Modeling dispersal using capture–recapture data: A comparison of dispersal models

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Abstract
Capture–recapture methods have been a cornerstone of field-based dispersal ecology. However, obtaining unbiased estimates of dispersal parameters from capture–recapture data is challenging because it is impossible to survey all possible range of dispersal in the field. There are several approaches to address this critical issue of capture–recapture methods. Still, a lack of formal comparisons among these modeling approaches has confused about which is the best practice given the available dataset. Here, I compared the performance of three dispersal models using test datasets simulated under various sampling designs. In the first approach, a probability distribution (a dispersal kernel) was simply fitted to the capture–recapture data (the “simple dispersal model”). In the second approach, a truncated probability distribution was used to account for the finite range of observations (the “truncated dispersal model”). Finally, the dispersal and observation processes were coupled to consider the spatial organization of sampling designs (the “dispersal–observation model”). The simulation study provided three important insights. First, the dispersal–observation model provided reliable estimates of dispersal parameters, even under sampling designs with a few recaptures. Second, the truncated dispersal model was also effective, but only when the number of recaptures was large. Finally, the use of the simple dispersal model caused a substantial underestimation of dispersal parameters regardless of sampling designs; this modeling approach should be avoided where possible. The results of this simulation study should help choose a suitable modeling approach.

KEYWORDS
Markov chain Monte Carlo, movement, simulation, spatial ecology, statistical inference

1 | INTRODUCTION

Ecological entities rarely exist independently. Dispersal—any movement of organisms across space (Bowler & Benton, 2005)—links populations (Hanski, 1999;
Hanski & Ovaskainen, 2000; Terui et al. 2014b; Terui et al. 2018a), communities (Leibold et al., 2004) and food webs (Nakano, Miyasaka, & Kuhara, 1999; Nakano & Murakami, 2001; Spiller et al., 2010; Terui et al. 2018b). Despite the inherent difficulty in quantifying dispersal in the wild (Nathan, 2001), dispersal research has evolved as a major field in ecology and has provided implications for critical applied issues, such as the metapopulation persistence of endangered species in fragmented landscapes (Hanski, 1999). More recently, synthetic works integrating behavioral and spatial ecology has identified crucial roles of plastic and context-dependent dispersal in driving spatial community dynamics (e.g., Amarasekare, 2004, 2010; Fronhofer et al., 2018; Little, Fronhofer, & Altermatt, 2019; Terui, Oue, Urabe, & Nakamura, 2017).

Hence, there is an increasing awareness that a detailed analysis of dispersal is integral to understanding spatial biodiversity patterns.

Capture–recapture (or mark–recapture) methods have been a cornerstone of field-based dispersal ecology. In classical capture–recapture studies, ecologists studied dispersal by simply fitting a probability distribution (a dispersal kernel) to the frequency distribution of displacement distance, which is calculated as the Euclidian distance of capture and recapture locations (reviewed in Nathan, Klein, Robledo-Arnuncio, & Revilla, 2012). This simple statistical approach, however, ignores critical problems inherent to capture–recapture data. First, this modeling does not account for individuals dispersing beyond the study area (the “permanent emigration”). In capture–recapture studies, it is virtually impossible to survey all possible range of dispersal in a landscape (Fujiwara, Anderson, Neubert, & Caswell, 2006; Gowan & Fausch, 1996; Hirsch, Visser, Kays, & Jansen, 2012; Schaub & Royle, 2014). As a result, a substantial portion of individuals, especially long-distance dispersers, can leave behind the study area. Ignoring this fundamental problem causes a serious underestimation of dispersal distance because recaptured individuals represent a non-random subset of a population (Fujiwara et al., 2006; Hirsch et al., 2012). Second, the sampling exposure of individuals depends on the spatial organization of the capture–recapture study (Pépino, Rodríguez, & Magnan, 2012; Schaub & Royle, 2014). For example, individuals that are captured and released near the center of the study area may be subject to greater sampling efforts as those are less likely to leave the study area. This issue arising from the nature of capture–recapture methods may introduce additional biases in statistical inference.

Several modeling approaches have been proposed to address the critiques on capture–recapture methods. The simplest solution would be the implementation of truncated probability distributions (Rodríguez, 2010; Terui et al. 2014a). Truncated probability distributions can account for the finite range of observations by restricting the values of recapture locations to be sampled. For example, suppose that observable recapture locations are confined to 0–100 m from a reference point. A statistical technique called “truncation” rescales the probability distribution function so that an integration of the rescaled probability distribution over this range gives a unity. Simulation experiments have shown that this modeling approach yields reasonable estimates of dispersal parameters, proving the usefulness of the truncation technique (e.g., Rodriguez, 2010). An alternative approach is to employ a modeling framework that couples dispersal and observation processes (Fujiwara et al., 2006; Pépino et al., 2012; Pépino, Rodríguez, & Magnan, 2016; Rodríguez, 2002). This dispersal–observation framework realizes the spatial organization of sampling designs, and therefore, enables us to account for individual-level heterogeneity in sampling exposure and imperfect recapture probability (i.e., the product of survival and detectability). More recently, dispersal–observation models have been further refined within a framework of Bayesian statistics to account for temporary and permanent emigrations (reviewed in Royle, Fuller, & Sutherland, 2018), although the original focus is to provide unbiased survival estimates using long-term encounter history data (Schaub & Royle, 2014). The Bayesian implementation allows for the use of latent variables, which substantially improves the flexibility of model specifications (Kéry & Schaub, 2012).

Despite all the benefits of the emerging modeling approaches, however, there have been no formal comparisons of model performance under different sampling designs. This knowledge gap is problematic because more sophisticated models are not always the “best” practice, given the differences in the amount and/or type of data. Under some scenarios, it is certainly possible that simpler models can yield results comparable to those derived from sophisticated models. Here, I aim to fill this gap by comparing the performance of dispersal models using simulated data. In doing so, I highlight in what context sophisticated dispersal models are required to obtain reliable estimates of dispersal parameters. The results should help determine which modeling approach is better suited to fulfill the purpose of an individual dispersal study.

2 | MODELS

I compared the performance of three dispersal models: (a) a simple dispersal model, (b) truncated dispersal model and (c) dispersal–observation model. Key parameters/variables in the models were listed in Table 1. All the models were assumed to use capture–recapture data
TABLE 1 Key parameters/variables used in the dispersal models

| Parameter/variable | Interpretation |
|--------------------|----------------|
| δ                  | Scale parameter of a Laplace distribution |
| σ                  | Standard deviation of a Gaussian distribution |
| X                  | Recapture location |
| X₀ᵢ                | Capture location |
| z                  | Latent variable indicating whether an individual remained in (z = 1) or left behind a study section (z = 0) |
| φ                  | Recapture probability (=ξz) |
| s                  | Survival probability |
| ξ                  | Detection probability |

collected in a one-dimensional system (e.g., a stream) and the notations of X₀ᵢ and Xᵢ were used to denote capture and recapture locations of individual i. In this study, I made two assumptions to make a clear case. First, I chose a one-dimensional system as an example because two-dimensional models are relatively complex, which may compromise the accessibility for unfamiliar readers. Second, to simplify model specifications, I used the notation of capture and recapture locations as if individuals are exposed to a single recapture attempt (i.e., X₀ᵢ and Xᵢ).

2.1 Simple dispersal model

In simple dispersal models, probability distributions with infinite support are commonly used as dispersal kernels (e.g., Laplace distribution) and are fitted to capture-recapture data. Here, I denote a probability distribution function (PDF) as \( f(Xᵢ|X₀ᵢ; θ) \). The notation \( Xᵢ|X₀ᵢ \) means that the recapture location \( Xᵢ \) is conditional on the release location \( X₀ᵢ \), and \( θ \) is a vector of parameters for the PDF. For example, let \( Xᵢ \) to follow a Laplace distribution as \( Xᵢ|X₀ᵢ; Δ \), in which \( Δ \) denotes a scale parameter (i.e., an expected dispersal distance). The PDF of the Laplace distribution is:

\[
f(Xᵢ|X₀ᵢ; Δ) = \frac{1}{2Δ} \exp \left(-\frac{1}{Δ} |Xᵢ - X₀ᵢ| \right).
\] (1)

Simple dispersal models are programmatically easy. As such, this modeling approach has been widely used in capture-recapture studies. An appropriate probability distribution may vary among organisms and ecological contexts. Choices may include Gaussian distributions, student-t distributions, Gaussian mixture distributions, Laplace distributions and Laplace mixture distributions, among others (see Nathan et al., 2012 for choices of dispersal kernels).

2.2 Truncated dispersal model

In truncated dispersal models, truncated probability distributions are used as dispersal kernels. For PDFs that are commonly used as dispersal kernels, the support extends from \(-∞ \) to \( ∞ \), which is inappropriate given the finite range of observations in most capture-recapture studies. If the observable range is restricted to \( 0 - L \) m from a reference location, recapture location \( Xᵢ \) is a realization of a random variable drawn from a probability distribution truncated at 0 and \( L \) m \([\Pr(Xᵢ < 0) = 0 \cap \Pr(Xᵢ > L) = 0]\). A statistical technique called “truncation” rescales the PDF so that the truncated PDF, \( g(Xᵢ|X₀ᵢ; θ) \), integrates to one over the interval of possible minimum and maximum values:

\[
g(Xᵢ|X₀ᵢ; θ) = \frac{f(Xᵢ|X₀ᵢ; θ)}{\int₀^L f(Xᵢ|X₀ᵢ; θ) dXᵢ}.
\] (2)

The truncated probability distribution reproduces random values restricted to the range of observation, and therefore, realizes that information on the likelihood can only come from those recaptured in the finite study area. Truncated dispersal models have been implemented in some capture-recapture studies (e.g., Terui, Miyazaki, Yoshioka, Kadoya, et al., 2014).

2.3 Dispersal–observation model

Dispersal–observation models are the most sophisticated approach to estimate dispersal parameters. In reality, released individuals disperse freely for a certain period and may leave the finite study area. Further, only survived individuals may be recaptured with some probability (i.e., imperfect detection) even when marked individuals stay in the study area. Thus, to be recaptured, individuals must (a) stay in the study area, (b) survive until being recaptured and (c) be detected if they survive and remain in the study area. Dispersal–observation models realize these dispersal and imperfect observation processes while accounting for the spatial organization of sampling designs (Pépino et al., 2012; Schaub & Royle, 2014).

Here, let the dispersal process follow a given probability distribution having a PDF of \( f(Xᵢ|X₀ᵢ; θ) \) with infinite support (e.g., a Laplace distribution). Then, individual
recapture history \( Y_i \) (\( Y_i = 1 \) if recaptured, otherwise 0) is used to model imperfect observation processes in the observation submodel. The response variable \( Y_i \) is modeled as a realization of a random variable drawn from a Bernoulli distribution:

\[
Y_i | z_i \sim \text{Bernoulli}(z_i s_i \xi_i),
\]

where \( z_i \) is the latent variable indicating whether individual \( i \) stays or not in the study area (\( z_i = 1 \) if present, otherwise 0), \( s_i \) is the survival probability between the time points of capture and recapture and \( \xi_i \) is the detection probability. The latent variable \( z_i \) accounts for permanent emigration; if \( z_i = 0 \), the multiplication \( z_i s_i \xi_i \) is inevitably zero (i.e., never be recaptured). Importantly, \( z_i \) is the latent variable sampled from the probability distribution used in the dispersal submodel:

\[
z_i = \begin{cases} 
1 & \text{if } 0 \leq X_i \leq L \text{(stay)} \\
0 & \text{if } X_i < 0 \text{ or } X_i > L \text{(leave)}.
\end{cases}
\]

Therefore, the variable \( z_i \) couples dispersal–observation processes. For recaptured individuals, \( z_i \) is deterministic and always one as they are known to be in the study section. For unrecaptured individuals, \( z_i \) can be either one or zero, and the probability of staying in the study section is related to the parameters in the dispersal submodel \( \theta \) as well as the initial location \( X_{0,i} \):

\[
p_i(\theta) = Pr(z_i = 1|X_{0,i}; \theta) = \int_0^L f(X_i|X_{0,i}; \theta) dX_i.
\]

In a framework of Bayesian statistics, the probability is naturally integrated through the process of Markov chain Monte Carlo (MCMC) simulations. The parameters \( s_i \) and \( \xi_i \) can be isolated if an independent dataset to estimate detection probability (e.g., multiple-pass removal data) is available (Dorazio, Jelks, & Jordan, 2005) or if there are multiple recapture attempts (Schaub & Royle, 2014). Otherwise, the two parameters need to be condensed into recapture probability \( \phi_i (=s_i \xi_i) \) so that:

\[
Y_i | z_i \sim \text{Bernoulli}(z_i \phi_i).
\]

The likelihood function of the dispersal–observation model, \( h(Y_i|X_{0,i}; \phi_i, \theta) \), is:

\[
h(Y_i|X_{0,i}; \phi_i, \theta) = (\phi_i p_i(\theta))^Y_i (1-\phi_i p_i(\theta))^{1-Y_i}.
\]

The model is parameter redundant and requires some constraint. Here, I assume that recapture probability \( \phi_i \) is the same for all individuals (i.e., \( \phi_i = \phi \)). Unlike the other two models, the dispersal–observation model allows us to extract information from individuals leaving behind the study area and corrects for the effect of permanent emigration on dispersal parameter estimates (Schaub & Royle, 2014). Furthermore, the observation submodel realizes that those released closer to the boundary of the study area are more likely to emigrate permanently as recapture location \( X_i \) is conditional on initial capture location \( X_{0,i} \). Note that the dispersal–observation model described above is a special case of spatial Cormack–Jolly–Seber (CJS) models (Schaub & Royle, 2014), which are originally developed to estimate unbiased survival probability using long-term spatial encounter history data.

### 2.4 Simulation experiment

I generated test datasets using simulations to compare the performance of the dispersal models. An overview of the data-generation procedure is the following. I considered a situation in which virtual ecologists conduct a capture–recapture study in a linear section with length \( L \) m. I first produced the initial locations \( (X_{0,i}) \) of \( N \) marked individuals as the distance from a reference point (0 m at the reference point), which was drawn from a uniform distribution as \( X_{0,i} \sim \text{Uniform}(0,L) \). Then, the dispersal process was simulated based on a chosen dispersal kernel (either a Laplace or Gaussian distribution; see below). After the relocation, I computed a process of imperfect recapture using a Bernoulli distribution; only those remained in the study section \( (0 \leq X_i \leq L) \) were exposed to recapture with success probability \( \phi \ (=s \xi) \). If recaptured, the recapture location \( X_i \) was assigned \( (Y_i = 1) \); otherwise, \( X_i \) was recorded as \( \text{NA} \) \( (Y_i = 0) \). As such, the source of \( X_i = \text{NA} \) and \( Y_i = 0 \) can be either permanent emigration, death, or undetected. These are indistinguishable in the simulated data and needs to be estimated. Capture and recapture locations \( (X_{0,i}) \) and \( X_i \) were rounded to the nearest meter in light of observation errors.

I used Laplace and Gaussian distributions when generating test datasets. A Laplace distribution has a symmetric exponential decay of probability density from the point of release (Figure 1). The PDF is:

\[
f(X_i|X_{0,i}; \delta) = \frac{1}{2\delta} \exp\left( -\frac{1}{\delta} |X_i - X_{0,i}| \right).
\]
I selected a Laplace distribution because it is widely used in the dispersal literature (Baguette, 2003; Hanski, 1999; Nathan et al., 2012; Pépino et al., 2012; Pépino et al., 2016; Rodríguez, 2002). A Gaussian distribution has the following PDF:

$$f(X_i | X_0; \sigma) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{(X_i - X_0)^2}{2\sigma^2}\right). \quad (10)$$

The expected value of absolute dispersal distance is related to the parameter $\sigma$ (standard deviation) as $E(|X_i - X_0|) = \sqrt{2\pi\sigma}$. A Gaussian distribution has characteristics of a low kurtosis and thin tails, which contrast with a Laplace distribution (Figure 1).

**FIGURE 1** Laplace and Gaussian dispersal kernels. Different line colors indicate dispersal kernels with different dispersal parameter values ($\delta$ for a Laplace dispersal kernel and $\sigma$ for a Gaussian dispersal kernel) [Color figure can be viewed at wileyonlinelibrary.com]

**FIGURE 2** Boxplots showing the proportion of stayers (red) or recaptures (gray) in relation to true dispersal parameter (Laplace). $\delta_{true}$ is the scale parameter of a Laplace distribution used to produce simulated data. Different panels show different sampling designs. Values of design factors are shown on the top of each panel ($N$ the number of individuals marked, $L$ the section length and $\phi$ the recapture probability) [Color figure can be viewed at wileyonlinelibrary.com]
Under a chosen dispersal kernel, I assessed the ability of each dispersal model to estimate the true dispersal parameter ($\delta_{\text{true}}$ or $\sigma_{\text{true}}$). The following values of design factors were used to simulate various sampling designs: (a) the number of individuals marked $N$ (100, 500 and 1,000 individuals), (b) the length of the study section $L$ (500 and 1,000 m) and (c) recapture probability $\phi$ (0.4 and 0.8). I used six values of true dispersal parameter under each sampling design ($\delta_{\text{true}}$ or $\sigma_{\text{true}} = 50, 100, 150, 200, 250$ and 300 m). This setup results in 72 parameter combinations of $N$, $L$, $\phi$ and the dispersal parameter ($\delta_{\text{true}}$ for a Laplace distribution or $\sigma_{\text{true}}$ for a Gaussian distribution). I produced 50 replicates under each parameter combination, resulting in a total of 3,600 simulated datasets (72 × 50) for each of the dispersal kernels.

I also considered a scenario in which individual-level heterogeneity in true recapture probability exists. When generating simulated datasets, true recapture probability $\phi_i$ for individual $i$ was drawn from a normal distribution as $\logit(\phi_i) \sim \text{Normal}(\logit(\phi), \sigma_{\phi}^2)$, where $\sigma_{\phi}$ was set to be 1.0 to ensure significant variation among individuals. I considered this alternative scenario to assess the robustness of the dispersal models against model misspecification, that is, fitting a model to the data that misrepresents the data-generating process. As stated above, the dispersal–observation model assumes a constant recapture probability among individuals ($\phi_i = \phi$), so this model structure misspecifies the data-generating process under this scenario. The consideration of this scenario is important because, in nature, it is likely that recapture probability varies among individuals. I produced the same set of 3,600 simulated datasets for each of the dispersal kernels.

The dispersal models were fitted to the simulated data using R 3.5.1 (R Core Team, 2019) and JAGS 4.3.0 (Plummer, 2003). I estimated the parameter $\delta$ or $\sigma$ (for all models) and recapture probability $\phi$ (for the dispersal–
observation model) and assessed the % bias of estimated dispersal parameter:

\[ \text{%bias} = \frac{100 \times (\theta_{\text{est}} - \theta_{\text{true}})}{\theta_{\text{true}}} \quad (11) \]

\( \theta_{\text{est}} \) and \( \theta_{\text{true}} \) are estimated and true dispersal parameters (\( \delta \) or \( \sigma \)), respectively. Vague priors were assigned to the parameters: a truncated normal distribution for log-transformed \( \delta \) (mean = 0, SD = 100, range = -10 to 10), a half-Cauchy distribution for \( \sigma \) (location parameter = 0, scale parameter = 1,000) and a uniform distribution for \( \phi \) (range = 0–1). For each scenario under each model, I initiated three Markov chain Monte Carlo (MCMC) chains with 15,000 iterations. I discarded the initial 5,000 samples as burn-in and kept the remainder every 20 steps to summarize the posterior distributions. I performed as many simulations as were necessary to achieve convergence, which was assessed by whether the R-hat indicator of each parameter had reached a value of <1.1 (Gelman, Carlin, Stern, & Rubin, 2003). Total MCMC samples stored after burn-in and thinning ranged from 1,500 to 54,000.

**FIGURE 4** Boxplots of % bias in the estimated dispersal parameter (Laplace). Results are shown in relation to true dispersal parameter (x-axis: \( \delta_{\text{true}} \)) and different sampling designs (panels). Boxplots show the median (thick line in the center of the box), the 25 and 75% quantiles (limits of boxes) and ranges within 1.5 times the height of the box (whiskers). Data points outside of whiskers are shown as dots. Values of design factors are shown on the top of each panel (\( N \) the number of individuals marked, \( L \) the section length and \( \phi \) the recapture probability). Dispersal parameter \( \delta_{\text{true}} \) (the scale parameter of a Laplace distribution used to produce simulated data) was estimated using three dispersal models (the simple dispersal model, gray box; the truncated dispersal model, blue box; the dispersal observation model, red box) [Color figure can be viewed at wileyonlinelibrary.com]
RESULTS

The simulated datasets showed a wide range of values in the proportion of stayers (individuals remained in the study section; 0.38–1.00) and recaptures (0.08–0.87). Overall patterns were similar between the simulated datasets produced by Laplace and Gaussian distributions (Figures 2 and 3). The proportion of stayers decreased with increasing true dispersal parameter ($\delta$ for a Laplace distribution and $\sigma$ for a Gaussian distribution), and this relationship was more evident when the length of the study section $L$ was short (Figures 2 and 3). Although the recapture probability $\phi$, the product of survival and detection probabilities, did not affect the proportion of stayers.

### Table 2

Percent bias of estimated dispersal parameters averaged across 72 simulation scenarios

| Kernel  | Model                | Average % bias |
|---------|----------------------|----------------|
| Laplace | Simple               | $-29.0\%$      |
|         | Truncated            | $16.4\%$       |
|         | Dispersal–observation| $5.7\%$        |
| Gaussian| Simple               | $-15.4\%$      |
|         | Truncated            | $17.9\%$       |
|         | Dispersal–observation| $5.3\%$        |

Note: Positive and negative values indicate over- and underestimation of dispersal parameters ($\delta$ for a Laplace distribution and $\sigma$ for a Gaussian distribution). Scenario-specific values of percent bias were provided in Tables S1–S6.
stayers, it reduced the proportion of recaptures (Figures 2 and 3). Hence, the number of recaptures, which represents the sample size for the dispersal models, is a function of the number of marked individuals \(N\), the true dispersal parameter \(\delta_{\text{true}}\) or \(\sigma_{\text{true}}\), the length of the study section \(L\) and the recapture probability \(\phi\).

The simulations identified the critical differences in the estimation accuracy and uncertainty of the three dispersal models. The simple dispersal model consistently underestimated the dispersal parameter regardless of sampling designs, and this result was consistent across dispersal kernels (Figures 4 and 5, gray). The degree of underestimation was substantial, especially when the true dispersal parameter was large relative to the study section length \(L\). Increasing the number of marked individuals \(N\) did not improve the performance of the simple dispersal model (Figures 4 and 5, gray). The mean % bias of estimated dispersal parameter across 72 simulation scenarios was \(-29.0\%\) for a Laplace distribution (range: \(-58.8\) to \(-4.6\%\); Tables 2 and S1–S6) and \(-15.4\%\) for a Gaussian distribution (range: \(-42.5\) to \(-1.4\%\); Tables 2 and S1–S6). Although the 95% CIs were narrower than other models (Figures S1 and S2), these are unreliable given the strong bias in the estimated dispersal parameters.

The truncated dispersal model provided less biased estimates of dispersal parameters in simulation scenarios with larger \(N\), \(L\) and \(\phi\) (Figures 4 and 5, blue), all of which contributed to the increased number of recaptures (Figures 2 and 3). However, in scenarios where the number of recaptures was limited (i.e., smaller \(N\), \(L\) and \(\phi\)),

**FIGURE 6** Boxplots of recapture probability \(\phi\) estimated by the dispersal–observation model (Laplace). \(\delta_{\text{true}}\) is the scale parameter of a Laplace distribution used to produce simulated data. Boxplots show the median (thick line in the center of the box), the 25 and 75% quantiles (limits of boxes) and ranges within 1.5 times the height of the box (whiskers). Data points outside of whiskers are shown as dots. Horizontal gray lines are the true recapture probability used when generating simulated datasets. Values of design factors are shown on the top of each panel (\(N\) the number of individuals marked, \(L\) the section length and \(\phi\) the recapture probability) [Color figure can be viewed at wileyonlinelibrary.com]
the estimates of dispersal parameters became highly variable (Figures 4 and 5, blue). In particular, substantial biases were observed when the observation section was short relative to the dispersal parameter $\delta_{\text{true}}$ or $\sigma_{\text{true}}$. For example, the truncated dispersal model overestimated large dispersal parameters ($\delta_{\text{true}}$ or $\sigma_{\text{true}} \geq 200$ m) substantially under the scenario with $N = 100$, $L = 500$ and $\phi = 0.4$ (Figures 4a and 5a). Overall, the estimated dispersal parameter was positively biased (i.e., overestimation). The mean % bias of estimated dispersal parameter across simulation scenarios was 16.4% for a Laplace distribution (range: $-1.5$ to $232.7$%; Tables 2 and S1–S6) and 17.9% for a Gaussian distribution (range: $-1.5$ to $212.1$%; Tables 2 and S1–S6). Further, the estimated 95% CIs were broader than those of other models in most simulation scenarios. The 95% CI increased with increasing true dispersal parameter (Figures S1 [Laplace] and S2 [Gaussian]), and this trend was exacerbated with smaller $N$, $L$ and $\phi$ (e.g., Figures S1a and S2a).

The dispersal–observation model provided the least biased estimates of dispersal parameters in almost all the simulation scenarios (Figures 4 and 5, red). Although non-negligible biases were observed with a limited number of recaptures (e.g., Figures 4a and 5a), the model performance was improved as the number of recaptures increased (i.e., large $N$ and $L$ with high recapture probability $\phi$). The degree of bias was smaller than other models (Table 2). The mean % bias of estimated dispersal parameter across simulation scenarios was 5.7% for a Laplace distribution (range: $-8.7$ to $58.3$%; Tables 2 and S1–S6) and 5.3% for a Gaussian distribution (range: $-2.9$ to $74.3$%; Tables 2 and S1–S6). As with the truncated dispersal model, the 95% CI increased with increasing true dispersal parameters (Figures S1 and S2). However, the 95% CIs were much narrower than those of the truncated dispersal model, especially under the scenarios with small $N$, $L$ and $\phi$ (Figures S1 and S2). Therefore, the dispersal–observation model provides a robust framework to estimate dispersal

**FIGURE 7** Boxplots of recapture probability $\phi$ estimated by the dispersal–observation model (Gaussian). $\sigma_{\text{true}}$ is the standard deviation of a Gaussian distribution used to produce simulated data. See Figure 6 for details [Color figure can be viewed at wileyonlinelibrary.com]
parameters. The estimated recapture probability $\phi$ was also comparable to the true recapture probability, although there was a tendency of overestimation when the true dispersal parameter was large (Figures 6 and 7).

The results were similar when true recapture probability varied among individuals (Figures S5–S8). In general, the simple dispersal model underestimated dispersal parameters (Figures S5–S8). The truncated dispersal model provided reasonable estimates only when the number of recaptures was sufficient (Figures S5–S8). The dispersal–observation model provided the most reliable estimates in almost all the scenarios considered (Figures S5–S8).

4 | DISCUSSION

The comparison of the dispersal models provided essential insights. First, the dispersal–observation model is the most reliable approach in estimating dispersal kernels; thus, this modeling approach is highly recommended for most cases. This result is unsurprising given the feature of the dispersal–observation model that maximizes the use of available information. It couples dispersal and observation processes to account for the spatial organization of the sampling designs, thereby extracting information from both recaptured and unrecaptured individuals (Royle et al., 2018; Schaub & Royle, 2014; Terui et al., 2017). Second, my simulation results indicated that the truncated dispersal model is also useful but only in scenarios where many recaptures are available. Finally, I do not recommend the use of the simple dispersal model when estimating dispersal parameters, although most studies use this modeling approach. It risks the substantial underestimation of dispersal distance regardless of sampling designs. These general patterns were consistent across different dispersal kernels. The information provided above should help choose a suitable modeling approach given the data availability.

In comparison to the truncated dispersal model, the dispersal–observation model provided more reliable estimates when estimating large dispersal parameters with a limited number of recaptures. This result may stem from the fact that the dispersal–observation model uses two data sources, that is, the recapture history $Y_i$ and the dispersal distance $X_i - X_{i,0}$, to inform the dispersal parameter (see Equation (7) for the likelihood function). The dual-use of these information sources is critical under small-sample-size scenarios because $Y_i$ has the information not only for recaptured individuals ($Y_i = 1$) but also for those unrecaptured ($Y_i = 0$). Hence, the dispersal–observation model may be able to narrow the plausible range of dispersal parameters by extracting partial information from unrecaptured individuals. In contrast, the parameter estimation of truncated dispersal models entirely ignores unrecaptured individuals, inflating the uncertainty of statistical inference with heavily censored data. Nevertheless, the difference in model performance became minimal as the number of recaptures increased. Therefore, as long as the study’s purpose is the estimation of dispersal distance, truncated dispersal models may yield results comparable to those derived from dispersal–observation models under scenarios with many recaptures (e.g., a large study area with a large number of marked individuals). The model structure of the truncated dispersal model is simple and can be easily implemented in the Bayesian statistical software, such as JAGS (Plummer, 2003). Truncated dispersal models are, therefore, a reasonable option if the dataset contains a sufficient number of recaptures.

Simple dispersal models are widely used in capture–recapture studies (Baguette, 2003; Comte & Olden, 2018a, 2018b; Radinger & Wolter, 2014; Schwalb, Poos, & Ackerman, 2011; Skalski & Gilliam, 2000). In my simulation, however, the simple dispersal model consistently underestimated dispersal distance, supporting the recent criticisms on this approach (Fujiiwara et al., 2006; Gowen & Fausch, 1996; Hirsch et al., 2012). As pointed by previous studies, the underestimation of the simple dispersal model is probably caused by the non-random censoring of the data by which long-distance dispersers are selectively removed (Fujiiwara et al., 2006). The observed bias was severer when a Laplace kernel was used to generate simulated datasets, probably because the heavier tails produce more long-distance dispersers leaving the observable area. Therefore, the risk of underestimation would be exacerbated with heavy-tailed dispersal kernels, although further explorations are needed to generalize this finding.

In some cases, it is infeasible to apply the ideal modeling approach to the data because capture–recapture locations are not always available. For example, displacement distance, instead of capture–recapture locations, can be the only available information for a meta-analysis (e.g., Comte & Olden, 2018a, 2018b; Radinger & Wolter, 2014). For individual studies, however, it is highly recommended to use either truncated dispersal or dispersal–observation models as those provide less biased estimates of dispersal distance. The data required for the implementation of these models are similar to those needed for simple dispersal models. Although dispersal–observation or truncated dispersal models require some programming skills, step-by-step guidance for the Bayesian analysis is now increasingly available (Gelman & Hill, 2007; Kéry, 2010; Kéry & Schaub, 2012).

Overall, truncation and dispersal–observation models seem promising. However, dispersal–observation models...
have a higher potential for further improvement. First, there was a tendency to overestimate the true dispersal parameter that is large relative to the study area, as observed in spatial CJS models (Schaub & Royle, 2014). While increasing sampling efforts (wider observation area and/or the increased number of marked individuals) may be the simplest solution, an alternative approach is to combine different capture-recapture methods. For example, individuals marked with Passive Integrated Transponder (PIT) tags can be detected at the boundary of the study area/section through stationary PIT antennas (Armstrong et al., 2013). Although this approach cannot identify exact recapture locations, it provides information on whether tagged individuals remained in or left behind the study area. The radiotelemetry tracking can also provide information on individuals unrecaptured in the study area/section. Such partial data may be used to inform the latent variable $z_j$ (the variable indicating whether individuals remained in or left behind the study area/section) and should increase the accuracy and flexibility of the dispersal-observation model. Second, the model can be developed to relax the assumption of the constant recapture probability. Although the dispersal-observation model was robust to random variation in recapture probability among individuals (Figures S5–S8), non-random variation might cause biases in statistical inference. For example, it is common to perform surveys by multiple investigators, which could introduce systematic differences in recapture probability among them. In such a case, the recapture probability may be modeled as \[ \logit \phi_{ji} \sim \text{Normal} \left( \mu_{\phi}, \sigma^2_{\phi} \right) \], where subscript $j$ represents investigator ID. A similar model structure may be applicable to other scenarios that cause nonrandom variation in recapture probability. Third, dispersal-observation models can be extended to 2D versions, and several studies validated its usefulness in a 2D space (Ergon & Gardner, 2014; Royle et al., 2018; Schaub & Royle, 2014). For example, Ergon and Gardner (2014) modeled dispersal distance and angle in a 2D space. Such an application may not be possible for truncated dispersal models because truncation distance changes not only by the initial location but also by the direction of movement. Finally, if long-term multiple recapture data are available, dispersal-observation models may be modified to model the Markovian movement process in state space (Ergon & Gardner, 2014; Royle et al., 2018; Schaub & Royle, 2014). This modeling approach has a certain merit. For example, it is possible to account for individuals who may emigrate and return to the study area during the observation period (Schaub & Royle, 2014).

A critical issue that applies to all the dispersal models is the misspecification of the dispersal kernel. I used a Laplace or Gaussian kernel for all the simulation scenarios; however, there are many possible dispersal kernels (Nathan et al., 2012), and it is difficult to know the best dispersal kernel a priori. The Widely Applicable Information Criterion (WAIC) (Watanabe, 2010) and cross-validation (Hooten & Hobb, 2015) may represent promising tools to choose which dispersal kernel is best supported by the data. An R-package for these methods is freely available (Vehtari, Gelman, & Gabry, 2016) and is now increasingly used in the field of ecology (Hooten & Hobb, 2015; Terui et al. 2018a; Terui, Finlay, Hansen, & Kozarek, 2019). Therefore, comparing the support of different dispersal kernels using the WAIC or cross-validation may be a reasonable step to select an appropriate dispersal kernel.

In summary, the comparison of the three dispersal models revealed the usefulness of dispersal-observation and truncated dispersal models. Their performance was either distinguishable or comparable, depending on sampling designs. Although dispersal-observation models are generally recommended, truncated dispersal models are also useful when many recaptures are available. Therefore, users may choose an appropriate modeling approach in light of the dataset, coding skills and purpose of the research.

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**DATA AVAILABILITY STATEMENT**

This study has no data. R and JAGS scripts are available at https://doi.org/10.5281/zenodo.3966052.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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