



# The integration of mark re-encounter and tracking data to quantify migratory connectivity



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## ABSTRACT

Animals which spend subsequent seasons in different areas connect geographical regions. The connection between breeding and non-breeding grounds is defined as migratory connectivity. The quantification of such connectivity is important, because movements between different locations can have strong consequences for the moving animal as well as the encountered habitats or ecosystems. Connectivity is usually investigated either on the basis of (few unsystematic) re-encounters of (often large numbers of) marked individuals or by observations of a few individuals tracked by remote sensing techniques, i.e. GPS or geolocation. The combination of qualitatively different data sets can reduce the limitations of each type of data and thus improve the accuracy of the estimated connectivity parameters considerably.

We formally combine individual tracking data and mark re-encounter data in a probabilistic model framework for quantifying connectivity. In a first example, we quantify migratory connectivity of a long-distance passerine migrant based on ring re-encounter and geolocator data. As a second example, we combine re-encounter data of ear-tagged wild boars with GPS tracking data to estimate the spatial distribution of wild boars during the hunting and the non-hunting seasons. These two examples illustrate the use of the model in two different framework: 1) long-distance migration and, 2) seasonal (e.g. hunting induced) non-migratory movements.

Results from the integrated analyses provided more information than the informal comparison of the results from independent analyses on each data set separately. Parameter estimates were more precise in the integrated analyses compared to the separate analyses and stronger conclusions could be drawn.

The integration of mark re-encounter and tracking data reduces sampling bias and increases the value of both data sets but the weighting of each data set needs further investigation.

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## 1. Introduction

Migratory connectivity describes the linkage of areas through the seasonal movement of individuals (Webster et al., 2002). Migratory connectivity has implications on population dynamics via carry-over effects (Harrison et al., 2011) and on ecosystems via nutrients, seeds, and microorganisms brought from other areas (Bauer and Hoyer, 2014). Herein the time periods when migrants encounter specific sites, determine the consequences of migratory connectivity (Bauer et al., 2016). Often, migratory connectivity is

used for describing the seasonal movement of individuals between breeding, stop-over and wintering sites. However, all seasonal movements of individuals can connect different areas, i.e. “movement connectivity”. For example, game species often avoid hunting pressure by moving to areas where hunting is less intensive. They stay there until the hunting season is over (e.g. Kilgo et al., 1998). These movements are repeated every year. Even though the underlying mechanisms of the hunting induced movements are different from migratory movements, the phenomenon might be more similar to migratory connectivity than to landscape connectivity which describes time-continuous, diffusion-like movements (Webster et al., 2002).

The study of migratory or other movement connectivity is important for informing conservation actions (e.g. Maxwell et al., 2011; Pendoley et al., 2014; Sawyer et al., 2009), for predicting the spread of diseases (Liu et al., 2005), and for understanding

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ecosystems visited by moving individuals (Bauer and Hoye, 2014). However, the quantification of the number of individuals migrating between areas can be difficult.

Various methods allow for the study of animal movements, but they differ in the gained information and in their inherent bias (Robinson et al., 2010).

Marking and re-encountering individuals, e.g. by using numbered or coloured tags, provides precise information about two or more locations the individuals have visited during their lives (e.g. Brewer et al., 2000; Bønløkke et al., 2006). To obtain a re-encounter of a marked individual it needs to be recaptured, re-sighted or its body has to be recovered after its death and its mark reported. The probability that a marked individual is re-encountered differs between regions and between seasons, e.g. due to varying hunting pressure or observation activity (Perdeck, 1977). Tracking individuals by satellite telemetry, on the other hand, yields detailed migratory routes. Such routes are unbiased because data is transmitted independently of human reporting activity. Several locations per day up to a few meters precision can be achieved if satellite telemetry is combined with Global Positioning System (GPS). However, the weight (at least 5–20 g) of the device may influence the animal's behaviour (Robinson et al., 2010), and the high financial costs often limit sample sizes. Sampling a large number of individuals within each population is a prerequisite for measuring migratory connectivity. Archival tags such as geolocators store but do not send measurements such as light intensities, date and time. From day length and time of midday the position on earth can be derived except during the equinox. Archival tags are lighter, the lightest are around 0.5 g, (Stutchbury et al., 2009; Bächler et al., 2010) than satellite transmitters and also yield migratory routes, albeit at a much coarser resolution (DeLong, 1992). To obtain archival data, however, the animal needs to be recaptured (Bridge et al., 2013). Thus the sample is biased towards individuals that survived and are recaptured.

Non-random and, therefore, biased data are the norm rather than the exception in studies of animals that move to areas outside the reach of the investigator. The integration of different data sources may help to assess and reduce such a bias (Boulet et al., 2006; Fiedler 2009; Robinson et al., 2010). Several studies have compared estimates of migratory connectivity from mark re-encounter data with results from other data sources and discussed discrepancies (comparing with satellite tracking data, Strandberg et al., 2009; geocator data, Ryder et al., 2011; or stable isotope data, Cunjak et al., 2005; Boulet et al., 2006; Norris, 2006; Procházka et al., 2013). While the comparison of more than one type of data qualitatively improved the interpretation of the results, such separate analyses might not exploit the full potential of the data. The combination of different types of data in an integrated stochastic model resulted in higher precision of parameters estimates. Further, some (e.g. latent) parameters that were not estimable in each of the separate analyses could be estimated in integrated models (Besbeas et al., 2005; Véran and Lebreton, 2008; Schaub and Abadi, 2011).

Recent studies successfully combined mark re-encounter and tracking data using integrated individual movement models (Kendall et al., 2006; McCrea et al., 2010; Powell et al., 2000; Sibert and Fournier 2001; Schick et al., 2008). These techniques aim to model the path of individuals and, therefore, require data with a high temporal resolution. This implies that the observation probability (e.g. recapture or re-sighting probability or the number of telemetry/GPS fixes) along the whole migratory pathway must be reasonably high. As explained above, such high resolution data often exist for a few individuals. Therefore, such data contain little information on migratory connectivity. Migratory connectivity is a characteristic of populations rather than of single individuals.

In contrast, re-encounter data from large numbers of individuals and over a broad geographic range exist on a low temporal resolution, e.g. from bird ringing schemes (e.g. du Feu et al., 2016) or from re-sightings of tagged mammals (Calambokidis et al., 2001). These data provide valuable large-scale quantitative information on migratory connectivity (Thorup et al., 2014).

Here, we present a simple method to quantify migratory connectivity from mark re-encounter data by accounting for spatial heterogeneity in re-encounter probability and integration of tracking data. Our model builds on the multi-state mark re-encounter model introduced by Arnason and Schwarz (Arnason 1972; Schwarz et al., 1993). A re-parameterized version of this model (Bauthian et al., 2007; Thorup and Conn 2009) was developed to handle cases where some states have very little observations (e.g. when no individuals were marked in some areas, or when re-encounter probability is extremely low).

The integration of individual tracking data with mark re-encounter data is straight forward because similar models can be used for both data types (see below).

To illustrate our approach, we use two examples: 1) We quantify migratory connectivity of a long-distant migrating passerine, the common nightingale *Luscinia megarhynchos* based on ring re-encounter and geocator data, and 2) we quantify hunting related movements of wild boar *Sus scrofa* by combining GPS tracking data with re-encounters of ear-tagged individuals.

## 2. The mark re-encounter model and the integration of tracking data

### 2.1. Model description

We define group  $g = 1, \dots, G$  of individuals belonging to the same “population” defined by the place and/or time of marking, i.e., the group represents the origin of an individual. Destination area  $d = 1, \dots, D$  is defined by the area where the individuals move to during a subsequent season. The aim is to estimate the proportion of individuals from population  $g$  that has migrated to destination area  $d$ ,  $m_{g,d}$ . Let  $R_{g,d}$  be the number of individuals re-encountered in area  $d$  out of  $N_g$  marked individuals in group  $g$ . Let  $Q_g$  be the number of marked individuals of group  $g$  that have never been found again, thus  $N_g = Q_g + \sum_{d=1}^D R_{g,d}$  (see Table 1 for notations). A product multinomial model can then be formulated using the proportions of individuals from group  $g$  migrating to area  $d$ ,  $m_{g,d}$ , and the probability of re-encountering a marked individual in area  $d$  given it is present in  $d$ ,  $r_d$ , as model parameters. The posterior distribution of the model parameters can be formulated up to proportionality (see Thorup and Conn, 2009 for a formulation of the likelihood in a frequentist framework):

$$p(m_{1:G,1:D}, r_{1:D} | R_{1:G,1:D}, Q_{1:G}) \\ \propto \prod_{g=1}^G \text{Multinom} \left( (R_{g,1:D}, Q_g) | N_g, \left( m_{g,1r_1}, \dots, m_{g,D}r_D, 1 - \sum_{d=1}^D m_{g,d}r_d \right) \right) \\ \times \prod_{d=1}^D \text{Beta}(r_d | 1, 1) \times \prod_{g=1}^G \text{Dirichlet}((m_{g,1}, \dots, m_{g,D}) | (1, \dots, 1))$$

In the above model, the Beta and the Dirichlet distributions are independent flat priors for  $r_d$  and  $m_{g,1:D}$ , respectively. Reliable estimates for  $r_d$  and  $m_{g,d}$  are obtained when  $G \geq D$  and  $m_{g,1:D}$  differ between the  $G$  groups (Korner-Nievergelt et al., 2010). A crucial model assumption is that the re-encounter probability, given an individual is present in area  $d$ ,  $r_d$ , is independent of group  $g$  (i.e.,  $r_d$  is independent of where the individual is coming from).

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