

Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models

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Abstract

1. Dynamic occupancy models are popular for estimating dynamic distribution rates (colonization and extinction) from repeated presence/absence surveys of unmarked animals. This approach assumes closure among repeated samples within primary periods, allowing estimation of dynamic rates between these periods. However, the impact of temporary emigration (TE; reversible changes in sampling availability) on dynamic rate estimates has not been tested.
2. Using simulated data, we investigated the degree to which TE could mislead researchers interested in quantifying dynamics. We then compared results from three avian point count datasets to evaluate the likelihood that TE confounds estimates of dynamics for 19 species under a popular sampling protocol.
3. Simulated experiments indicated that when secondary periods were open to TE, presence of dynamics was correctly identified $\geq 95.1\%$ of the time, and dynamic rate estimates were accurate. However, dynamic rate estimates were biased when secondary periods were closed to TE. In empirical datasets, dynamic occupancy models had greater support than closed models for all species when secondary sampling periods occurred in immediate succession (i.e. 3 samples within 10 min); however, our results suggest that this is because dynamic estimates were heavily influenced by TE. When counts within a primary period were separated by 24–48 hr, we found evidence of dynamics for less than half of these species. We recommend an alternative sampling approach that allows accurate estimation of dynamic rates when TE is of no interest, and introduce a novel model for estimating both processes simultaneously in rare cases where they are both of biological interest.
4. Concern for violating the occupancy modelling closure assumption has led to widespread recommendations that samples within primary periods be conducted extremely close in time. However, this may not be the best approach when interest is in quantifying dynamic rates. While dynamic occupancy models provide estimates of “colonization” and “extinction,” these values do not inherently represent dynamics unless TE has been explicitly modelled or accounted for with sampling design. Naiveté to this fact can result in incorrect conclusions about biological processes.

KEYWORDS

closure assumption, colonization, detection probability, dynamic occupancy models, extinction, metapopulation, Pollock's robust design, temporary emigration

1 | INTRODUCTION

Many ecological studies rely on presence–absence surveys to identify species distribution patterns and how they vary in space and time. Failing to account for individuals that are present but undetected leads to underestimated distributions, biased estimates of colonization and extinction probabilities and poor parameterization of resource-use models (e.g. Gu & Swihart, 2004; Kéry, Royle, & Schmid, 2005; MacKenzie, 2005; Moilanen, 2002; Tyre et al., 2003). This realization led to development of a landmark occupancy modelling framework (MacKenzie et al., 2002; Tyre et al., 2003), wherein occupancy and detection probability can be simultaneously estimated from repeated samples of sites that are assumed closed to changes in occupancy. Since its inception, there has been an explosion in use and development of these models to meet numerous estimation needs (Bailey, MacKenzie, & Nichols, 2014).

Because the *closure assumption* is one of the most important and criticized requirements of occupancy models, much effort has been dedicated to identifying and modelling closure violations. In the strictest interpretation of closure, it is assumed that presence of the species within spatially discrete sampling units does not change between repeated sampling occasions, resulting in an instantaneous “snapshot” of a species’ distribution (Latif, Ellis, & Amundson, 2016; MacKenzie & Royle, 2005). Several recent studies have demonstrated that common sampling protocols for birds (McClure & Hill, 2012; Rota, Fletcher, Dorazio, & Betts, 2009), salamanders (Otto, Bailey, & Roloff, 2013), anurans (Kendall, Hines, Nichols, & Grant, 2013) and insects (Bried & Pellet, 2012) violate the closure assumption, leading some to consider abandoning the method altogether (Hayes & Monfils, 2015; Hutto, 2016).

Under this strict interpretation, there are two processes that could cause closure violations, the first stemming from temporary changes in sampling availability. A site may be considered *used* (even if not occupied at some instant) if one or more individuals have non-zero probability of being exposed to sampling (Latif et al., 2016; MacKenzie

& Royle, 2005; Nichols et al., 2008). *Temporary emigration* (TE) occurs when all individuals using the site are unavailable for sampling at an instant, and violates the closure assumption when changes in availability occur between sampling visits. Often this arises from a mismatch between the spatial scales of sampling units and animal territories (Chandler, Royle, & King, 2011; Efford & Dawson, 2012; Nichols, Thomas, & Conn, 2009). For example, if spatially discrete avian point count stations are considered sites, individual territories may only partly overlap the sample space resulting in species presence during only some sampling occasions (Nichols et al., 2009; Figure 1). Similar spatial mismatches can result from any stationary sampling of mobile organisms, such as camera, net or hair snare trapping (Chandler et al., 2011; Efford & Dawson, 2012; Kendall, Nichols, & Hines, 1997). However, TE can also arise when at least one individual is spatially present, but otherwise unavailable for detection (Kendall et al., 1997; Kéry & Royle, 2016; O’Donnell, Thompson, & Semlitsch, 2015), for example, due to vertical migration into burrows or below the water surface (O’Donnell et al., 2015). Critically, in each of these scenarios, TE is a reversible process that results in changes to the occupancy state, but not site use.

Several methods have been proposed for accommodating availability changes in occupancy models. Researchers have made use of multiple detection methods or sampling time scales to simultaneously estimate occupancy and use (Mordecai, Mattsson, Tzilkowski, & Cooper, 2011; Nichols et al., 2008). When site occupancy changes in a non-Markovian way between samples, others recommend simply relaxing the closure assumption and re-interpreting the occupancy parameter as probability of site use (Latif et al., 2016; MacKenzie, Bailey, & Nichols, 2004; MacKenzie & Royle, 2005). In these cases, the detection parameter is also re-interpreted as the product of the probability of availability (p_a ; the complement of the TE rate) and probability of detection given availability (p_d ; Kendall, 1999; Nichols et al., 2009). Yet because the number of used sites will always be greater than or equal to the number of occupied sites, site use rates are often considered inferior estimates of a species’ distribution (Latif et al., 2016;

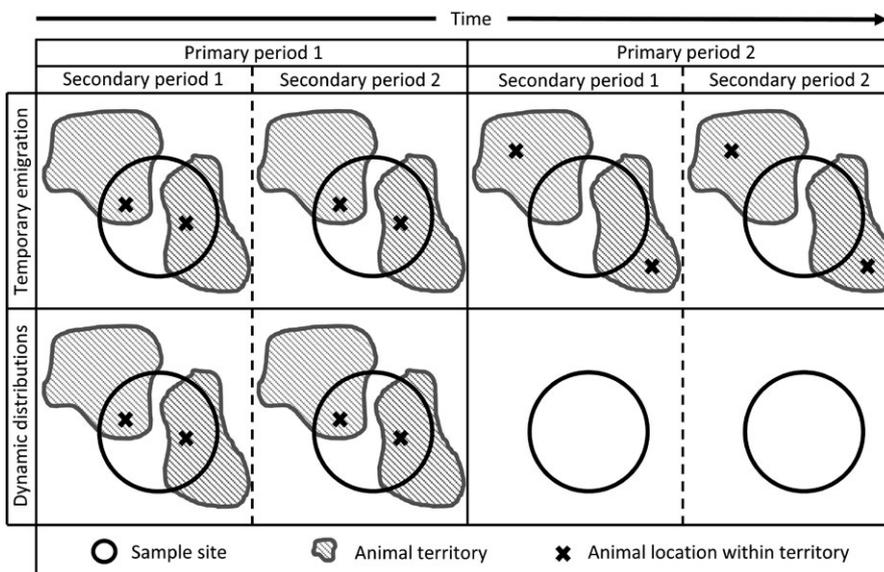


FIGURE 1 When practitioners of dynamic occupancy models ensure complete site closure within primary periods, changes in sampling availability stemming from temporary emigration may not be distinguishable from distributional changes in territory locations. In the two scenarios depicted, there is some probability of detecting the species during both samples in the first primary period, but no possibility of detecting it during either sample in the second. Yet only in the bottom scenario does the actual distribution of the species change

MacKenzie, 2005; MacKenzie & Royle, 2005). Thus, others recommend conducting repeated samples simultaneously, or over extremely short time intervals, creating estimates of occupancy not confounded by TE (Kendall et al., 2013; MacKenzie, 2005; MacKenzie & Royle, 2005; Rota et al., 2009).

Distribution dynamics can also result in closure violations. We define *distribution dynamics* (henceforth, *dynamics*) as distributional shifts resulting from dispersal or other demographic processes (i.e. births, deaths) that lead to unused sites becoming used, or vice versa. In occupancy models, dynamics can also be accommodated by reducing the interval between sampling periods, or acknowledged by altering the interpretation of occupancy. Alternatively, MacKenzie, Nichols, Hines, Knutson, and Franklin (2003) developed a dynamic occupancy model that explicitly estimates dynamic rates by utilizing Pollock's (1982) robust sampling design. This model assumes site closure over repeated secondary sampling periods nested within primary periods, between which dynamic rates are modelled as colonization and extinction. Since development, dynamic occupancy models have been used to test the predictions of island biogeography and metapopulation theory (Ferraz et al., 2007; Pellet, Fleishman, Dobkin, Gander, & Murphy, 2007), validate metapopulation models (Ozgul, Armitage, Blumstein, Vanvuren, & Oli, 2006), identify source and sink populations (Fisher, Volpe, & Fisher, 2014; Kerbiriou, Le Viol, Bonnet, & Robert, 2012; Peterman, Rittenhouse, Earl, & Semlitsch, 2013), estimate population growth rates (Kerbiriou et al., 2012; Kéry et al., 2010) and model biological invasions (Fisher et al., 2014; Yackulic et al., 2012).

Inherent in each of these applications of the dynamic occupancy model is an implicit assumption that the rates modelled between primary periods represent shifting distributions rather than temporary changes in sampling availability. Yet there is nothing explicit in the model itself that guarantees this. Combining a dynamic occupancy model with a sampling window that ensures complete site closure within primary periods means that both dynamics and TE only occur between primary periods. Therefore, both processes may influence colonization and extinction estimates (Figure 1). Numerous recent studies have taken this type of sampling approach. For instance, Otto et al. (2013) estimated salamander extinction rates from secondary periods occurring within 24 hr. In more extreme cases, estimates of amphibian (Gould et al., 2012) and avian (Betts, Rodenhouse, Sillett, Doran, & Holmes, 2008; McClure & Hill, 2012; Otto & Roloff, 2012; Rota et al., 2009) dynamic rates were generated from secondary periods occurring within minutes of one another. In these scenarios, dynamics may not be distinguishable from TE (Figure 1); yet tests comparing static and dynamic occupancy models, and the colonization and extinction estimates generated by dynamic models, are frequently assumed to represent distribution dynamics (Betts et al., 2008; Gould et al., 2012; McClure & Hill, 2012; Otto & Roloff, 2012; Rota et al., 2009). While some authors have acknowledged this potential confounding (Betts et al., 2008; Rota et al., 2009), there has been no evaluation of how TE might impact model results. Here we use simulated and empirical data to test the hypothesis that failing to account for TE via sampling design results in misleading comparisons of static and dynamic occupancy models and biased estimates of distribution dynamics. We

then provide recommendations for unbiased sampling and modelling schemes for estimating dynamic rates of unmarked populations in the presence of TE.

2 | MATERIALS AND METHODS

2.1 | Simulated data

We simulated presence/absence datasets under two different robust-design sampling scenarios (Pollock, 1982), one where the strict closure assumption is met within primary periods (*occupancy* scenario) and one where primary periods were closed to dynamics, but availability changes could occur between secondary samples (*use* scenario). The *occupancy* scenario allowed us to evaluate how TE influences colonization and extinction estimates, while the *use* scenario allowed us to test whether a simple sampling alteration could improve those estimates. Our simulations explicitly assume that availability changes occur over finer time scales than dynamics, and that the researcher is interested in estimating dynamic rates, rather than changes in sampling availability.

Each simulated dataset contained 500 sites and nine sampling occasions, where three secondary samples were nested within each of three primary periods. We simulated initial site use from a Bernoulli distribution with probabilities of $\psi_0 = 0.3$ or 0.7 . We simulated dynamics as transitions in site use between primary sampling periods to represent distributional shifts. Transitions from used to unused were simulated from a Bernoulli distribution with probabilities of $\varepsilon_0 = 0.0, 0.2$ or 0.4 . Transitions from unused to used were simulated similarly with probabilities of $\gamma_0 = 0.0, 0.09, 0.17, 0.47$ or 0.93 , where γ_0 was calculated so the site use rate remained constant across primary periods. We use ψ_0 , ε_0 and γ_0 to distinguish probability of site use and probability of changes in site use from the occupancy (ψ), extinction (ε) and colonization (γ) notation used in dynamic occupancy models (MacKenzie et al., 2003).

Given a site was used, we simulated sampling availability from a Bernoulli distribution with probabilities of $p_a = .5$ or $.8$. In *occupancy* sampling scenarios, availability could only change every third visit, allowing instantaneous estimates of the species' distribution within primary periods. Thus, the occupancy state of a site could change between subsequent primary periods via changes in availability, even if the site was used during both. In the *use* scenarios, availability was simulated independently on each sampling occasion. Finally, given that the species was available for sampling, detection during each secondary period was simulated from a Bernoulli distribution with probabilities of $p_d = .5$ or $.8$. We generated 1,000 datasets for each combination of 24 parameter values under each sampling scenario using R (v. 3.1.2).

We fit static (MacKenzie et al., 2002) and dynamic (MacKenzie et al., 2003) occupancy models to each of the respective 24,000 datasets using the *unmarked* R package (v. 0.10-6; Fiske & Chandler, 2011). Static models assumed no occupancy changes between any visits and open models allowed distributions to change every third visit. Because multiple studies (e.g. McClure & Hill, 2012; Rota et al., 2009)

compare static and dynamic occupancy models to test for evidence of dynamics, we compared model pairs with a common approach (Dail & Madsen, 2011; Rota et al., 2009; Self & Liang, 1987). Static occupancy models are special cases of their dynamic counterparts where dynamic parameters are constrained to be zero. To test for dynamics, we calculated a test statistic as $T = -2\ln(\Lambda)$, where Λ is the ratio of the maximized likelihood for the static model to that of the dynamic model. Because the null hypothesis is that the dynamic parameters are on the boundaries of their parameter spaces, this test does not meet the likelihood ratio test regularity conditions. Instead, this test statistic asymptotically approaches a mixture χ_0^2 , χ_1^2 and χ_2^2 distributions with mixing proportions equal to $0.5-\delta$, 0.5 and δ , with δ calculated from the dynamic model's Hessian matrix (Dail & Madsen, 2011; Self & Liang, 1987). When δ could not be estimated (<1% of comparisons), it was fixed at 0.5 to minimize the probability of rejecting the null (static) model. We accepted a $p < .05$ as evidence for dynamic distributions.

For each parameter combination under each sampling scenario we calculated the percentage of correct models selected. Again, we assumed interest is in quantifying dynamics, so the dynamic model was deemed "incorrect" when the simulation parameters γ_0 and ε_0 equalled zero. We compared estimates of occupancy, colonization, extinction and detection with the simulation parameters, and specifically compared estimates of colonization and extinction with those used to simulate dynamics (γ_0 and ε_0). We estimated bias by subtracting the simulation parameter from each estimate and averaging these values over all 1,000 datasets. We calculated variance among the estimates themselves, and mean squared error as the sum of the variance and the squared bias. We disregarded parameter estimates from models with non-invertible Hessian matrices (<2% of fitted models). Full simulation and analysis code are provided in Appendix S1 in the Supporting Information.

2.2 | Dynamic, multi-scale occupancy model

When a researcher is interested in quantifying temporal dynamics in both use and occupancy, the simple design-based solution simulated above ("use" scenarios) would not be sufficient. At present, we are unaware of any models that explicitly estimate both TE and dynamic rates simultaneously. Thus, we developed one that relies on an extension of Pollock's robust design (Pollock, 1982) to include tertiary sampling periods closed to both TE and dynamics, and secondary periods closed only to dynamics. Note that sampling considerations for this model are nearly identical to those described in the use sampling scenario above. In both cases, all secondary samples within a primary period must be closed to dynamics, but open to changes in availability. Thus, this model provides no benefit for estimating dynamic rates. Instead, it imposes additional burden by requiring more frequent sampling within secondary periods to estimate "availability" and "detection given availability" separately, rather than estimating their product as a single parameter (Nichols et al., 2009; Schmidt, McIntyre, & MacCluskie, 2013). Use of this model is thus unnecessary in most cases, but we refer interested readers to Appendix S2 for full model development and testing.

2.3 | Empirical case study

2.3.1 | Field Sampling

In the summer of 2014, we established 193 point count stations (≥ 200 m apart) in the central hardwoods region of southern Indiana. We used a popular sampling protocol (e.g. Betts et al., 2008; McClure & Hill, 2012; Otto & Roloff, 2012; Rota et al., 2009) where trained observers conducted three 3:20 point counts during each of three 10-min site visits (9 total point counts). We recorded all birds within 50 m, and counts took place between sunrise and 10.00 hr from 16 June to 16 July in suitable weather conditions (i.e. no rain and minimal wind). For clarity, we will refer to 10-min site visits as *visits* and repeated 3:20 point counts within each visit as *intervals*. The first two visits to each station were conducted within two mornings of each other, and the third visit was conducted 15–19 (median 17) days after the first.

This sampling scheme was designed under three assumptions. First, because repeated intervals within a visit occurred over 10 min, it is reasonable to assume complete site closure within visits. Second, because survey sites were stationary (50 m radius circles), but birds are mobile, availability changes could occur between site visits due to individuals moving in and out of the sample space (Figure 1). Finally, dynamic rates should be approximately zero over the 24–48 hr period between our first and second site visits, but changes in site use may occur over the 19 days between the first and third visits (McClure & Hill, 2012; Rota et al., 2009). Using these assumptions, we constructed three unique presence/absence datasets from the point count data (Figure 2) and label them with the processes being modelled by dynamic occupancy model colonization and extinction parameters.

The first dataset treated the first and third visits as primary periods, and intervals as secondary periods (visit two ignored). Multiple researchers have compared static and dynamic occupancy models fit to data collected analogously, and concluded there was evidence for within-breeding season territorial changes in bird communities (e.g. Betts et al., 2008; McClure & Hill, 2012; Rota et al., 2009). Analysing this dataset allowed us to replicate such results. Under our assumptions, both dynamics and TE could only occur between primary periods, and we refer to this as the *confounded TE/dynamics* dataset.

The second dataset was similar to the first, except that the first and second visits were considered primary periods (visit three ignored). Under our assumptions, any closure violations detected could be explained primarily by changes in availability. Thus, analysing this dataset allowed us to evaluate the impacts of TE on tests of within-breeding season territorial shifts. We refer to this as the *isolated TE* dataset.

The final dataset combined all three visits and ignored the repeated intervals. We treated the first two visits as a single primary period containing two secondary periods. The third visit was a unique primary period containing only one secondary period. While the first two datasets were designed to generate estimates of instantaneous occupancy within primary periods (by assuring complete site closure), this dataset is designed to estimate site use within primary periods (by allowing availability changes between secondary samples). Thus, the

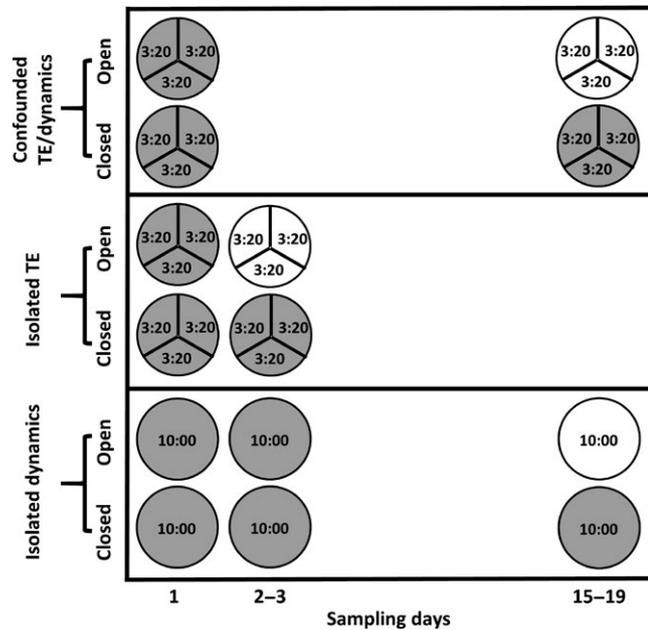


FIGURE 2 A schematic outlining the structure of the three occupancy datasets constructed from repeated point counts at 193 locations in southern Indiana in the summer of 2014. Circles represent 10-min site visits, some of which were split into 3:20 subintervals. Circles and circle parts shaded similarly were included in the same primary period. Datasets were designed to quantify either distribution dynamics, temporary emigration (TE) or both between primary periods. Time on the x-axis is not necessarily to scale

TE rate should be estimated with detection in the dynamic occupancy model (Nichols et al., 2009), and colonization/extinction estimates should only be influenced by distribution dynamics. We refer to this as the *isolated dynamics* dataset.

We limited analyses to the 19 species detected on >20% of sample sites (Table S1). Using the approach described earlier, we tested for distribution dynamics in each of these 57 datasets (three per species) by comparing static occupancy models that assumed site closure over all samples (MacKenzie et al., 2002) to dynamic occupancy models allowing colonization and extinction between primary periods (MacKenzie et al., 2003). In each model, time of day and observer were included as covariates for detection probability, but for simplicity, initial occupancy, colonization and extinction were modelled as constants. All analyses were conducted using the *unmarked* package (v. 0.10-6) in R (v. 3.1.2).

3 | RESULTS

3.1 | Simulated data

In the *use* sampling scenarios, site closure tests performed very well. Where distribution dynamics did not occur, the static occupancy models were appropriately selected $\geq 95.1\%$ of the time (Table 1), and when dynamics were present, the dynamic occupancy model was selected $\geq 97.2\%$ of the time (Table S2). In both cases, the estimates of initial occupancy approximated ψ_0 while detection estimates

approximated $p_a p_d$. Accordingly, dynamic parameter estimates were highly accurate and precise estimates of the dynamic rates.

When secondary sampling periods were closed to availability changes (*occupancy* scenarios), site closure tests and dynamic parameter estimates resulted in misleading conclusions about dynamic rates. Where dynamics were absent, the closed models were appropriately selected $\leq 1.3\%$ of the time (Table 1), and when dynamics were present, the dynamic model was selected 100% of the time (Table S2). In both cases, estimates of initial occupancy tended to approximate $\psi_0 p_a$ while the detection estimate approximated p_d . However, the dynamic occupancy models tended to produce biased estimates of γ_0 and ϵ_0 .

3.2 | Dynamic, multi-scale occupancy model

By augmenting the dynamic occupancy model to include tertiary sampling periods, we were able to estimate TE and dynamic rates simultaneously (Appendix S2). This extended model performed well under simulated sampling scenarios that involved three primary, three secondary and three tertiary periods (Table S2.1). However, dynamic rate estimates showed no accuracy improvements over those generated by combining *use* sampling with a dynamic occupancy model, as described earlier. Therefore, we chose not to pursue further testing.

3.3 | Empirical case study

Results from the analysis of our confounded TE/dynamics and isolated TE datasets were very similar. The null hypothesis (i.e. that closure could be assumed among site visits) was rejected for all 19 species using both datasets ($p < .02$; Table S1). That is, the dynamic occupancy models had greater support for all species even when the interval between primary sampling periods was limited to 24–48 hr. Estimates of extinction probability from the confounded TE/dynamics datasets tended to be greater than the estimates from the isolated TE datasets (Figure 3), as might be expected if multiple processes influenced the former but not the latter. However, estimates of detection, initial occupancy and colonization were similar between these models. Therefore, in most cases, the parameter estimates generated by dynamic models were extremely similar when primary periods were separated by 2 days vs. 17 days. This suggests that the colonization and extinction estimates were heavily influenced by TE when all secondary samples occurred within 10 min.

In contrast, we only found evidence for closure violations for nine species using the isolated dynamics datasets (Table S1). That is, for most species there was no evidence for dynamics over the ~17-day period when the effects of TE were excluded. Although some parameter estimates from isolated dynamics models had poor precision due to a smaller number of secondary periods, strong patterns emerged. Estimates of detection and extinction tended to be greater, while initial occupancy tended to be lower in models fit to the confounded TE/dynamics datasets than when fit to the isolated dynamics datasets (Figure 4). In our simulation study, we saw a similar pattern when we compared the *occupancy* and *use* scenarios (Table S2). This supports our assumption that the colonization and extinction parameters from

TABLE 1 A comparison of static and dynamic occupancy models fit to simulated presence-absence survey data where distribution dynamics were absent. For each set of simulation parameters, we generated 1,000 datasets. In use sampling, availability was independent during each sampling period. As a result, the static models were chosen the majority of the time. In occupancy sampling, availability could only change between primary periods and the dynamic models were selected nearly 100% of the time. Metrics provided are on the original parameter scale

Simulation parameters				% Open selected			Occ (ψ)			Det (p)			Colonization (γ)			Extinction (ϵ)		
ψ_0	p_a	p_d	γ_0	ϵ_0	Mean	Var	Mean	Var	Mean	Var	Mean	Var	Mean/Bias	MSE	Mean/Bias	Var	MSE	
Use scenarios																		
0.3	0.5	0.5	0.0	0.0	0.30	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.3	0.5	0.8	0.0	0.0	0.30	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.3	0.8	0.5	0.0	0.0	0.30	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.3	0.8	0.8	0.0	0.0	0.30	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.7	0.5	0.5	0.0	0.0	0.70	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.7	0.5	0.8	0.0	0.0	0.70	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.7	0.8	0.5	0.0	0.0	0.70	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.7	0.8	0.8	0.0	0.0	0.70	0.00	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Occupancy scenarios																		
0.3	0.5	0.5	0.0	0.0	0.16	0.00	0.47	0.00	0.00	0.00	0.07	0.00	0.00	0.01	0.39	0.00	0.15	0.15
0.3	0.5	0.8	0.0	0.0	0.15	0.00	0.80	0.00	0.00	0.00	0.09	0.00	0.00	0.01	0.49	0.00	0.24	0.24
0.3	0.8	0.5	0.0	0.0	0.26	0.00	0.46	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.08	0.00	0.01	0.01
0.3	0.8	0.8	0.0	0.0	0.24	0.00	0.78	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.15	0.00	0.02	0.02
0.7	0.5	0.5	0.0	0.0	0.35	0.00	0.50	0.00	0.00	0.00	0.26	0.00	0.00	0.07	0.48	0.00	0.24	0.24
0.7	0.5	0.8	0.0	0.0	0.35	0.00	0.80	0.00	0.00	0.00	0.27	0.00	0.00	0.07	0.50	0.00	0.25	0.25
0.7	0.8	0.5	0.0	0.0	0.58	0.00	0.47	0.00	0.00	0.00	0.17	0.00	0.00	0.03	0.11	0.00	0.01	0.01
0.7	0.8	0.8	0.0	0.0	0.56	0.00	0.80	0.00	0.00	0.00	0.25	0.00	0.00	0.06	0.19	0.00	0.04	0.04

MSE, mean squared error.

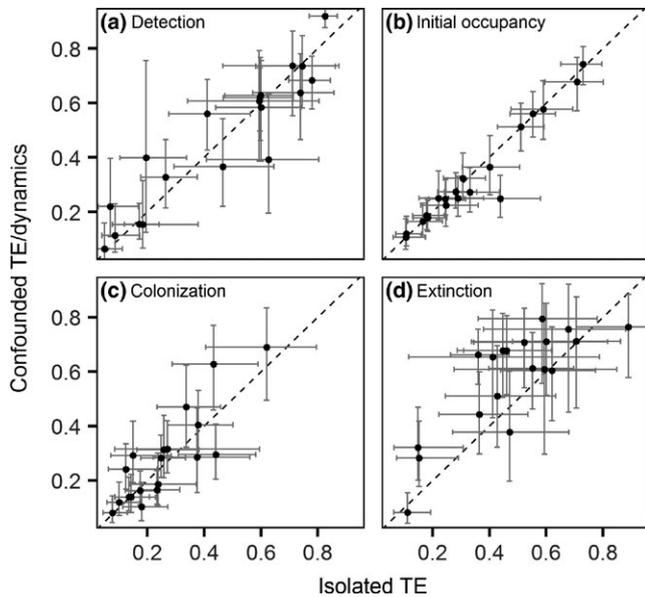


FIGURE 3 A comparison of the parameter estimates generated by open occupancy models fit to the confounded temporary emigration (TE)/dynamics and isolated TE empirical datasets for 19 forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates of (a) detection probability, (b) initial occupancy, (c) colonization, and (d) extinction. Most parameter estimates were similar under this sampling scheme when primary periods were separated by 2 days vs. 17 days

the isolated dynamics models are likely quantifying changes in site use between primary periods, while estimates generated from the other two datasets are likely measuring changes in instantaneous occupancy.

4 | DISCUSSION

Concern about overestimating species distributions due to closure assumption violations has led to widespread recommendations that secondary samples be conducted extremely close in time (Kendall et al., 2013; MacKenzie, 2005; MacKenzie & Royle, 2005; Rota et al., 2009). This enables instantaneous estimates of species occupancy patterns, which are valuable for generating a snapshot of the species' distribution at a moment in time. However, as our simulations demonstrate, this may be a poor sampling approach for quantifying distributional shifts. When instantaneous occupancy is estimated within primary periods, dynamic occupancy models estimate colonization and extinction rates as changes in instantaneous occupancy, which can be influenced by both distribution dynamics and TE; naiveté to this fact could mislead interpretations of the biological process being modelled.

Results from our empirical data analysis demonstrate how this problem could emerge in observational studies. By varying the temporal duration between primary and secondary periods, we showed that colonization and extinction estimates generated using a popular avian sampling technique are potentially heavily influenced by TE. Nevertheless, numerous studies have interpreted these dynamic rates as evidence of within-season dispersal (e.g. Betts et al., 2008; McClure & Hill, 2012;

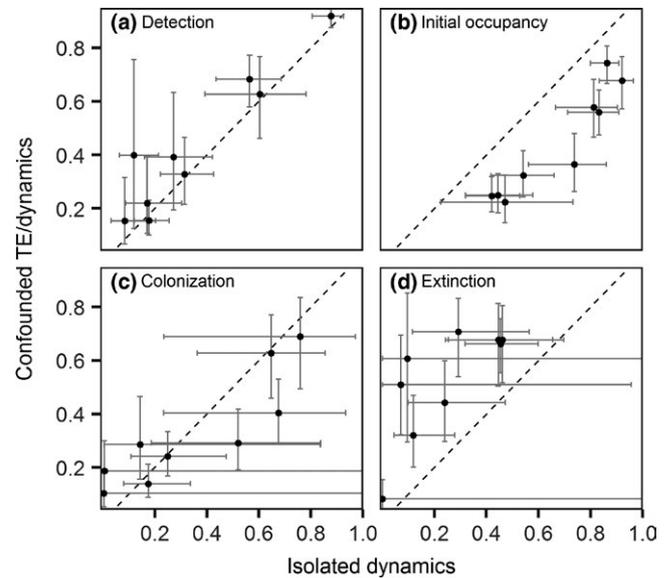


FIGURE 4 A comparison of the parameter estimates generated by open occupancy models fit to the confounded temporary emigration (TE)/dynamics and isolated dynamics datasets for nine forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates of (a) detection probability, (b) initial occupancy, (c) colonization, and (d) extinction. Detection and extinction estimates tended to be larger, while initial occupancy estimates tended to be lower in the confounded TE/dynamics models

Otto & Roloff, 2012; Rota et al., 2009). Indeed, Rota et al. (2009) thoroughly considered the influence TE had on their results, and concluded that it was likely not the process being modelled between their 10-min primary periods. Yet, our results indicate TE may be the only process being modelled between primary periods for some species. Note, that sequential surveys may additionally violate the assumption that detections are independent (MacKenzie et al., 2002), which could also explain the inflated detection and deflated occupancy estimates observed under this protocol (Figure 4). Regardless of the mechanism, this sampling approach is poorly adapted for modelling distribution dynamics.

Designing sampling schemes for dynamic occupancy modelling requires a more nuanced consideration of the closure assumption; researchers must also consider the biological process being modelled by the colonization and extinction parameters. In cases where TE is the only process occurring between primary periods (e.g. in our isolated TE datasets), models that explicitly estimate this parameter (Mordecai et al., 2011; Nichols et al., 2008) may be more appropriate than the dynamic occupancy model. Estimating TE rates directly may be valuable for designing survey protocols (Riddle, Stanislav, Pollock, Moorman, & Perkins, 2010) or for generating instantaneous occupancy estimates (Nichols et al., 2008). Yet, for many research questions interest lies in distributional changes in space use rather than short-term reversible changes in availability. Applications of dynamic occupancy models for quantifying dispersal (Betts et al., 2008; Rota et al., 2009), metapopulation dynamics (Ferraz et al., 2007; Pellet et al., 2007) or source/sink rates (Kerbioui et al., 2012; Peterman et al., 2013) all seek colonization and extinction estimates representing distribution dynamics. In

these cases, TE is a nuisance parameter that should be accounted for to estimate dynamics accurately.

As demonstrated in Appendix S2, by extending the dynamic occupancy model to include tertiary sampling periods, rates of dynamics and TE can be estimated simultaneously. However, for all parameters to be identifiable, the model requires collecting additional data (tertiary samples) that contribute no information to dynamic rate estimates. Therefore, when researchers wish to estimate distribution dynamics, and TE is of no interest, we strongly recommend adjusting the sampling design rather than fitting a more complex model. Nevertheless, the model performed well in initial simulations, and we encourage further testing to more thoroughly explore its utility and limitations.

As we and others (e.g. Kendall, 1999; Schmidt et al., 2013) have demonstrated, dynamic rates can be isolated simply by designing studies to estimate site use within primary periods rather than instantaneous occupancy. This approach requires estimating detection probability as $p_a p_d$, and therefore that the probability the species is available for sampling is random and independent during each secondary period (MacKenzie, 2005; Nichols et al., 2009). Where there is a spatial mismatch between the size of sample sites and the space used by targeted individuals (e.g. Figure 1), this means allowing time for spatial redistribution of individuals such that their locations during two sampling events are uncorrelated (Figure 5). Spatial autocorrelation in such within-home range locations should decrease over time, but the length of time required to achieve statistical independence will be longer for slower moving species (Swihart & Slade, 1985). When the sampling technique itself is destructive or induces a “trap response” (e.g. Otto et al., 2013), the duration between samples may need to be further extended to ensure that availability on each sampling occasion is not negatively influenced by a previous sampling event. Indeed, in all situations, increasing the time between samples should reduce correlation in availability (e.g. the likelihood that an animal is vocalizing); yet critically, the total time interval within a primary period must be sufficiently short that dynamic rates are negligible. Otherwise, these processes will also be estimated as a component of detection probability (Kendall, 1999; Rota et al., 2009).

Importantly, these recommendations assume a study system in which TE occurs over a finer time-scale than distribution dynamics, and that the two are sufficiently distinguishable (Figure 5). Designing an appropriate sampling scheme thus requires substantial knowledge about the study system and species. In our empirical study of territorial breeding birds, we assumed 24–48 hr periods were long enough to ensure independence among successive individual bird locations within territories, yet short enough that dynamic rates were negligible. Although we did not evaluate this assumption in the field, a 2-day period should allow ample movement for highly vagile species like birds, while substantial changes in site use are unlikely. In other sampling scenarios, however, these processes may not be uniquely identifiable, even with a robust sampling design. For instance, Kendall et al. (1997) noted that non-nesting birds could be considered temporary emigrants when sampling techniques focus on nesting individuals (e.g. Spendlow & Nichols, 1989). However, the temporal scale of mating and nest-building may not be distinguishable from that of changes

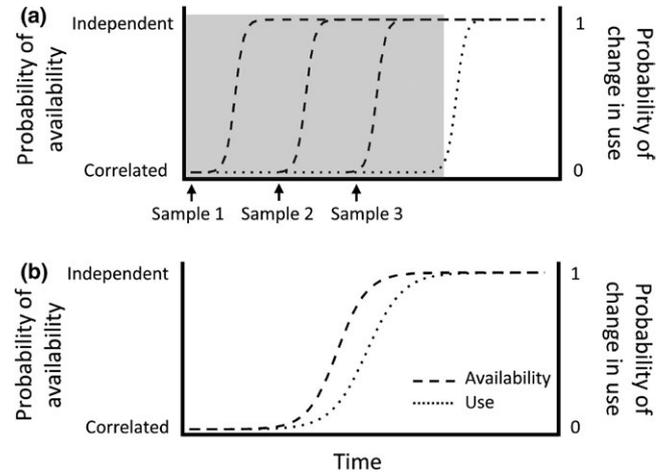


FIGURE 5 To quantify distribution dynamics independently from temporary emigration (TE), secondary samples should be spaced far enough apart in time that probability of availability is independent on each repeated visit, but true changes in site use are negligible. In (a), the grey box represents the maximum length of a primary sampling period, and three secondary samples are spaced so that probability of availability is independent on each occasion. If samples are conducted closer together in time, dynamic rates will be confounded by TE. If secondary samples occur outside of the grey box, dynamic rates will be confounded with detection probability. In (b), TE and dynamics occur at similar rates, and the two processes cannot be distinguished using Pollock’s (1982) robust sampling design

in population distributions. Similarly, for species with poorly defined territories or home ranges, TE and dynamics may not be biologically distinct processes. Future work should identify appropriate temporal sampling scales for different species and sampling techniques to help separate TE from dynamic rates.

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AUTHORS’ CONTRIBUTIONS

All authors conceived the ideas, contributed to drafts and gave final approval for publication. J.J.V. designed methodology, collected and analysed the data and led manuscript writing.

DATA ACCESSIBILITY

Data simulation R code is provided in Appendices S1 and S2. Data for the empirical case study are deposited in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.5d8s7> (Valente, Hutchinson, & Betts, 2017).

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SUPPORTING INFORMATION

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