



Estimating survival in continuous space from mark-dead-recovery data — Towards a continuous version of the multinomial dead recovery model

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ABSTRACT

Understanding spatially varying survival is crucial for understanding the ecology and evolution of migratory animals, which may ultimately help to conserve such species. We develop an approach to estimate an annual survival probability function varying continuously in geographic space, if the recovery probability is constant over space. This estimate is based on a density function over continuous geographic space and the discrete age at death obtained from dead recovery data. From the same density function, we obtain an estimate for animal distribution in space corrected for survival, i.e., migratory connectivity. This is possible, when migratory connectivity can be separated from recovery probability. In this article, we present the method how spatially and continuously varying survival and the migratory connectivity corrected for survival can be obtained, if a constant recovery probability can be assumed reasonably. The model is a stepping stone in developing a model allowing for disentangling spatially heterogeneous survival and migratory connectivity corrected for survival from a spatially heterogeneous recovery probability. We implement the method using kernel density estimates in the R-package CONSURE. Any other density estimation technique can be used as an alternative. In a simulation study, the estimators are unbiased but show edge effects in survival and migratory connectivity. Applying the method to a real-world data set of European robins *Erithacus rubecula* results in biologically reasonable continuous heat-maps for survival and migratory connectivity.

1. Introduction

1.1. The biological relevance of spatial variability in survival in the context of migratory species

Even if survival is one of the most fundamental demographic parameters and continuously varying in geographical space, the usage of survival maps is not very common. Despite approaches modeling spatially varying survival on a discrete spatial domain (Thorup and Conn, 2009; Bauthian et al., 2007; Korner-Nievergelt et al., 2010b), only in a few studies continuous survival maps are created by spline functions to visualize the relationship between two-dimensional explanatory variables, e.g., geographical space, and survival (Gimenez et al., 2009; Péron et al., 2011). Such maps would facilitate to evaluate demographic monitoring of entire species with large, already existing data sets like the EURING data set (Du Feu et al., 2016) of marked

birds recovered dead and reported. Such a demographic monitoring may help to analyze population dynamics of species using space on a broad scale like migratory animals and may even help to assess the conservation status of these species. However, the distribution of raw recovery data is a result of an interplay between continuously varying survival across geographical space, the space use by the animal and the spatially heterogeneous observation process. To obtain a survival map, the three parameters, survival, space use and the observation process, must be separable. We, here, present how to disentangle the three parameters under the constraint of a constant recovery probability. This is a stepping stone in future model development, where all three parameters can be disentangled without this constraint.

Migratory behavior leads to a particularly complex relationship between environment and biology of migratory species. We define

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migratory behavior as a directed seasonal recurring movement, sometimes involving large spatial scales like the whole two continents Europe and Africa. As the spatial distribution of migratory species changes between seasons, they connect distant areas with each other through migratory connectivity (Webster et al., 2002) and impact the local ecosystems there (Bauer and Hoyer, 2014; Riotte-Lambert and Matthiopoulos, 2020). In turn, abiotic and biotic environmental factors of these distant areas influence the ecology and evolution of migratory species by affecting demography and movement patterns (Alerstam et al., 2003; Gaillard et al., 2010). Demography and movement also interact with each other. Thereby, survival impacts animal movement (Hewson et al., 2016; Healy et al., 2017) and the decision on where and when to move influences survival (Bauer et al., 2016). Understanding these relations helps understanding population dynamics, and also raises the awareness to vital factors in conserving migratory species (Newson et al., 2009; Xu et al., 2019).

Investigating the interplay of survival and animal movement by observing the spatial distribution of the species inevitably requires considering the observation process. Both survival and animal movement shape the distribution of a species in space (Fletcher et al., 2019). As a consequence, how species are distributed contains information on both processes. However, the species distribution only becomes visible through observational data. So, the observation process biases the distribution, while creating the data of species distribution being analyzed. This bias can be reduced by addressing the observation process explicitly (Buckland et al., 2015; Korner-Nievergelt et al., 2010a; Patterson et al., 2008).

All processes (survival, animal movement and observation) are spatio-temporally varying and continuous in space by nature (Tjørnølv et al., 2020; Veit et al., 1994). Environmental factors influencing these processes like elevation (Chandler et al., 2018), precipitation (Rockwell et al., 2017), habitat (DeCesare et al., 2014), or predation risk (DeCesare et al., 2014) vary continuously in space. Even if individual factors are piecewise constant in space, e.g., like fragmented habitat types, all processes being influenced by so many environmental factors can be seen as truly spatially continuous parameters.

Spatially continuous biological processes should be modeled by spatially continuous models to reflect the true pattern of the parameter. Nevertheless, continuous parameters are often discretized for practical reasons in quantitative analyses (Saracco et al., 2010; Allen et al., 2019; Baker and Thompson, 2006). For example, in classical mark-recapture modeling, time intervals are regularly discretized even if capturing has taken place continuously, e.g., by a camera trap. The discretization depends on a priori decisions on the class boundaries and is often arbitrary, sometimes leading to a poor model fit (Teller et al., 2016). In temporal models this issue is well known making continuous time models an area of active research (e.g., Blackwell et al., 2016; Borchers et al., 2014; Mews et al., 2022; Schofield et al., 2018). Similarly, discretization in space, e.g., demographic parameters per grid cell of a map, may not realistically reflect the spatial pattern of that parameter. Even if there are suitable modeling frameworks like partial differential equations (e.g., INLA) or splines, to our knowledge, there is only one approach generating continuous survival maps by spline functions (Gimenez et al., 2009; Péron et al., 2011).

Learning about the ecology and evolution of migratory animals requires taking all three processes, survival, migratory connectivity and observation, into account. The multinomial dead recovery model described in the next section approaches this problem for discrete destination areas. In this study, we further develop that model to allow modeling survival, migratory connectivity and observation in a continuous space using point processes.

1.2. The multinomial dead recovery model

Spatially varying survival can be estimated, when the destination space is split into a few discrete destination areas, while simultaneously

estimating migratory connectivity and controlling for the observation process. For that, individually marked animals can be used. When these marked animals die, they may be found by humans, who report the code to the institutions managing recovery databases (Du Feu et al., 2016). The records of these dead marked animals are called dead recovery data. For dead recoveries of marked individuals, Thorup and Conn (2009), Bauthian et al. (2007) and Korner-Nievergelt et al. (2010b) developed the multinomial dead recovery model, which allows estimating spatially explicit survival probabilities. In the discrete case, disentangling the spatial distribution of animals from the spatial heterogeneous probability that humans find and report a dead marked animal is possible. A mathematical description of the multinomial dead recovery model can be found in Schirmer et al. (2022a).

In particular, the multinomial dead recovery model describes the following scenario: animals are marked in discrete populations of origin. Individuals of one population may migrate to different destination areas, while individuals of different populations may share the same discrete destination areas. Individuals do not change destination areas between years. The distribution of one population over the destination areas is called migratory connectivity. Individual annual survival in the destination area is independent of the origin of the individual. When individuals die, the probability of dying within one year is the inverse of the annual survival probability. Dead individuals are found and reported with a certain probability, the recovery probability. The multinomial dead recovery model enables estimating separate survival probabilities, migratory connectivity and recovery probabilities for all predefined destination areas. The parameters are identifiable when an equal or higher number of populations of origin than destination areas is available and no two populations of origin show the same migratory connectivity pattern.

Spatial explicit survival analyses should benefit from a continuous version of the multinomial dead recovery model, which makes use of more information in the given data and thereby better fits the data. The multinomial dead recovery model acts on the population level, only making use of the counts of marked individuals in the areas of origin and recovered individuals per destination area. However, geographical coordinates are often known for locations, where individuals were recovered dead. These geographical coordinates provide additional information which can be used to estimate a continuous distribution in space. Moreover, defining discrete destination areas, e.g., by country boundaries, is arbitrary and averaging over these areas may not reflect the underlying ecological characteristics of these areas. Developing a model in continuous space, e.g., by point processes, uses all spatial information available in the data and meets the characteristics of the continuous parameters. Therefore, it may reveal survival patterns not seen in discrete space.

1.3. Point processes

One approach to obtain spatially continuous models are spatial point processes. They can model spatial point patterns produced by individual based observations such as counts of unmarked animals and live recaptures, resightings or dead recoveries of marked animals (e.g., Illian et al., 2008). Binomial or Poisson point processes are commonly used in ecological applications. Mostly, it suffices to describe this point process by its intensity. The intensity corresponds to the expected number of points in an area, called the intensity measure. An associated intensity function exists, which integrates to the intensity measure over the specified area. This intensity function is a density function, which can be estimated using classical parametric or non-parametric statistical methods, e.g., the simple technique of kernel density estimation (see the literature on density estimation for more complex methods). For example, point processes are used in distance sampling to model the abundance of a species or the species distribution in a certain area (Buckland et al., 2015). Another area of application is spatial capture recapture, modeling the home ranges or

use of space by individuals (Royle et al., 2013). Johnson et al. (2010) and Yuan et al. (2017) use thinned Poisson point processes to model count data, where the detection probability obtained from distance sampling design scales the intensity function.

We here use a similar thinned binomial mixed point process model to estimate survival from a species distribution, when the species distribution (and the intensity function) is seen as a product of multiple biological and/or methodological processes.

1.4. Aims

Based on the multinomial dead recovery model, our aim is to formulate a fully stochastic spatially continuous model for survival and for migratory connectivity corrected for survival. We try to balance between a not too complicated mathematical approach and a model, which covers enough biological complexity to be applied to real world data. For an easier understanding of our work, we keep the modeling framework simple and achieve this aim under the constraint of a constant observation process over space and time (for a relaxation of this assumption using optimization see Schirmer, 2022). Additionally, we aim to cover all steps from theoretical model development to model application to real world data. Therefore, we develop our work in three main parts. The first part (Section 3) is of theoretic nature: here, we formulate a fully stochastic model by using the intensity function of a thinned mixed binomial point process to provide estimates for all parameters. The second part (Section 4) functions as a bridge between the theoretic model and the applied model to real world data. There, we generate from known parameter values an intensity function of a point process, from which we sample spatial locations for hypothetical dead recoveries of individuals. From these spatial locations we estimate the density, which corresponds to the intensity function of the point process. To the estimated density we apply the method to estimate the parameters developed in Section 3. This enables us to investigate the performance of the model by comparing the estimated to the known parameter values. Finally, in Section 5 we apply the model to a real-world data set of European robins *Erithacus rubecula*. In the data set, every single marked bird generates one data point if it is found dead and reported in winter.

2. Model

In the following, $\mathbb{N}_{>0}$ denotes all positive integers excluding zero and $\mathbb{N}_{\geq 0}$ denotes all positive integers including zero. Let us consider $n = \sum_{b=1}^B n_b$ marked individuals, where $n_b \in \mathbb{N}_{>0}$ individuals are marked in an area of origin b out of a discrete set of investigated areas of origin $B = \{1, \dots, b, \dots, B\}$, where B is the number of areas of origin. All individuals migrate to a continuous destination space $\mathcal{W}$, which can be one-dimensional ($\mathcal{W} \in \mathbb{R}$, e.g., corresponding to the distance to the spring of a river) or two-dimensional ($\mathcal{W} \in \mathbb{R}^2$, e.g., corresponding to longitude and latitude in geographical space). In the destination space, the individuals can stay or die at exact geographical coordinates $w \in \mathcal{W}$ during time spent at the destination location. The continuous nature of space makes that migratory connectivity may lead to individuals of one area of origin using geographically dispersed points in destination space, while the points of individuals of different areas of origin may be close to each other. Migratory connectivity is the density of individuals originating from one population of origin over the whole destination space. It contains migration as a seasonal, directed, recurring movement and implicitly, also small random movements in the destination space. A random number $k \in \mathbb{N}_{\geq 0}$ of individuals are found as dead recoveries in the destination space. The recovery status of an individual is indicated by the random variable Z , where $Z = 1$ if an individual is found dead, and $Z = 0$ if it is not found. Every individual recovered dead originates from an area of origin, is found at geographic coordinates in the destination area, and displays an age at death. The age at death is an element of the set of observed years $\mathcal{T} = \{1, \dots, t, \dots, T\}$,

where T denotes the length of the observation period. Therefore, the dead recoveries are written as $(x_i)_{i=1}^k = ((b_1, w_1, t_1), \dots, (b_k, w_k, t_k)) \in B \times \mathcal{W} \times \mathcal{T}$, where i denotes the i th dead recovery of the whole population in an arbitrary numeration. When only considering dead recoveries belonging to a specific area of origin b , we write $(x_i^{(b)})_{i=1}^{k_b} = ((w_1, t_1), \dots, (w_{k_b}, t_{k_b})) \in \mathcal{W} \times \mathcal{T}$, where i denotes the i th dead recovery of the b th population in an arbitrary numeration. The parameters of the model are functions of space: the annual survival probability $s : w \mapsto (0, 1)$, the constant recovery probability $r \in (0, 1)$ and, for each $b \in B$, the density migratory connectivity $m_b : w \mapsto \mathbb{R}$. This means, $m_b(w) \geq 0$ and $\int_{\mathcal{W}} m_b(w) dw = 1$. When a model or parameter describes aggregated data ignoring the assigned area of origin, we use B as a subscript, e.g., m_B is the migratory connectivity function of the whole data set.

3. Method

We model the point pattern of the dead recoveries as the intensity function of a point process composed of a product of processes described by the parameters survival, migratory connectivity and recovery probability. Estimating the intensity function can be done by any density estimation method. We choose the kernel density estimator to keep the method simple and to focus on parameter estimation. Similar to the approach of the multinomial dead recovery model, the parameters are estimated stepwise: in a first step, we estimate survival using parts of the intensity function. In a second step, we estimate a joint function of migratory connectivity and recovery probability using parts of the intensity function and the survival estimate from step 1. In a third step, we disentangle migratory connectivity and recovery probability from the joint function estimated in step 2. To keep the focus of the paper on survival estimation, we assume a constant recovery probability. Step 3 can be enhanced to more complex scenarios, e.g., by combining this approach with the discrete domain multinomial dead recovery model and using optimization (Schirmer, 2022).

3.1. The intensity function

The geographic coordinates and ages at death of the dead recoveries can be seen as a random pattern of points in a two- or three-dimensional sample space. The geographic space can have one or two dimensions, whereas one dimension always reflects the age at death of the recoveries. Vividly, we obtain a density function consisting of a stack of discrete layers reflecting the ages at death (see Appendix E). For example, the area under the layer of the individuals which died at age 1 is the proportion of individuals dying at age 1 in the total population. Consequently, the sum of the areas under all layers is 1. Formulating this stacked density function is fundamental for estimating survival. We model this density as the intensity function of a mixed binomial point process (for an even more detailed explanation see Schirmer, 2022). For this we theoretically formulate how we define a mixed binomial point process:

Definition 1 (Mixed Binomial Point Process). Let $(\Omega, \mathcal{F})$ be a measurable space, where Ω is the sample space and $\mathcal{F}$ the corresponding sigma algebra. Let $K \in \mathbb{N}$ be a random number independent of X , the random numbers $X = (X_1, X_2, \dots, X_K) \in \Omega$ be independent identically distributed with $X_i \sim P$ and $k \in \mathbb{N}_{\geq 0}$. The indicator function is a random measure defined by:

$$\mathbb{1}_A(x) := \begin{cases} 1 & \text{if } x \in A \\ 0 & \text{if } x \notin A. \end{cases}$$

The number of points in a subset $A \in \mathcal{F}$ is given by the counting measure $\varphi_A(X) := \sum_{i=1}^K \mathbb{1}_A(x_i)$.

The distribution of these numbers is called mixed binomial point process given by P and the distribution of K . It is written as the random measure

$$\beta_{K,P}(\{\varphi : \varphi_A(X) = k\}) = \mathbb{P}(\{|i : X_i \in A| = k\}).$$

Observe that the probabilities $\mathbb{P}$ are binomial characterizing β .

Now, we define the distribution of dead recoveries as a mixed binomial point process as in [Definition 1](#). In simple terms, this point process describes how the number of individuals marked gives rise to the number of individuals recovered, and how the density function of these recovered individuals looks like in terms of space and age class.

Definition 2. Let $k_b \in \mathbb{N}_{\geq 0}$, $i \in \{1, \dots, k_b\}$, $n_b \in \mathbb{N}_{>0}$ and consider an area of origin $b \in \mathcal{P}(\mathcal{B}) \setminus \emptyset$. For $X = (x_i^{(b)})_{i=1}^{k_b} = (w_i, t_i)_{i=1}^{k_b} \in A \subseteq \mathcal{W} \times \mathcal{T}$, X is independent identically distributed with $(X_i)_{i=1}^{k_b} \sim P_{rec}$, where the density

$$P_{rec}(w, t) = \frac{m_b(w)s(w)^{t-1}(1-s(w))^r}{P(Z=1, b)}, \quad (1)$$

where

$$P(Z=1, b) = \int_{\mathcal{W}} m_b(w)(1-s(w))^T r dw$$

is the normalizing factor.

The count of found individuals of one area of origin b is a random variable

$$k_b \sim \text{Bin}(n_b, P(Z=1, b)). \quad (2)$$

The mixed binomial point process given by k_b and P_{rec} is denoted $\beta_{k_b, P_{rec}}(\{\varphi : \varphi_A(x^{(b)}) = k\})$.

The subdensity of found individuals consists of the terms for survival, migratory connectivity, and recovery probability. We obtain a valid density in Eq. (1) by normalizing the subdensity with the overall probability to be found. This probability, $P(Z=1, b)$ is a marginalized probability independent of the observation period and the destination area and should not be confused with the recovery probability $r = P(Z=1 | t \leq T, w, b)$, which is conditional on dying within the observation time and within the observation space. It is important to consider only the found individuals for the density, and simultaneously address the probability of the found individuals explicitly. Combining the distributions of found individuals from different populations makes absences of found individuals of other populations informative. Eq. (2) contains information of the not found individuals.

Remark 1. For each $w \in \mathcal{W}$ the density P_{rec} (Eq. (1)) is spatially locally log-linear in the age at death t :

$$\begin{aligned} \ln(P_{rec})(w, t) &= \ln m_B(w) + \ln(1-s(w)) + \ln(r) \\ &\quad - \ln \left(\int_{\mathcal{W}} m_B(\tilde{w})(1-s(\tilde{w}))^T r d\tilde{w} \right) \end{aligned} \quad (3)$$

$$+ (t-1) \ln(s(w)) \quad (4)$$

So, we can interpret $\ln(P_{rec})(w, t)$ as a locally linear model $y_t(w)$ in a point w of the form $y_t(w) = \beta_0(w) + \beta_1(w)(t-1)$. The intercept β_0 corresponds to the first part of Eq. (3) and the slope β_1 to $\ln(s(w))$ in Eq. (4).

3.2. Parameter estimation

3.2.1. Estimation of the survival probability function

Assuming the survival probability to be independent of the areas of origin, enables survival estimation by jointly considering all dead recoveries available at all possible time steps:

Theorem 1. Let us use the data set of dead recoveries aggregated over all areas of origin and let

$$y_{t,B}(w) = \ln(P_{rec})(w, t) = \beta_{0,B}(w) + \beta_1(w)(t-1),$$

be a model (see [Remark 1](#)), which is at point $w \in \mathcal{W}$ linear in t . Then the estimator of the survival probability function in a point $w \in \mathcal{W}$ is $\hat{s}(w) = e^{\beta_1(w)}$.

For the proof of [Theorem 1](#) see [Appendix A](#).

The assumption that survival is independent of the area of origin means that estimated survival will reflect an average value over all individuals from different areas of origin that migrated to the same destination. This must be kept in mind when interpreting the estimated survival values. Alternatively, one model can be fitted to every area of origin, if the sample size for each area is sufficiently high.

3.2.2. Estimation of the migratory connectivity density function corrected for survival

Knowing the survival probability and the properties of the migratory connectivity density function, enables us to estimate the latter while assuming (for simplicity) a constant recovery probability over space:

Theorem 2. For every area of origin $b \in \mathcal{B}$ we use the data set of dead recoveries marked in this area of origin and the model from [Theorem 1](#) conditioned on the b th area of origin

$$y_{t,b}(w) = \ln(P_{rec,b})(w, t) = \beta_{0,b}(w) + \beta_1(w)(t-1).$$

Let $\hat{s}(w)$ be as in [Theorem 1](#), $\int_{\mathcal{W}} m_b(w) dw = 1$ and $r \in (0, 1)$. The migratory connectivity density function can be estimated by $\hat{m}_b(w) = e^{\beta_{0,b}(w)} / (c_b(1 - \hat{s}(w)))$, where the constant $c_b = \int_{\mathcal{W}} e^{\beta_{0,b}(w)} / (1 - \hat{s}(w)) dw$.

For the proof of [Theorem 2](#) see [Appendix B](#).

3.2.3. Estimation of the constant recovery probability

Theorem 3. Let the model $y_{t,b}(w)$ and c_b be like in [Theorem 2](#). n_b is the count of marked individuals in the area of origin b and k_b the number of recovered dead individuals marked in the area of origin b . Then the maximum likelihood estimator for the recovery probability function is $\hat{r} = \hat{r}_b = c_b k_b / n_b$.

For the proof of [Theorem 3](#) see [Appendix C](#).

4. Numerical simulations

4.1. Method

Two simulation studies, in one- and two-dimensional space respectively, show the performance of the model. For simplicity, the destination area is a unit interval or a unit square, respectively. We simulate data using the stochastic relationships from [Definition 2](#) (values in [Table 1](#)). The simulation algorithm consists of two main steps repeated for every area of origin:

- Choose B , $\mathcal{W}$, T , r , $s(w)$.
- For every $b \in \{1, \dots, B\}$:
 - Choose n_b , $m_b(w)$.
 - Determine the count of individuals marked in b found anywhere in $\mathcal{W} \times \{1, \dots, T\}$ by $k_b \sim \text{Bin}(n_b, P(Z=1, b))$ ([Definition 2](#), Eq. (2)).
 - Sample k_b data points representing the recovered individuals $X = (w_i, t_i)_{i=1}^{k_b} \sim P_{rec}$ ([Definition 2](#), Eq. (1)).

As P_{rec} is a probability density function of potential complex shape, the sampling process can be done by rejection sampling ([Von Neumann, 1951](#)). We propose as a proposal distribution a product of one or two beta distributions depending on the dimensionality of space and a geometric distribution truncated at the maximum observation time T . Hereby, the beta distributions cover the spatial component, while the truncated geometric distribution covers the temporal component.

To estimate the intensity function of the point process, we used the functions for spatio-temporal kernel density estimation of the R-package `sparr` ([Davies et al., 2018](#)). We automatically selected a

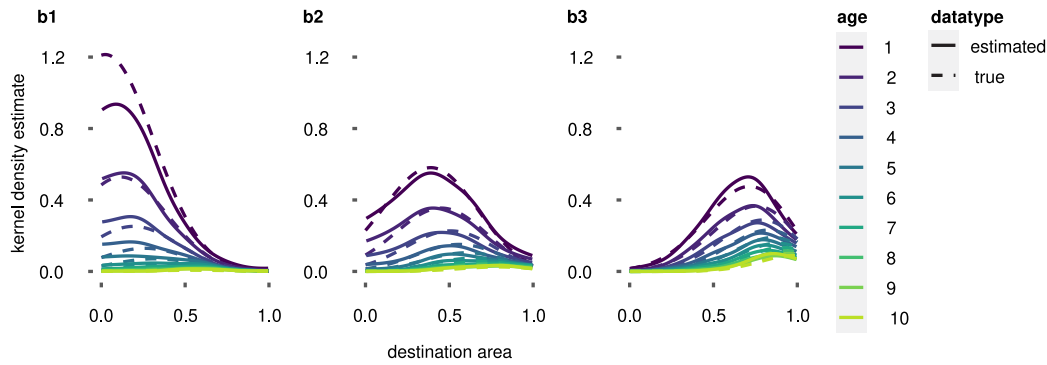


Fig. 1. True (dashed line) and estimated (solid line) kernel density for a simulated data set of three single areas of origin (b1, b2, b3) in one-dimensional space. Age at death is indicated by color, where darker colors indicate a lower age at death. This figure appears in color in the electronic version of this article, and color refers to that version.

Table 1

Values for simulation study in one- and two-dimensional continuous space, respectively. pdf: probability density function. $\mathcal{N}^{trunc}$: normal distribution truncated by the borders of $\mathcal{W}$.

	One-dimensional	Two-dimensional
B	3	3
T	10	10
n_b	10^5	10^5
μ	(0.1, 0.5, 0.9)	(0.1, 0.5, 0.9)
$\mathcal{W}$	[0, 1]	$[0, 1] \times [0, 1]$
$s(w)$	$0.4 + 0.5w$	$0.4 + 0.2 \sum_{i=1}^2 w_i$
$m(b, w)$	pdf of $\mathcal{N}^{trunc}(\mu_b, 0.3)$	pdf of $\mathcal{N}^{trunc}\left(\mu_b, \begin{pmatrix} 0.3 & 0 \\ 0 & 0.3 \end{pmatrix}\right)$
r	0.01	0.01

constant spatial bandwidth using an oversmoothing bandwidth selector (Davies and Hazelton, 2010; Terrell, 1990). We set the temporal bandwidth to 1.1 slightly oversmoothing the temporal component with a true temporal bandwidth of 1. To limit computation time, the resolution was set to 100 points per unit interval in both spatial directions. We estimate all parameters using the continuous space approach described above and implemented in the R-package CONSURE (Schirmer, 2021). Survival is estimated using robust linear regression by computing an MM-type regression estimator (Maechler et al., 2019).

We evaluate the variability of all parameters by non-parametric bootstrapping the simulated data set and generating 999 bootstrap-data sets. For every area of origin, we sample with replacement n_b individuals from the marked individuals in this area of origin. The set of dead recoveries and the age at death are sampled indirectly: a dead recovery will be part of the data set, if the corresponding marked individual is sampled and the age at death is the age corresponding to the original dead recovery. In this approach of a stratified bootstrap the number of marked individuals per area of origin remains fixed, while all other parameters (survival, migratory connectivity and recovery probability) vary by the sampling approach. For every initialization data set, the parameters are estimated. The bootstrap confidence interval is the 0.025- and the 0.975-quantile of the 999 estimated parameters of all bootstrapped data sets in this specific point, reflecting the variability of one parameter in a specific point.

4.2. Results

The results do not differ in one- and two-dimensional space. We, therefore, only illustrate the kernel density estimates of the one-dimensional case, because visualizing the kernel density in two dimensions would need a not easily readable large number of plots. The kernel density fits the shape of the true density, but is slightly biased at the edges of the destination area (Fig. 1). This bias influences the estimates of all parameters at the edges of the study area, whereas the parameter estimates in the main part of the study area are reliable.

The survival estimator approximates the true values in the center of the spatial distribution well. However, close to the edges, biased estimates occur for high and low values. Overestimation and underestimation is associated with larger bootstrap confidence intervals and lower R^2 values of the linear regression (Figs. 2 and 3). Overall, R^2 values are near 1 indicating a good fit.

The estimates of migratory connectivity corrected for survival (Figs. 4 and 5) also fit the shape of the true values. Likewise, they are biased near the edges.

The recovery probability is estimated in one-dimensional space as 0.0099 (bootstrap interval: 0.0094–0.0107) and in two-dimensional space as 0.0100 (bootstrap interval: 0.0097–0.0107).

5. Real world data analysis

5.1. Data set

We apply the method to the same data set (Schirmer et al., 2022b) used in Schirmer et al. (2022a) to be able to compare the results between the multinomial dead recovery model and the spatially continuous model presented in this article. This small and simple data set shows that our model is applicable to real-world data. The following description is already published in Schirmer et al. (2022a): The data set of robins is gathered at the island Greifswalder Oie in the Baltic Sea 54°15'N 13°55'E, Germany. This data set contains 98 399 individuals banded during fall migration from 1994 to 2018. Until 2018, in total, 48 of these individuals were found dead during the period from November to February of any year after marking. Migrating robins should have reached their destination areas by November, and should not start migrating back to their areas of origin before March. The island Greifswalder Oie is used as a stopover site by robins during migration. Therefore, the area of origin of the individuals is unknown. However, we can assume that individuals with different passage dates have different areas of origin (Korner-Nievergelt et al., 2014; Remisiewicz, 2002; Pettersson and Lindholm, 1983). Commonly, the earlier individuals start migrating in fall, the further north they breed. Arbitrarily, we define three discrete areas of origin corresponding to early, intermediate and late passage dates by using the 1/3- and 2/3- quantile of individual passage dates, respectively. For example, we assume an individual to migrate early when it belongs to the 1/3 earliest migrating individuals marked on the island across all years. This results in a time span from the 1st August to 23rd September for early passage ($n = 34\,177$), from 24th September to 6th October for intermediate passage ($n = 32\,389$) and from 7th October to 6th November for late passage ($n = 31\,833$). The banding season, i.e., days with capture effort, truncates the passage dates at the 1st August and the 6th November.

We model an equal annual survival for juvenile and adult robins, although typically most juveniles are considered to have a much lower survival than adults. This difference is mostly explained by high mortality in the pre- and post-fledgling period in juvenile songbirds (see

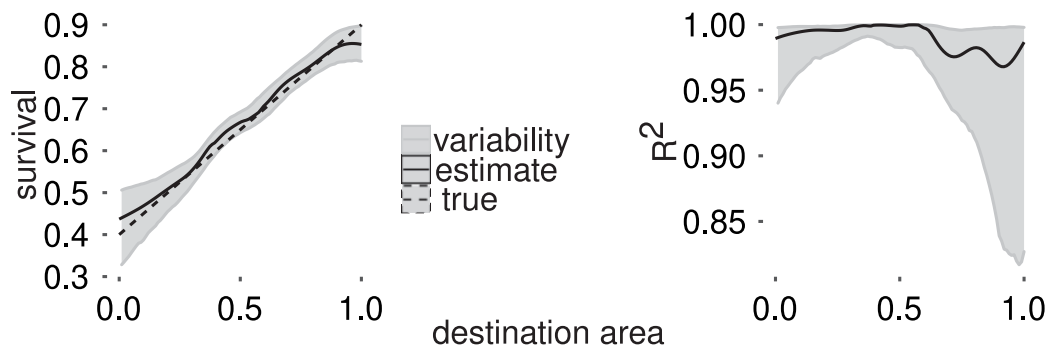


Fig. 2. Survival probability s (left) and goodness of fit (right) for a simulated data set in one-dimensional space. True (dashed line) and estimated (solid line) annual survival probability s with the 0.025- and 0.975- quantile of 999 bootstrapped data sets (gray area). The R^2 -values of the linear model show the goodness of fit, with a perfect fit indicated by a value of 1.

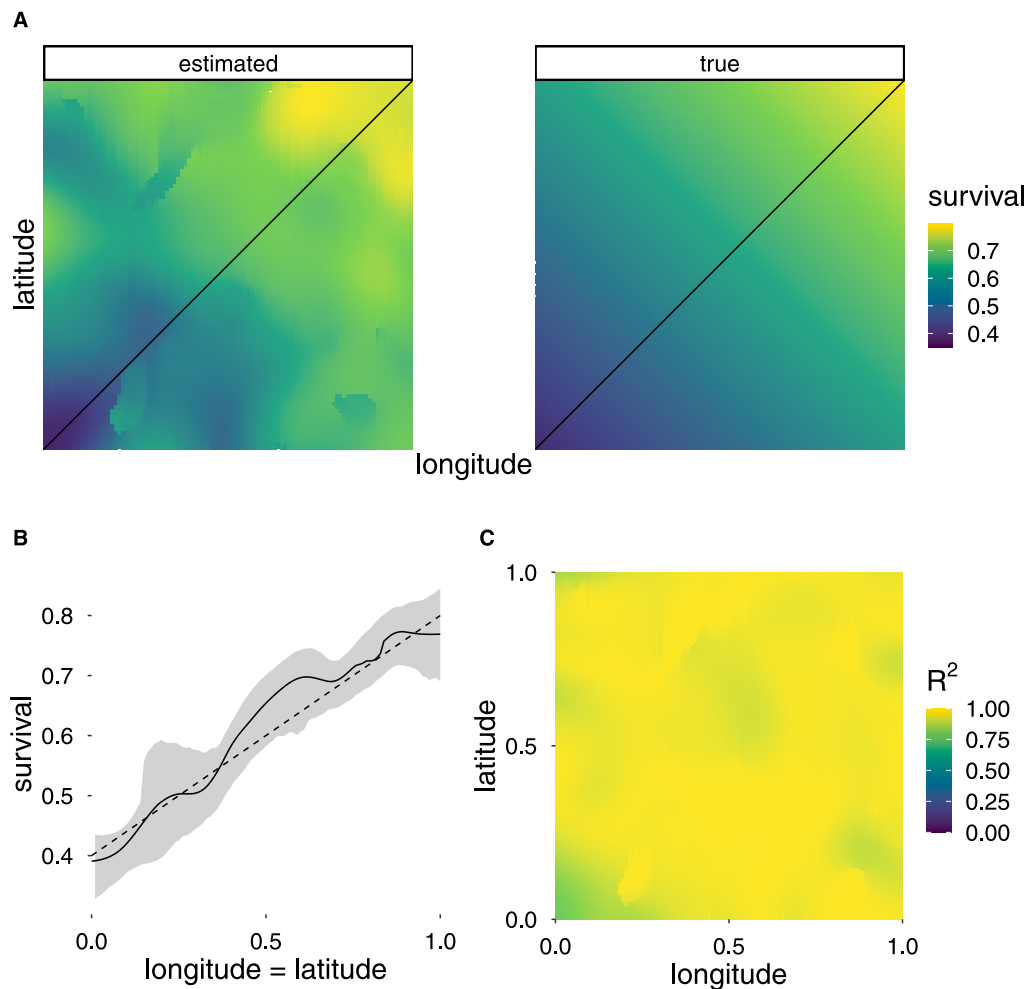


Fig. 3. Survival probability s (A), exemplary bootstrap confidence interval for s (B) and goodness of fit (C) of a simulated data set in two-dimensional space. (A): Estimated (left) and true (right) annual survival probability s , lighter colors indicate higher values. The black line in the left plot and the dashed line in the right plot show the profile line, which is the basis for plot B. (B): Variability of survival exemplarily given for the profile line shown in plot A. Estimated survival (solid line) and 0.025- and 0.975- bootstrap confidence interval (gray area) and true survival (dashed line). (C): The R^2 -values of the linear model show the goodness of fit, with a perfect fit indicated by a value of 1. This figure appears in color in the electronic version of this article, and color refers to that version.

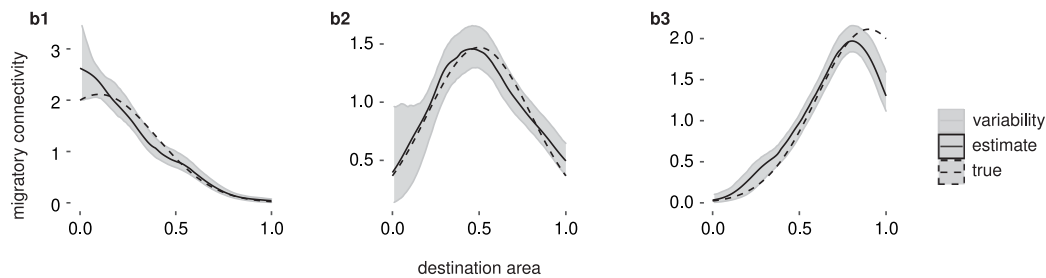


Fig. 4. Migratory connectivity for a simulated data set in one-dimensional space for the areas of origin b1 (left), b2 (center), and b3 (right). True migratory connectivity m (dashed line), estimated migratory connectivity m (solid line) and the 0.025- and 0.975- bootstrap confidence interval (gray area).

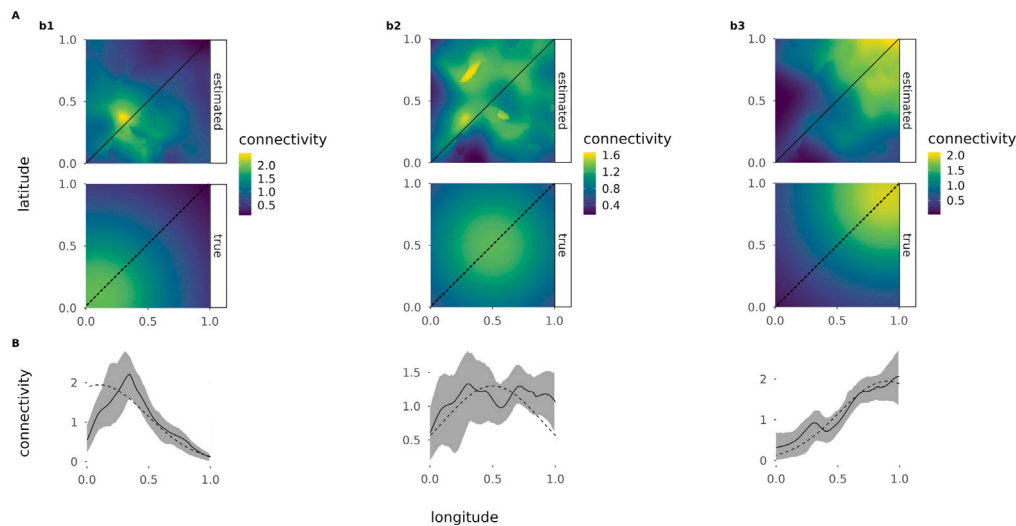


Fig. 5. Migratory connectivity m (A) and exemplary bootstrap confidence interval for m (B) for a simulated data set in two-dimensional space. The left panel displays the area of origin b1, the central panel the area of origin, and the right panel the area of origin b3. (A): Estimated (upper row) and true (lower row) migratory connectivity. Lighter colors indicate higher values. The black line in the upper plot and the dashed line in the lower plot show the profile line, which is the basis for plot B. (B): Variability of survival exemplarily given for the profile line shown in plot A. Estimated migratory connectivity (solid line) and 0.025- and 0.975- bootstrap confidence interval (gray area). This figure appears in color in the electronic version of this article, and color refers to that version.

the review of Naef-Daenzer and Gruebler, 2016). In our study, juveniles are marked during migration, so juveniles which do not survive the pre- and post-fledgling period are not represented in the data set. Therefore, the survival of juveniles in this particular data set is likely to be similar to the survival of adults. Such a pattern of equal non-breeding survival between juveniles and adults is also supported by Gruebler et al. (e.g., 2014).

The model only considers the age at death of the individual, not the specific years. The age at death is reconstructed from the year of marking and the year of recovery. During fall migration, robins can be assigned into two age classes, i.e., first-year individuals hatched within the same year and individuals hatched at least in the preceding year (Svensson, 1992). Therefore, the exact year of birth is only known for the first-year individuals. All other individuals only have a minimum age, which we used as the age. Nevertheless, we consider all birds for analysis to increase the sample size.

We define the destination area by outlining the area where robins ringed on the Greifswalder Oie potentially occur. For that, all locations of alive and dead ring re-encounters of robins marked on the island Greifswalder Oie ($n = 142$) and found during the whole annual cycle are considered. We calculate a buffer of 3.5° around these locations using qGIS (QGIS Development Team, 2021) (see Schirmer et al., 2022a).

Because robins were banded every fall between 1994 and 2018, and we only include dead recoveries until 2019, observation time varies between one and 24 years. All robins except one were recovered dead one to four years after marking and therefore, we use an observation

period of five years. For technical reasons, we discarded the only older bird reaching an age of at least 16. We use this data set as a simple example data set and ignore for this purpose time-dependent effects, which may have occurred during the 24-year-period of observation.

5.2. Parameter estimation

We estimate survival, migratory connectivity corrected for survival and recovery probability in two-dimensional space as described in Sections 3 and 4. The spatial resolution is 100×100 points over the entire destination area.

The variability of the parameters for survival, migratory connectivity and recovery probability is evaluated by non-parametric bootstrapping as described in the simulation study.

5.3. Results

The raw data (Fig. 6) suggests that early passing robins are found mostly in Spain, Portugal, and France. The intermediate passing robins overwinter mainly in France, whereas the late passing robins remain in Germany, Belgium, and the Netherlands. There are no dead recoveries east of Germany and Italy or North to Denmark between November and February.

The estimated survival pattern (Fig. 7A) shows high annual survival of around 0.5 for robins wintering in Portugal and Spain. The values decrease towards northeastern and southeastern directions to values

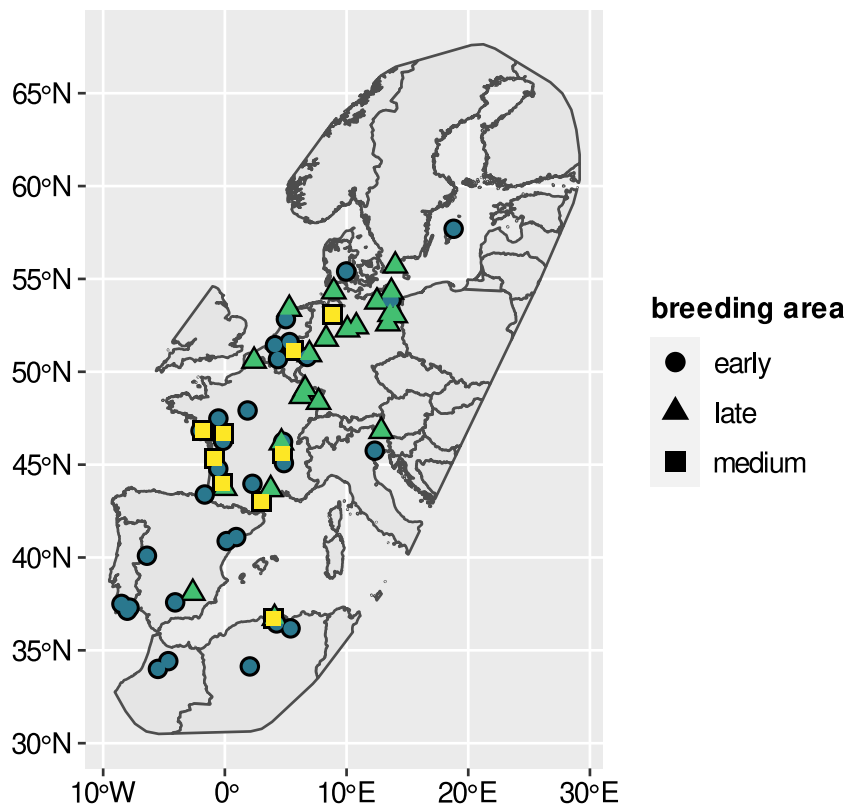


Fig. 6. Distribution of the raw data of dead recoveries of European robins marked on the island Greifswalder Oie during autumn migration. Different areas of origin are indicated by the shape and color: early (dark circle), intermediate (light square), late (medium light triangle). This figure appears in color in the electronic version of this article.

around 0.3 for individuals wintering in Northern Germany and Northern Africa. The goodness of fit (Fig. 7B) is quite high overall. Slightly lower values occur in Great Britain, northwestern Portugal and Spain, northwestern Africa and the northwestern edge of the Balkan peninsula, where no dead recoveries occurred (see Fig. 6).

According to the migratory connectivity pattern corrected for survival (Fig. 8) most robins migrate to the Atlantic coast of France or stay at the coasts of the Baltic Sea and the North Sea (note the different scales between the subplots in Fig. 8). The early migrating birds overwinter most southerly in Spain, Portugal, Northern Africa and the French west coast. The intermediate migrating birds stay in central destination areas, mainly at the French west coast. The late migrating robins overwinter the closest to the stopover site in Germany, the Netherlands, Denmark, Belgium and Eastern France.

The recovery probability is estimated as 0.0005 (bootstrap confidence interval: 0.0004–0.0007).

6. Discussion

The study extends the discrete domain multinomial dead recovery model (e.g., Schirmer et al., 2022a) to the continuous domain using thinned mixed binomial point processes. Our method uses a density estimated from the point pattern generated by dead recoveries of marked animals. This density directly links all model parameters survival, migratory connectivity and the recovery probability. The model parameters are estimated step by step: firstly, spatially varying survival from the information of age at death, secondly, the joint function of migratory connectivity and recovery probability and thirdly this joint function is disentangled in a migratory connectivity function corrected for the survival estimates and the recovery probability. This approach

produces continuous survival maps and maps of migratory connectivity corrected for survival. For simplicity, we here assume a constant recovery probability and we describe how to relax this assumption elsewhere.

In contrast to most models in the mark-recapture framework, the approach presented in this study estimates spatial variation in survival, while simultaneously operating on a continuous spatial domain. This supports the approach of Péron et al. (2011), who investigates spatially continuously varying survival and imperfect detection, but no space use. Other models that allow spatial variability in survival are mostly multinomial models that operate on a discrete spatial domain, such as the multi-state models (Schwarz et al., 1993; Gauthier and Lebreton, 2008; Conn and Cooch, 2009) especially the multinomial dead recovery model (Thorup and Conn, 2009; Bauthian et al., 2007; Korner-Nievergelt et al., 2010b). Models like the closed population spatial capture recapture models (Royle et al., 2013) or the open population spatial capture recapture models (Gardner et al., 2018) operate on the continuous domain, but focus mainly on estimating spatial movement processes, while survival is space-independent. This means they estimate one constant survival over space, which is corrected for biases generated by animals moving in space. These two views on survival do not necessarily contradict each other, but only illuminate different aspects of the complex interplay between demography and animal movement.

Results from numerical simulations in one- and two-dimensional space and the application to real-world data show that the presented model successfully estimates spatial survival and migratory connectivity corrected for survival. The numerical simulations indicate unbiased model estimates at a sufficient distance from the edge. The shape and location of the estimated intensity function, survival, migratory

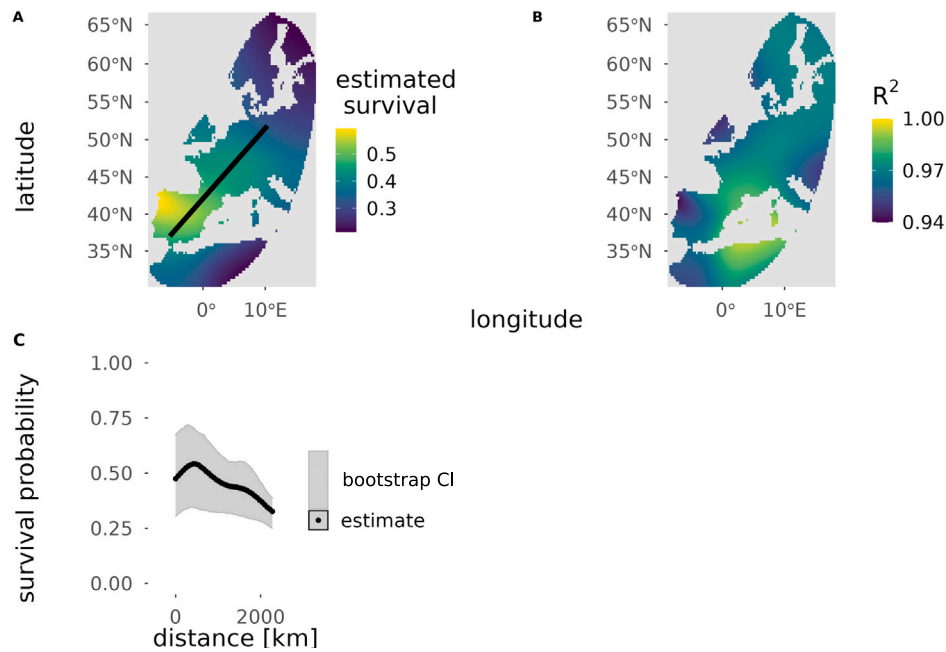


Fig. 7. Survival probability s (A), exemplary bootstrap confidence interval for s (C) and goodness of fit (B) of European robins found dead between November and February. The robins are marked on the island Greifswalder Oie during autumn migration. (A): Estimated annual survival probability s , lighter colors indicate higher values. The black line in the left plot shows the profile line, which is the basis for plot B. (B): The R^2 -values of the linear model show the goodness of fit, with a perfect fit indicated by a value of 1. This figure appears in color in the electronic version of this article, and color refers to that version. (C): Exemplary plot of the variability of estimated survival along the profile line shown in plot A. Estimated survival (solid line) and 0.025- and 0.975- bootstrap confidence interval (gray area).

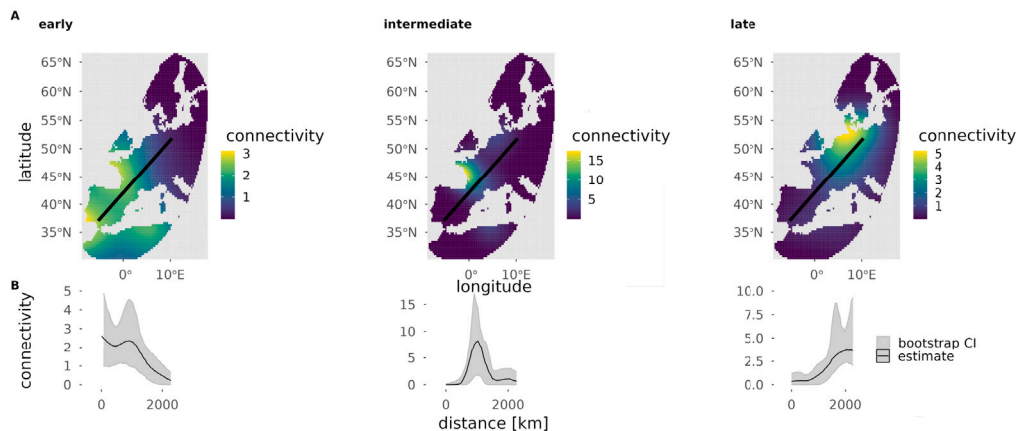


Fig. 8. Migratory connectivity m (A) and exemplary bootstrap confidence interval for m (B) of European robins marked on the island Greifswalder Oie during different periods of autumn migration (early (left), intermediate (central), late (right)) and found dead from November to February. (A): Estimated migratory connectivity. Lighter colors indicate higher values. The black line in the plot shows the profile line, which is the basis for plot B. (B): Variability of survival exemplarily given for the profile line shown in plot A. Estimated migratory connectivity (solid line) and 0.025- and 0.975- bootstrap confidence interval (gray area). This figure appears in color in the electronic version of this article, and color refers to that version.

connectivity and recovery probability is approximately correct with a lower model fit at the edges and at extreme values. Results of the analysis of the robins data are in line with the results of the discrete domain model (see Fig. 9, Schirmer et al. (2022a)). The continuous map of survival reveals a continuous survival gradient from southwest to northeast, while the discrete model indicate a stepwise decline of survival in the same direction. The migratory connectivity estimates corrected for survival match with the already described leapfrog migration pattern of European robins (Korner-Nievergelt et al., 2014; Schirmer et al., 2022a). This pattern is indicated by more Northern breeding birds wintering further South, so that they overtake the more Southern breeding birds.

The consistent results between discrete and continuous domain model occur even though the two models differ elementarily in the assumption for the recovery probability. The continuous domain model

assumes a constant recovery probability, whereas the discrete domain model enables spatially variable recovery probabilities for the different areas, which are estimated as not constant for the robins' data set (recovery probability North: 0.0010 (0.95-CrI: 0.0003–0.0031), Central: 0.0005 (0.95-CrI: 0.0002–0.0015), South: 0.0006 (0.95-CrI: 0.0002–0.0013), see Schirmer et al., 2022a). Therefore, the qualitative effect of survival and migratory connectivity seems to be strong enough to become visible under both assumptions, spatially constant or non-constant recovery probability.

The continuous survival map resulting from our method is a novelty in mark recapture modeling. Continuous varying survival from the theoretical intensity function of the thinned mixed binomial point process formulated in the method section, is identifiable and independent of identifiability issues in disentangling migratory connectivity and recovery probability. This allows us to describe spatial variation in

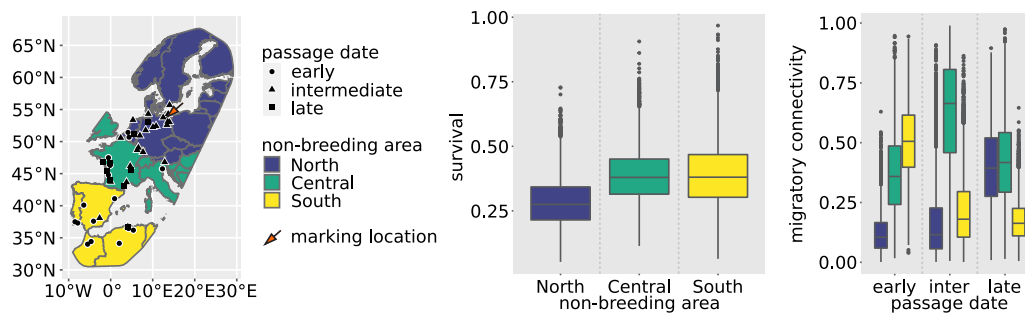


Fig. 9. Results of the discrete domain model: discrete partitioning of the destination space (left), survival estimates (middle) and migratory connectivity estimates (right).

survival of a certain species independent of their movement behavior, e.g., in our example data set, robins survive better the more south they overwinter. Such a result opens up the possibility to investigate survival in the context of other spatial continuous covariates. For example, the survival pattern of the robins may be correlated with winter temperature or snow cover.

The migratory connectivity maps corrected for survival, support the approach of Rushing et al. (2021), who discuss how spatial variation in survival can distort the picture suggested by observational data on animal distributions. Therefore, our model allows interpreting survival and migratory connectivity separately from each other. The survival and migratory connectivity maps of the example data set show that early migrating robins more likely migrate to wintering areas, where survival is higher. A pattern like that may be linked to life-history strategies of different populations in further research studies.

By formulating the recovery model in continuous space, some assumptions made by the multinomial dead recovery model can be omitted: firstly, the complete geographic information from the data can be used and survival can be estimated continuously varying in space. This allows for more detailed statements on survival, for which arbitrary spatial divisions such as country boundaries become unnecessary. For example, in our example data set, robins survive better the more south they overwinter. Secondly, as the destination area is a single continuous space, the number of available populations of origin no longer limits the spatial resolution of the model parameters. Thereby, the possible spatial resolution increases enormously from approximately 3–5 in the discrete scenario to theoretically infinite, depending on the sample size of dead recoveries. Besides that, the model can also be used for one single population of origin or for more than one population showing the same migratory connectivity pattern. By eliminating these assumptions, the continuous model operates directly on the raw data, has fewer demands on the data structure and the results are less dependent on the data preparation done by the modeler.

To increase understandability of the complex parameter estimation method, we have used a simple model structure. Firstly, the recovery probability is constant in space. This is a restrictive assumption not reflecting the current knowledge over observation processes (reviewed by Korner-Nievergelt et al., 2010a). However, in the example data set of robins this assumption does not have a qualitative effect in the resulting survival and migratory connectivity estimates compared to the results from the discrete domain multinomial dead recovery model. Secondly, all model parameters are time-independent and have no age structure. Therefore, time or age effects cannot be explored, which limits the interpretability of the results in the robins data set to spatial effects on survival and migratory connectivity. As the purpose of this work is to introduce the techniques allowing to disentangle migratory connectivity from survival on a continuous spatial scale, we kept other structures of the model simple. However, more complexity of these structures could be added to the model at a later stage. For example, we already implemented estimation under spatially heterogeneous recovery probability in the R-package CONSURE (Schirmer, 2021).

Although this method can theoretically achieve a very high spatial resolution, the spatial resolution that can be achieved in practice is limited by the available sample size of the dead recoveries. The lower the sample size the stronger needs to be the smoothing over the space. It is well-known that estimating the intensity function of a point process from imperfect data can only approximate the true underlying intensity function (e.g., Farrell, 1972) and it is beyond the scope of this study to deal with this problem in detail. The fewer dead recoveries, the coarser the resulting maps of survival and migratory connectivity. The very small sample of the robin data set is only suitable for a very coarse spatial resolution. Therefore, we only interpret the rough increase of survival from the north-east to the south-west, but no small-scale details of the maps. Thus, the results of the continuous domain model do not provide more detailed information than the discrete domain model when sample size is low, but the level of detail will increase with increasing sample size.

The results of this study are also limited by the use of dead recovery data only. Survival estimates from dead recovery data can potentially be biased by an overrepresented cause of death in the data set, which produces a higher or lower mortality than the average (Schaub and Pradel, 2004). For example, if human-made obstacles like windows cause a very high mortality in robins wintering in villages, but most robins winter in forests, where they die naturally, it is likely that more robins dying because of windows are represented in the data set than the proportion in the whole population would predict. One possibility to overcome this issue, is to integrate alive resightings or recaptures, which should contain a more representative set of individuals dying of all causes. Moreover, integrating other data sources like tracking data may also help to balance methodological sources of biases. Such extensions require developing a higher model complexity, which will eventually open up new possibilities in parameter estimation like seasonal survival.

Choosing the kernel density estimation method as a simple, fast and already implemented way to estimate the intensity function for the point process, leads to biases in estimating survival and migratory connectivity at the edges and at extreme values. The edge effects arise despite using uniform edge correction when estimating the kernel density. Besides that, the fixed bandwidth of the kernel density estimator is not very flexible in reaching very high and very low values. As the very high and low values are at the edges in our simulation study, these effects multiply. See Appendix D for a more detailed consideration. Both issues, bandwidth selection and edge effects, are well known and discussed in the literature concerning kernel density estimation. They are the result of the implementation of the density estimation by means of kernel density estimation, but they do not inherently originate from the method developed in this work.

Further research is needed to establish a more complex model framework, which better reflects the biological complexity of the investigated studies. Using information on cohorts of time and age classes may enable a time-dependent and age-structured model, if appropriate

data is available (Cole et al., 2012). An even bigger increase in fit between model and data includes relaxing the assumption of constant recovery probability. This may be done by estimating recovery probability externally, e.g., from human population densities (Korner-Nievergelt et al., 2010b) or by disentangling migratory connectivity from a non-constant recovery probability by combining the discrete and the continuous domain model and using optimization (Schirmer, 2022). This combined approach of the discrete multinomial dead recovery model and the continuous spatial model presented here can relax the assumption of a constant recovery probability, and estimate a continuous recovery probability map while maintaining the continuous maps for survival and migratory connectivity.

Future studies should also invest in optimizing the density estimation process. Applying more sophisticated edge correction methods may reduce edge effects. Implementing adaptive bandwidth selection may improve the behavior at extreme values. It may also be possible to integrate this method into the framework of inlabru (Bachl et al., 2019), a methodology that deals intensively with the estimation of densities from point patterns. Yuan et al. (2017) uses this already to estimate the intensity function of a point process for spatio-temporal distance sampling, which would need further adjustment to cope with mark-dead recovery data.

We recommend using the continuous model if the available data set is big enough and if knowing the continuous variability of survival and migratory connectivity is crucial for investigating the research question. Moreover, the assumption of a constant recovery probability in space and time must be reasonable or relaxed as discussed above. In every case, carefully interpreting the results with the spatial coverage of the raw data in mind and visualizing the goodness of fit (R^2 -value) of the linear model may help to identify areas with a poor fit. If sample size is small, applying the discrete domain multinomial dead recovery model may give comparable results.

7. Conclusion

In most literature survival is not considered to be spatially varying. Doing so, opens up various possibilities to study the causes and consequences of this spatial variability in survival. The method presented in this study enables us to estimate survival on a continuous spatial domain and correct migratory connectivity for biases caused by survival. Thereby, survival can be investigated in the context of other continuous covariates and the relationship between survival and migratory connectivity can be studied. Future research should enhance the complexity of the model structure to increase the fit of the model to the huge amount of already existing mark-dead recovery-data.

CRedit authorship contribution statement

Saskia Schirmer: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing – original draft. **Fränzi Korner-Nievergelt:** Conceptualization, Methodology, Writing – review & editing. **Jan A.C. von Rönne:** Conceptualization, Investigation, Data curation, Visualization, Writing – review & editing. **Volkmar Liebscher:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The R code of the method and a tutorial of the method can be found on Github: <https://saskiaschirmer.github.io/CONSURE/>. The data referenced in Section 5 is available on zenodo: <https://doi.org/10.5281/zenodo.6414151>.

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Appendix A. Proof of Theorem 1 (survival estimator)

Theorem 1. Let us use the data set of dead recoveries pooled over all areas of origin, so that $b = B$ and let

$$y_{t,B}(w) = \ln(P_{rec})(t, w) = \beta_0 + \beta_1(t - 1),$$

be a model (see Remark 1), which is at point $w \in \mathcal{W}$ linear in t . Then the estimator of the survival probability function in a point $w \in \mathcal{W}$ is

$$\hat{s}(w) = \exp(\hat{\beta}_1(w)).$$

Proof. We know from Remark 1 that $\beta_1 = \ln(s(w))$. So, survival is the inverse of the logarithm of the slope of the linear model. $\square$

Appendix B. Proof of Theorem 2 (estimator of migratory connectivity)

Theorem 2. For every area of origin $b \in B$ we use the data set of dead recoveries marked in this area of origin and the model from Remark 1

$$y_{t,b}(w) = \ln(P_{rec,b})(t, w) = \beta_0 + \beta_1(t - 1).$$

Let $\hat{s}(w)$ be like in Theorem 1, $\int_{\mathcal{W}} m_b(w) dw = 1$ and $r = c \in (0, 1)$. The migratory connectivity density function can be estimated by:

$$\hat{m}_b(w) = \exp(\hat{\beta}_0(w)) / (c(1 - \hat{s}(w))),$$

where the constant

$$c = \int_{\mathcal{W}} \exp(\hat{\beta}_0(w)) / (1 - \hat{s}(w)) dw.$$

Proof. We know from Eq. (3) that it is possible to estimate β_0 by:

$$\begin{aligned} \hat{\beta}_0(w) &= \ln(\hat{m}_b(w)) + \ln(1 - \hat{s}(w)) + \ln(\hat{r}) \\ &\quad - \ln\left(\int_{\mathcal{W}} \hat{m}_b(\tilde{w})(1 - \hat{s}(\tilde{w})^T) \hat{r} d\tilde{w}\right). \end{aligned} \quad (\text{B.1})$$

Therefore, we rearrange Eq. (B.1) and take the inverse of the logarithm:

$$\hat{m}_b(w) = \frac{\left(\int_{\mathcal{W}} \hat{m}_b(\tilde{w})(1 - \hat{s}(\tilde{w})^T) \hat{r} d\tilde{w}\right)}{\hat{r}} \frac{e^{\hat{\beta}_0(w)}}{(1 - \hat{s}(w))}. \quad (\text{B.2})$$

We do not have to know $\hat{r}$ explicitly. We define the first factor as the normalizing constant $\frac{1}{c_b}$, where

$$c_b := \hat{r} / \left(\int_{\mathcal{W}} \hat{m}_b(\tilde{w})(1 - \hat{s}(\tilde{w})^T) \hat{r} d\tilde{w}\right). \quad (\text{B.3})$$

To satisfy the assumption that $\int_{\mathcal{W}} \hat{m}_b(w) dw = 1$, c has to obtain the value:

$$c_b = \int_{\mathcal{W}} \exp(\hat{\beta}_0(w)) / (1 - \hat{s}(w)) dw. \quad \square \quad (\text{B.4})$$

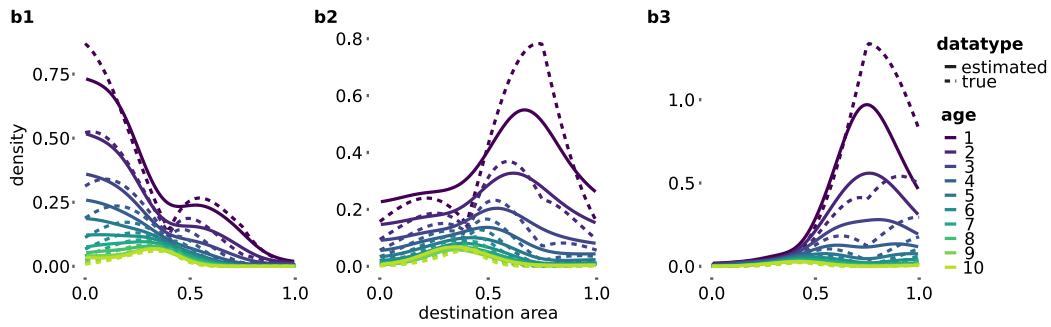


Fig. D.10. True (dashed line) and estimated (solid line) kernel density for a simulated data set for the three single areas of origin in one-dimensional space with a zigzag-shaped survival probability (see Fig. D.11). Age at death is indicated by color, where darker colors indicate a lower age at death.

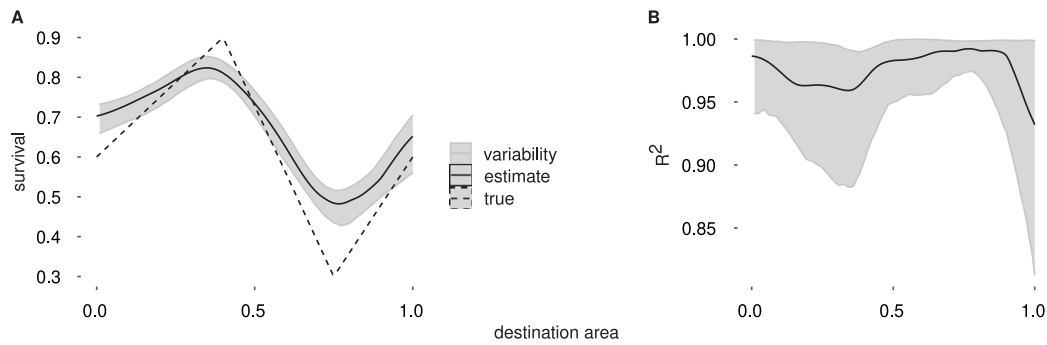


Fig. D.11. Survival probability s (A) and goodness of fit (B) for a simulated data set in one-dimensional space with a zigzag-shaped survival probability. True (dashed line) and estimated (solid line) annual survival probability s with the 0.025- and 0.975- quantile of 999 bootstrapped data sets (gray area). The R^2 -values of the linear model show the goodness of fit, with a perfect fit indicated by a value of 1.

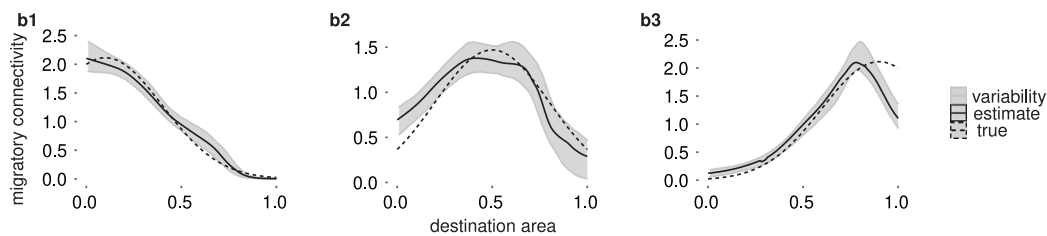


Fig. D.12. Migratory connectivity for a simulated data set in one-dimensional space with a zigzag-shaped survival probability (see Fig. D.11) for the areas of origin b1 (left), b2 (center), and b3 (right). True migratory connectivity m (dashed line), estimated migratory connectivity m (solid line) and the 0.025- and 0.975- bootstrap confidence interval (gray area).

Appendix C. Proof of Theorem 3 (estimator of the recovery probability)

Theorem 3. Let the model $y_{i,b}(w)$ be like in Theorem 1 and c be like in Theorem 2. n_b is the count of marked individuals in area of origin b and k_b the number of recovered individuals marked there. Then the maximum likelihood estimator for the recovery probability function is

$$\hat{r}_b = c_b k_b / n_b.$$

Proof. By rearranging Eq. (B.3) we get

$$\hat{r} = c_b \int_{\mathcal{W}} m_b(\tilde{w})(1 - s(\tilde{w})^T) \hat{r} d\tilde{w} = c_b P(Z = 1, b),$$

Because of Eq. (2), we can estimate $P(Z = 1, b)$ by the Maximum Likelihood estimator:

$$\widehat{P(Z = 1, b)} = k_b / n_b.$$

As r is assumed to be constant, it is independent of w . So

$$\hat{r}_b = c_b k_b / n_b,$$

where the value of c_b is known by Eq. (B.4). $\square$

Appendix D. Zigzag shaped survival probability

To differentiate between edge effects in the kernel density estimator and biases when values are very high or very low, we performed a simulation study in one-dimensional space using a zigzag shaped survival probability. This survival pattern has intermediate estimates at the edges, increases to very high values and drops to very low values in the middle.

The kernel density shows sharp shifts of direction, when the survival pattern changes from increasing to decreasing. These sharp changes cannot be followed by the kernel density estimator with fixed bandwidth and uniform edge correction, so that values are overestimated (Fig. D.10). Therefore, the survival estimator has problems to reach the

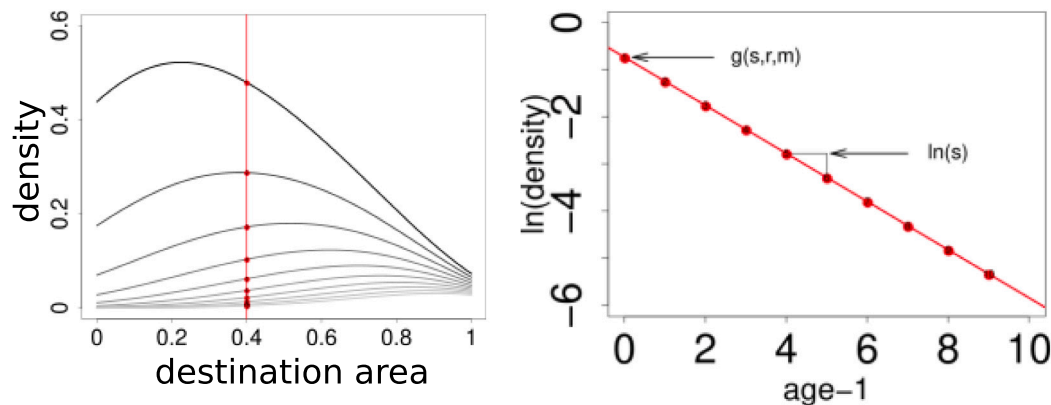


Fig. E.13. Example of the shape of an intensity function in one-dimensional destination space (left) and how the log-linear model evolves from the intensity function (right). The intensity function contains 10 age at death - classes, where the first age class has the highest values and the 10th has the lowest values.

very high and very low values in the middle (Fig. D.11). Moreover, the kernel density estimator shows edge effects, which induce edge effects in the survival estimator (Fig. D.11) and the estimator of migratory connectivity (Fig. D.12).

A kernel density estimator with adaptive bandwidth taking smaller bandwidths values around the peaks and another type of edge correction may help to overcome these issues.

Appendix E. Intensity function

Fig. E.13.

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