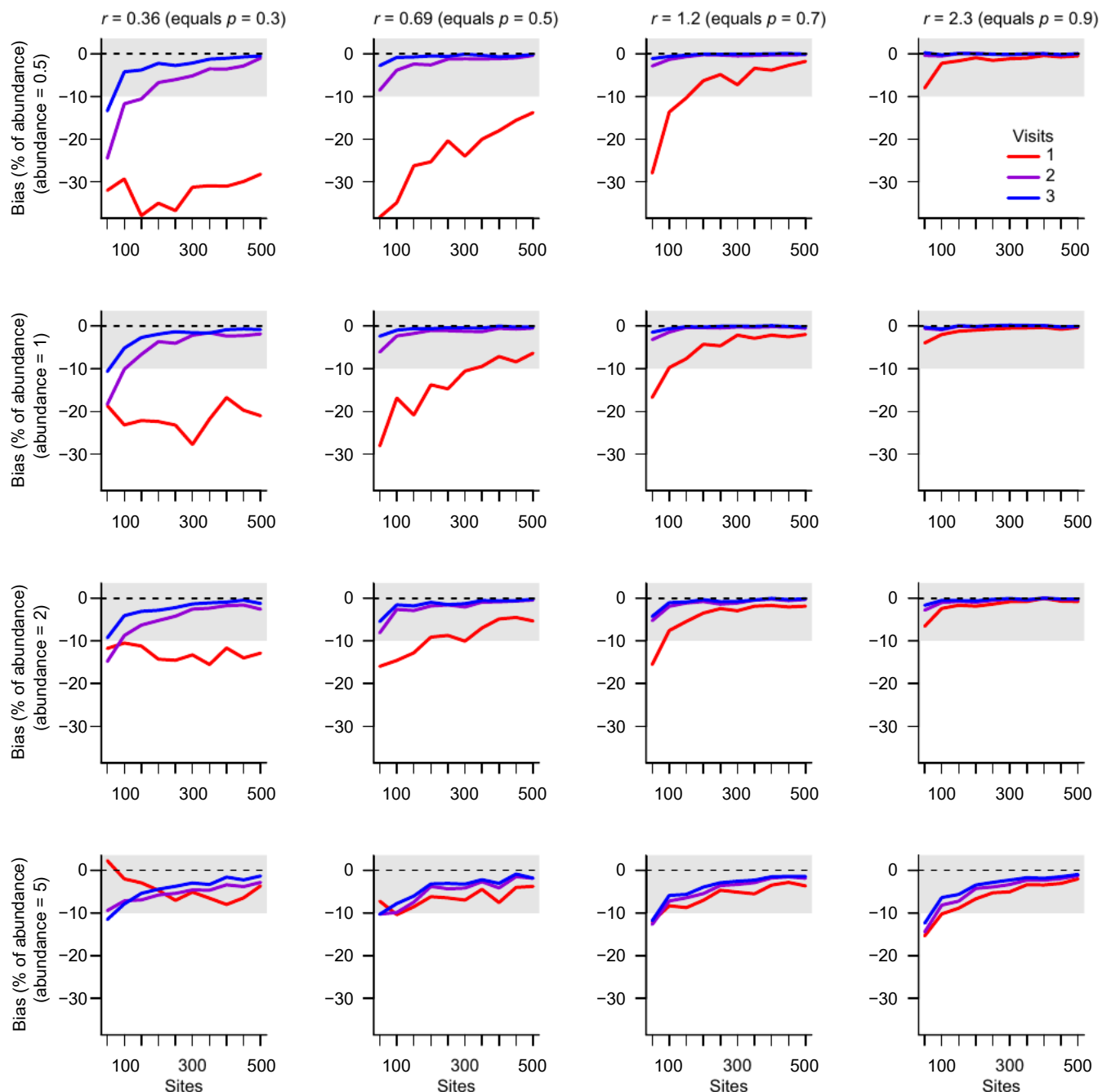
3 | RESULTS

3.1 | Simulations

3.1.1 | Simulation 1

Simulation 1 revealed what we consider adequate performance of our model with two or more visits under the following conditions (see Figure 1): Bias was less than −10% (threshold of |10%| chosen for illustrative purpose) for all parameter combinations as long as individual detection probability p was ≥0.5. When the number of sites was ≥100, bias was less than −10% also when p was 0.3. Under the single-visit protocol, performance was reduced and bias of the estimates was less than −10% of simulated abundance only under the following conditions: when p was 0.9 and the number of sites was ≥100; when p was 0.7, the number of sites was ≥100 and simulated abundance was ≥1; when p was 0.5 and simulated abundance was 5 (for all settings of sample size in terms of number of sites), or simulated abundance was 2 and number of sites was ≥200, or simulated abundance was 1 and number of sites was ≥300; and when p was 0.3 and simulated abundance was 5 (for all settings of sample size). Additional simulations with p set to 0.1 showed negative bias under the multi-visit protocol and partially positive bias under the single-visit protocol (Strebel et al. 2021).

Under the multi-visit protocol with $p = 0.9$ or $p = 0.7$, RMSE (Figure 2) was below ~20% (threshold chosen for illustrative purpose) when simulated abundance was between 0.5 and 2 (for all settings of sample size) and when abundance was 5 and number of sites was ≥250. When p was 0.5, under the multi-visit protocol, RMSE was below 20% when sample size was high, mainly 200 sites or above. When p was 0.3, RMSE was below 20% only when the number of visits was 3 and sample size was ≥200 (for abundance between 0.5 and 2) or sample size was ≥350 (for abundance = 5).

Under the single-visit protocol, RMSE was below 20% of simulated abundance when p was 0.9, number of sites was ≥100 and
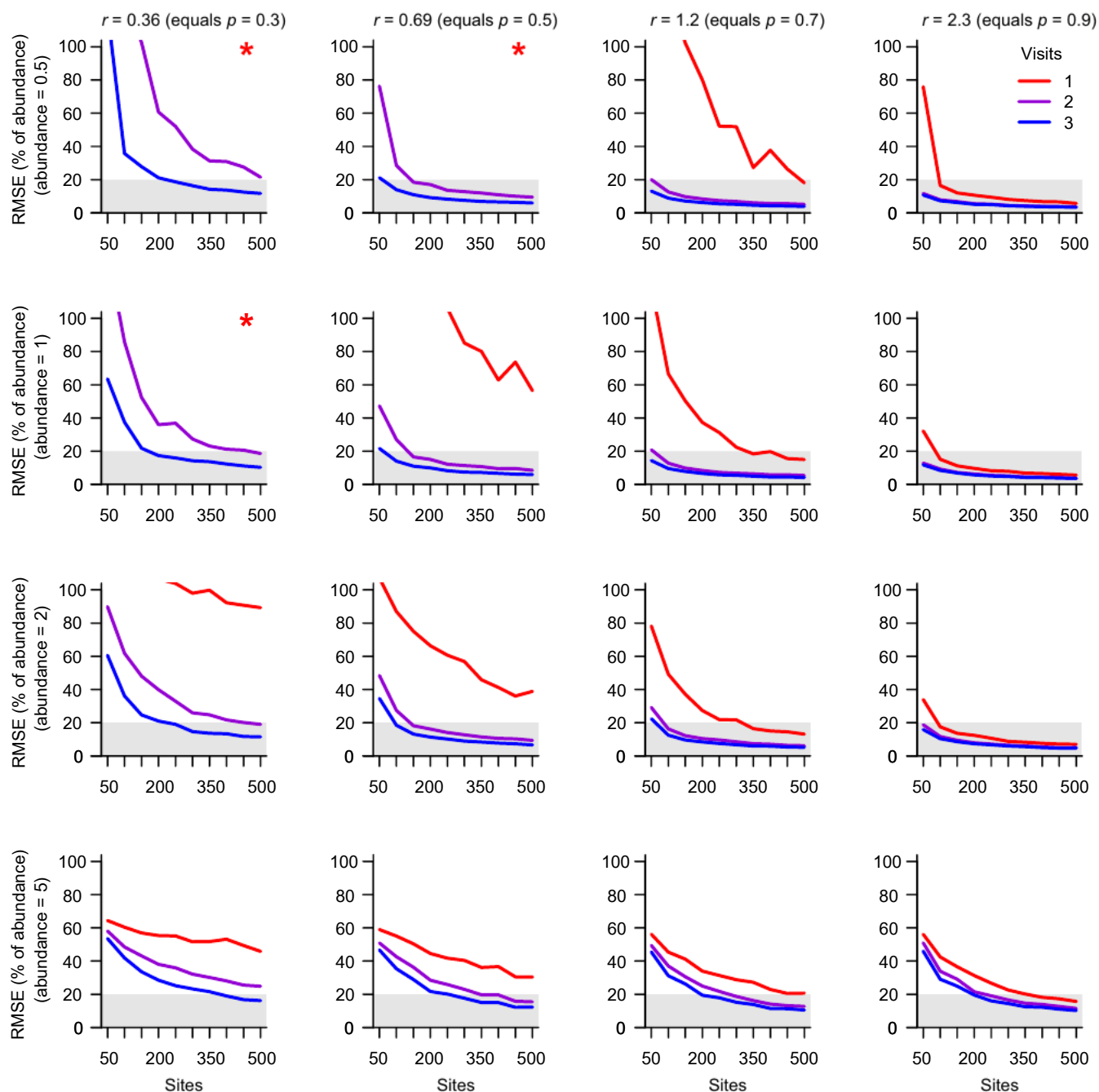
FIGURE 1 Results from Simulation 1, showing relative bias of estimated abundance (as a percentage of simulated abundance) under different settings of sample size (number of sites and number of replicated visits), simulated abundance and detection rate r with $Tmax = 1$ in a TTD N-mixture model. Grey shading: Bias ≤|10%| of simulated abundance. For each design point, 1,000 datasets were simulated and analysed

simulated abundance was between 0.5 and 2. When simulated abundance was 5, RMSE mostly exceeded 20% of simulated abundance. When p was 0.7, RMSE was below ~20% when simulated abundance was 1 or 2 and number of sites was ≥350. For lower values of p, RMSE exceeded 20% under the parameter settings chosen.

Simulation 1 suggests that individual detection probability p should be at least around 0.7 and sample size should be in the hundreds of sites to estimate abundance reasonably accurately from single-visit data using our model. At $p = 0.9$, the estimates are more accurate and less biased. Increasing the number of sites also increases accuracy and reduces bias. However, increasing the number of study sites particularly improves the accuracy of the estimates when mean abundance is below 5.

Visiting sites two times instead of once leads to an increase in accuracy and a decrease in bias of the estimates, particularly when abundance is below 5. Visiting plots two times but reducing the number of sites might thus often pay off. In absolute terms, the increase

FIGURE 2 Results from Simulation 1, showing the accuracy (root mean square error, RMSE, expressed as a percentage of simulated abundance) of estimated abundance under different settings for sample size (number of sites and number of replicated visits), simulated abundance and detection rate r, with $Tmax = 1$, in a TTD N-mixture model. Grey shading: RMSE ≤ 20% of simulated abundance. For each design point, 1,000 datasets were simulated and analysed. To enhance readability, we cropped y-axes at 100. *RMSE values for the corresponding number of visits always >100% of simulated abundance

in accuracy from one to two visits is mostly bigger than the increase from two to three visits.

3.1.2 | Simulation 2

Simulation 2 shows that the accuracy of the estimates under a TTD N-mixture model with two visits is almost identical to that of

a Royle-Nichols model fit to detection/non-detection data when simulated mean abundance is ≤1 (Figure 3). This is also the case when simulated abundance is 2; however, accuracy of the estimates from the TTD N-mixture model tends to be slightly better under low sample size (50 sites) and a per-individual detection probability p of 0.5 or 0.7. When simulated abundance is 5, the estimates of the TTD N-mixture model are more accurate than those of the Royle-Nichols model. Accuracy of the estimates of the binomial
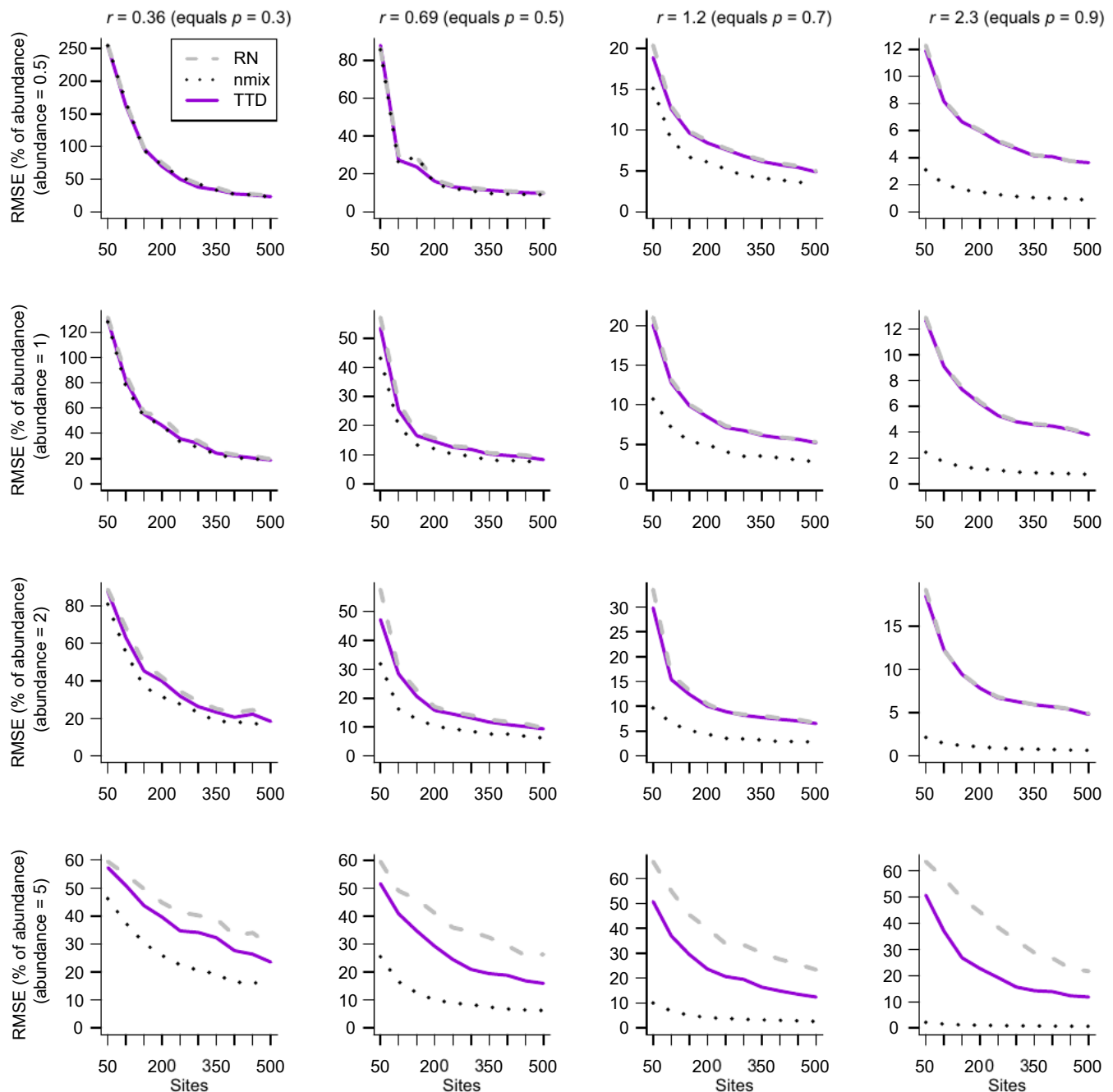
FIGURE 3 Results from Simulation 2, showing the accuracy (root mean square error, RMSE, expressed as a percentage of simulated abundance) of estimated abundance under different simulation settings. Data were simulated for two visits per site and analysed with a binomial mixture model (nmix), a Royle-Nichols Model (RN) and with the TTD N-mixture model (TTD). We simulated and analysed 1,000 datasets for each design point. Note different scales of *y*-axes

mixture model fit to count data is either similar or better compared to the Royle-Nichols and the TTD N-mixture model. Relative accuracy of the estimates of the binomial mixture model increases with higher abundance or detection probability. At a high *p* of 0.9, the estimates of the binomial mixture model were more accurate than those of the other models under all of the chosen settings for abundance and number of sites. When *p* is 0.5, the estimates of the binomial mixture model were substantially more accurate with a simulated abundance of 5, slightly more accurate with a simulated

abundance of 2, but accuracy was similar when simulated abundance was below 2.

3.2 | Case study

Models considering data from both visits generally yielded higher abundance estimates than the single-visit TTD analyses. This finding was consistent over six of eight forest bird species analysed. For
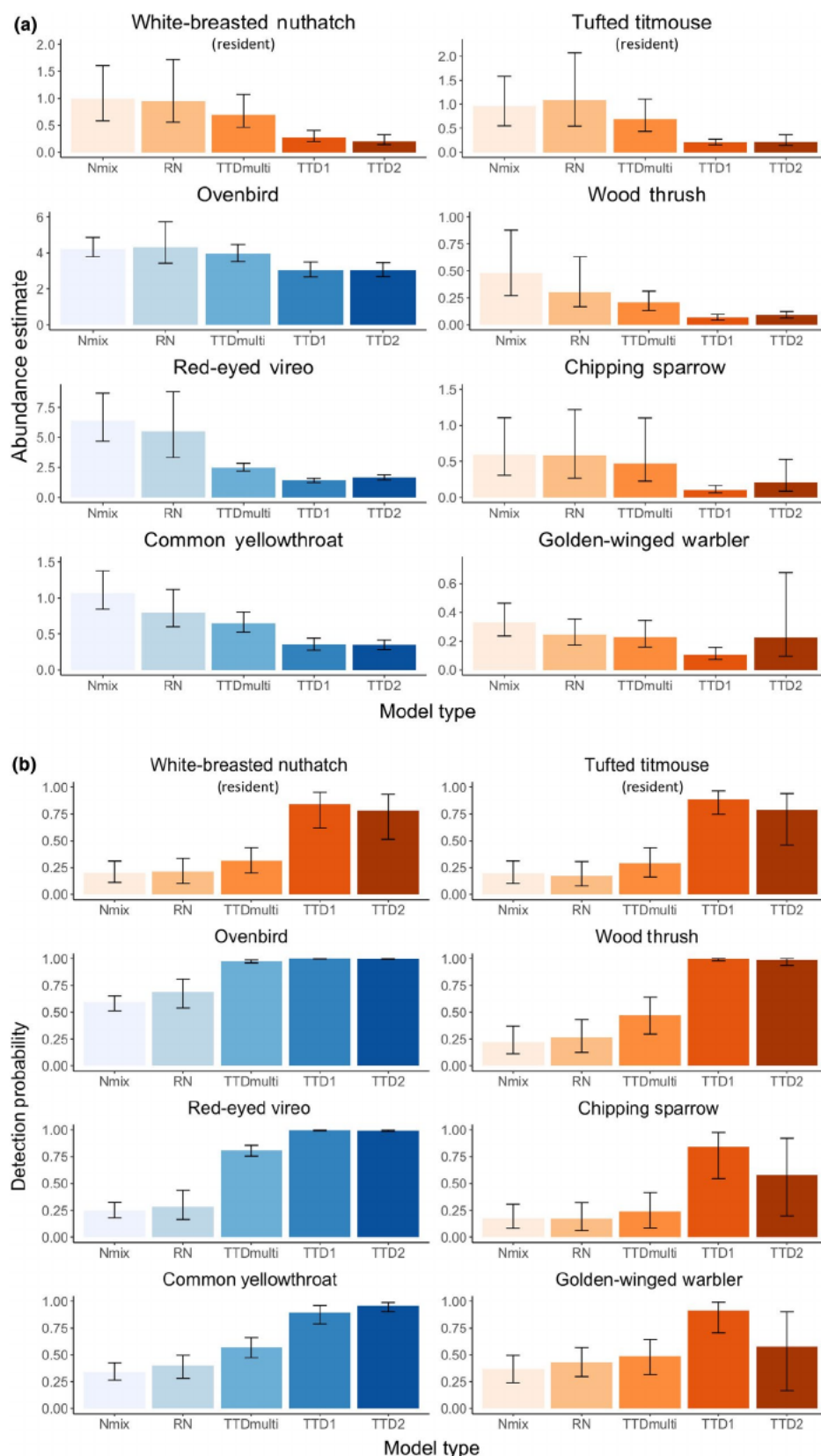
FIGURE 4 Estimates of abundance (Figure 4a) and detection probability over a 10-min session (Figure 4b) for eight forest-dwelling passerines representative of two classes of migratory behaviour (migrant and resident) compared between traditional multi-visit binomial mixture models (nmix, RN) and our new model using multiple visits (TTDmulti), and each visit separately (TTD1, TTD2). Species with orange graphs were rare (<25% observed occupancy) and species with blue graphs were common (>40% observed occupancy). Error bars represent 95% confidence intervals

chipping sparrow (rare; observed occupancy < 25%), the double-visit approaches estimated higher abundance, but confidence intervals overlapped with the single-visit approach using data from visit 2. For golden-winged warbler (rare), the estimate from the single-visit approach using data from visit 2 was similar to the estimates from the double-visit approaches (Figure 4). Our new model, when fit using both visits, generally yielded abundance estimates that were more similar to those of traditional multi-visit models as opposed to our model fit using either of the single visits alone. Specifically, confidence intervals for our model using both visits overlapped those of the traditional double-visit models in all but one common (observed occupancy > 40%) species, the red-eyed vireo.

Estimated detection probability was lowest for the traditional multi-visit methods (species-specific averages ranged from 0.18 to 0.53), and highest for the single-visit TTD approaches (0.53 to 0.99), again with overlapping confidence intervals for chipping sparrow and golden-winged warbler. When compared to traditional double-visit models, the double-visit version of our model tended to produce higher estimates of detection probability for common species (i.e. observed occupancy > 40%), but similar estimates for rare species (i.e. observed occupancy < 25%). Double-visit models typically had larger uncertainty than did our single-visit models. However, single-visit TTD models for very rare species (golden-winged warbler with observed occupancy = 14% and chipping sparrow with observed occupancy = 14%) had considerable error. Based on data from either visit 1 or visit 2, the estimates of our new TTD approach were very similar between both time periods (visit 1 and visit 2) for six of eight species, with associated 95% confidence intervals overlapping in all eight species.

4 | DISCUSSION

Quantifying abundance, distribution and population trends of animal and plant species is a pivotal task for ecologists and wildlife managers. Time and funding limitations restrict the number of sites that can be surveyed, and this is further exacerbated by the need for repeated visits by most survey protocols that aim at correcting for imperfect detection for estimating abundance. Hence, analytical methods that provide reliable abundance estimates from inexpensive data are desirable, where inexpensive may refer to the protocol required during a visit or also to the number of visits.

We developed a binomial mixture model to estimate abundance from spatially replicated, species-level TTD data. The performance of our model was between the Royle-Nichols and the binomial mixture model, using data that are less expensive than count data required for traditional binomial mixture models and hardly more expensive than detection/non-detections required for the Royle-Nichols model. Additionally, our model enables estimation of abundance even from single-visit data, albeit in this case performance found in the simulation was much reduced compared to the multi-visit case. Distance sampling (Buckland et al., 2001, 2004) and the analysis of TTD data are the primary two approaches that allow correcting for

imperfect detection based on single-visit data. Distance sampling is powerful and widely used, but requires (among other things) accurate distance measurements, which can be hard to get especially for surveys that are by ear mostly, as is usually the case in forests (Nichols et al., 2009). In addition, the assumption of perfect detection at distance zero may often not hold when a bird does not sing (Baechler & Liechti, 2007).

These assumptions are not required in the framework of TTD analyses; thus data collection is simpler and can also be done by novel datalogging methods like camera traps and autonomous recording units (ARUs; Darras et al., 2016; Shonfield & Bayne, 2017) that produce huge amounts of data naturally amenable to TTD modelling. Given its advantages compared to other approaches for surveying species occurrence, the concept of collecting and analysing TTD data has long been underutilized. The additional information content of TTD data, compared to detection/non-detection data, translates into more accurate parameter estimates (Halstead et al., 2018). However, our simulations illustrate that it might still pay off to visit sites more than once to improve accuracy of the estimates based on TTD data, or to invest the time in counting individuals to analyse the data with a traditional binomial mixture model (Royle, 2004), particularly for abundant species that are easy to detect. However, counting individuals of mobile, acoustically perceived species (e.g. songbirds) is error-prone (Simons et al., 2009), an issue that is obsolete when collecting species-level TTD data. Thus our approach still provides an attractive and efficient alternative. Additionally, it can naturally serve as part of an 'integrated model', where multiple datasets collected under different protocols are linked in a hierarchical model with a shared process (Kéry & Royle, 2016: chapter 10; Pacifici et al., 2017; Miller et al., 2019).

An extension of the multiple-visit version of our model allows quantifying random temporary emigration at sites (or rather its converse, availability probability; Supporting Information 1). In traditional binomial mixture models, this parameter can only be estimated separately from detection probability if covariates are available that explain variation in each of the two components temporary emigration and detection probability (Nichols et al., 2009; O'Donnell et al., 2015), or if replicated surveys take place at two temporal scales (Chandler et al., 2011). In contrast, our model allows estimating temporary emigration without such additional information.

In the case study, we found that traditional multiple-visit approaches resulted in similar or higher estimates of abundance and, correspondingly, in similar or lower estimates of detection probability compared to our new multi-visit method. Using our approach to analyse data from a single visit resulted in lower abundance estimates compared to the multi-visit methods, though estimates were generally consistent between first and second visits. Single-visit estimates, thus, appear to provide a reliable index of differences in abundance across space, time and covariate values.

There are several potential reasons for the discrepancies of our case study results between the traditional multi-visit models and the TTD single- and double-visit models. In multi-visit methods, the estimated detection probability represents the product

of detection probability of an available individual and of availability probability (Chandler et al., 2011; O'Donnell et al., 2015). If temporary emigration is random, these methods will estimate the superpopulation size, that is, the number of individuals present during the study period. If there is temporary emigration, the estimated TTD (time until an available individual is detected) is biased high, because the distinction between the cases 'temporary not there' and 'there but not detected before T_{max}' is not possible. In contrast, the abundance estimate resulting from analysing single-visit data represents the number of individuals available during a particular survey only and the resulting estimate for TTD is unbiased. Likewise, Henry et al. (2020) found much lower occupancy estimates and much higher detection probability estimates when analysing single-visit TTD data compared to analysing multiple-visit data that were collected over a study period of 8 months. For binomial mixture models, Duarte et al. (2018) showed that estimated abundance is biased high when true abundance between visits changes, which is quite certain when the study period is longer than the breeding period. We assume that in our case abundance between visits remained rather stable, as repeated visits were conducted within a relatively short time interval of 2 weeks during the breeding period, and because abundance estimated from single visits was similar in six of eight species.

If the assumptions of the multiple-visit models are met, one would expect similar estimates of abundance among them, and in fact except for the case of the very abundant red-eyed vireo, estimates of the Royle-Nichols model and our double-visit model were statistically similar. Yet, the binomial mixture model estimated a greater abundance than the double-visit version of our model for many species. We suspect that due to the large radius of the point counts and the low visibility in the forests of our study area, multiple counting of the same individual during one point count may have biased high the estimates under the binomial mixture model. Human error related to the counting of individual birds in a forested setting can be considerable (Simons et al., 2009). This could explain why the presence–absence-based method (Royle-Nichols) similarly produced slightly lower abundance estimates than the count-based method (binomial mixture), albeit with less precision.

As our simulations demonstrated, however, traditional binomial mixture models may perform better than Royle-Nichols or TTD models, perhaps because models using detection/non-detection data become unreliable as occupancy nears 1.0. Thus, in the case of the red-eyed vireo with a mean abundance of around 5 per plot estimated by traditional methods, the TTD-based method may have been less reliable.

Two of the eight species experienced lower detection probability, and less precise abundance estimates during the second visit (chipping sparrow and golden-winged warbler; Figure 4). While it is not exactly clear what lead to this change, we suspect that availability may have changed between the first and second visit, possibly due to behavioural changes between visits 1 and 2, from breeding and guarding territories to searching for food and provisioning young. The decrease in detection probability that we observed for these two species between visits 1 and visit 2 agrees with the decrease in singing activity during breeding season often described in the literature (Keast, 1994).

Abundance estimates from binomial mixture models are sensitive to unmodelled heterogeneity in detection probability (Duarte et al., 2018). Similarly, analysing TTD data is sensitive to unmodelled heterogeneity in the detection rate among surveys (Medina-Romero et al., 2019). Thus, known factors influencing detection rate should be accounted for as covariates. Also, correcting for an increase or decrease in detection rate during the survey (e.g. habituation of the study species, or observer losing concentration) is straightforward by estimating detection rate using the Weibull instead of the exponential distribution (Bischof et al., 2014; example code in the mini-tutorial in the archive, Strebel et al., 2021). Another way to deal with non-exponential detection rates is to implement an exponential log-normal mixture by adding a normal residual to the linear predictor for detection rate (section 14.1 in Kéry, 2010), assuming that songs are overdispersed Poisson log-normal. Medina-Romero et al. (2019) found that unmodelled heterogeneity in the detection rate leads to an overestimation of detection rate and to an underestimation of occupancy probability. This is a reflection of Royle (2006), where occupancy estimates were found to be biased low by unmodelled detection heterogeneity at the site level. However, one major source of detection heterogeneity, variation in abundance among sites, was ignored in most of the analyses conducted by Medina-Romero et al. (2019), but is naturally corrected for in our model. Thus, if abundance of the study species is likely to be >1 at least on some study sites, the model presented here should be preferred over a traditional TTD occupancy model.

In summary, we think that our approach to estimate abundance from TTD data using a binomial mixture model is valuable for the analysis of species-level TTD data when the aim of a study is estimating abundance rather than just occupancy. Species-level TTD data can be extracted from ARU data streams in a reasonably parsimonious manner. Our new model is thus a natural candidate for such data types, the amount of which is expected to greatly increase in the near future.

AUTHORS' CONTRIBUTIONS

J.C. and N.S. independently conceived of the possibility to estimate abundance from TTD data; N.S. implemented the model in JAGS, and K.F.K. developed its marginal likelihood and implemented it in unmarked; C.J.F., J.L.L. and J.C. contributed the case study. All the authors together developed the simulation studies, and contributed to the writing of the manuscript, the first draft of which was written by N.S.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The following documents are archived at http://doi.org/10.5281/ze-nodo.4549508 (Strebel et al., 2021): R code to conduct Simulations 1 and 2 (plus the resulting figures, with a wider range of parameter settings compared to the manuscript); data and associated R code used for the case study; a mini-tutorial that contains commented code to simulate data under different distributions and analyse it with JAGS and unmarked.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.