

# Migratory connectivity derived from sparse ring reencounter data with unknown numbers of ringed birds

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**Abstract** The large databases on ring reencounters, e.g. Euring database, contain extant information on the spatial distribution and potentially, on migratory connectivity of birds. However, reencounter data are normally sparse due to low reencounter probability. Further, to extract unbiased information about the spatial distribution of birds, spatial variation in reencounter probability has to be corrected for. To do so, knowledge of the total numbers of ringed birds is crucial but often not available. We present a general, combined statistical model to estimate population specific migration patterns based on the European reencounter data for which the number of ringed birds is unknown. Our approach combines a Cormack–Jolly–Seber model with a multinomial model. We present, for the first time, estimates and credible intervals of the spatial distribution of different populations of a migrant bird during the non-breeding period based on imperfect ringing data. Here, we used the Common Nightingale (*Luscinia megarhynchos*) as a representative long-distance migrant. The model allowed estimation of which proportions of the different breeding populations use a western, central or eastern flyway. Sensitivity analysis based on simulated data showed that most of these estimates were robust against violation of the most important model assumptions, i.e. homogeneity in recapture probability, homogeneity in breeding area return

probability, and in reencounter probability within the flyways. We provide a general technique to account for spatial variation in reencounter probability when analysing migratory connectivity based on ring reencounter data with unknown numbers of ringed individuals. It is applicable for almost all migrating species with reencounter data.

**Keywords** Cormack–Jolly–Seber model · Flyway use · Multinomial mark–reencounter model · Non-breeding distribution · Reencounter probability · Ring reencounter data · *Luscinia megarhynchos*

## Zusammenfassung

### Ableitung der Zug-Konnektivität zwischen Brut- und Nichtbrutgebiet aus spärlichen Ringwiederfunddaten und unbekannter Gesamtzahl beringter Individuen

Umfassende Ringfunddatenbanken, wie die Euring-Datenbank, enthalten wertvolle Information über die räumliche Verteilung von Zugvögeln und potentiell zur Verbindungsstärke zwischen Brut- und Nichtbrutgebiet (Zug-Konnektivität). Wegen geringer Ringfundwahrscheinlichkeiten ist die Stichprobengröße von Ringfunddaten jedoch oft klein. Wenn die räumliche Verteilung der Vögel basierend auf Ringwiederfunddaten beschrieben werden soll, muss eine räumliche Heterogenität der Ringfundwahrscheinlichkeit berücksichtigt werden. Um die Ringfundwahrscheinlichkeit schätzen zu können, sollte die Gesamtzahl beringter Vögel bekannt sein. Diese Anzahl ist jedoch in den meisten Ringfunddatenbanken nicht oder nicht detailliert enthalten. Wir stellen hier ein statistisches Modell vor, das populationspezifische Zugmuster basierend auf den europäischen Ringfunddaten mit unbekannter Anzahl beringter Vögel zu schätzen erlaubt. Unser Ansatz

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beinhaltet eine Kombination eines Cormack-Jolly-Seber Modells zur Schätzung der Zahl zur Brutzeit beringter Vögel, mit einem multinominalen Modell zur Beschreibung der räumlichen Verteilung der Vögel ausserhalb der Brutzeit. Am Beispiel der Nachtigall (*Luscinia megarhynchos*) als typischer Langstreckenzieher präsentieren wir erstmalig Schätzwerte und Vertrauensintervalle für die räumliche Verteilung der Individuen verschiedener Populationen ausserhalb der Brutzeit, die auf nicht standardisierten Ringfunddaten basieren. Eine nachfolgende Sensitivitätsanalyse zeigte, dass die meisten Modellschätzwerte robust gegenüber Verletzungen der Modellannahmen zu homogenen Wiederfangwahrscheinlichkeiten im Brutgebiet, homogener Rückkehrate ins Brutgebiet und homogener Wiederfundwahrscheinlichkeiten innerhalb eines Zugweges waren.

## Introduction

Marking birds individually with rings is still the most widely used technique to get information on population dynamics, migration patterns, orientation behaviour and site fidelity (Baillie et al. 1999, 2009; Bairlein and Schaub 2009; Thomson et al. 2009). About 115 million birds have been ringed in Europe to date (Baillie et al. 2007). From these, almost 5 million reencounters (“reencounter” is the umbrella term for live recapture, re-sighting and dead recovery) of almost 500 species have been recorded and stored in the Euring database (<http://www.euring.org>; Baillie et al. 2007).

This database contains extensive information on the spatial distribution during the non-breeding period of birds ringed in their breeding area, i.e. on the linkage between breeding and wintering/non-breeding populations, also called migratory connectivity (Webster et al. 2002). However, researchers analysing migratory connectivity based on ring reencounter data are challenged by the non-systematic nature of this type of data (Perdeck 1977), often combined with low sample sizes due to low reencounter probability. The probability that a ringed bird is found and its ring reported to a ringing scheme is highly variable in space and time (Baillie and Green 1987; McCulloch et al. 1992; Robinson et al. 2009; Sales 1973). Therefore, the proportions of ring reencounters in different areas do not reflect the proportions of birds that have migrated to the different areas. The spatial variation in reencounter probability must be taken into account when deducing information on migration patterns, and appropriate measurements for uncertainty should be reported. Hence, a range of statistical methods has been developed recently to overcome bias in such spatial ring reencounter analyses (see, e.g.,

Korner-Nievergelt et al. 2010a; Patterson et al. 2007; Thomson et al. 2009). Specifically, to estimate the spatial distribution of birds, Busse and Kania (1977), Kania and Busse (1986), Bauthian et al. (2007) and Thorup and Conn (2009) developed statistical methods that account for different reencounter probabilities between distinct areas such as flyways, breeding or non-breeding areas. All these methods are based on the same core assumption that makes reencounter probabilities estimable: the probability of being reencountered is equal for all birds present in the same area and independent of the birds’ origin. Further, more than one group of birds that differ in their spatial distribution have to be analysed to make reencounter probabilities and proportions of birds in different areas estimable (Bauthian et al. 2007; Busse and Kania 1977; Korner-Nievergelt et al. 2010b; Thorup and Conn 2009).

However, these methods require the total number of ringed birds to be known. Unfortunately, the Euring database does not contain these numbers, and for many species it is not possible to obtain these numbers with reasonable effort because data are not yet computerized or have even been lost. Recently, a fair amount of research has been done on mark–recovery or mark–recapture models to estimate population sizes when the numbers of birds ringed are unknown (Burnham 1990; Mazzetta 2010; Morgan and Ridout 2008). The software MARK even provides a model to analyse survival probability when the number of ringed birds is unknown, the so-called “BTO recovery model” (<http://www.phidot.org>; Cooch and White 2010). Here, we present how to use the multinomial model, developed by Thorup and Conn (2009), for ring reencounter data with unknown numbers of ringed birds. We use Bayesian methods to combine a mark–recapture model to estimate the number of ringed birds with the multinomial model to estimate bird distribution.

We introduce our widely applicable model to exemplarily estimate population-specific migration patterns of Common Nightingales (*Luscinia megarhynchos*, Brehm 1831), a typical Palaearctic long-distance migrant with approximately 40 million individuals migrating to sub-Saharan Africa (Hahn et al. 2009). Ring reencounter data of this species represent a typical sparse dataset for passerines, including only 28 reencounters during the non-breeding period even after collecting data over more than 100 years. Due to its broad breeding range from the Atlantic to the Black Sea coast, migration routes of nightingales from geographically distant breeding populations likely differ (Zink 1973). Birds from western breeding sites probably migrate via the Iberian Peninsula, whereas eastern breeders are assumed to travel via the eastern Mediterranean to sub-Saharan Africa (Zink 1973). Central European birds, however, may use the western, the eastern or a central migration direction along the Apennine peninsula.

An important part of this study consists of assessing the sensitivity of our model to violation of the most important model assumptions by simulations and by an analytical exercise.

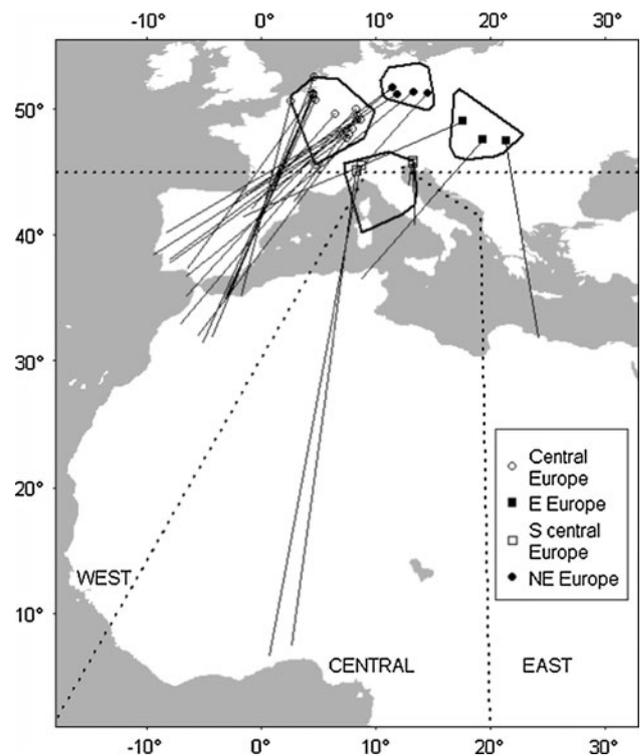
## Methods

### Data

The Euring database is a collection of ring reencounter records gathered by the national ringing schemes of European countries. An individual bird produces an entry in the Euring database only if it is ringed, the ring has been reencountered, the information is reported to a national ringing scheme, and finally the ringing scheme has sent the data to the Euring database. Consequently, a ringed bird that is not reencountered or its ring is not reported does not enter the Euring database, and thus the Euring database does not contain information about the number of ringed birds (however, very recently, the annual ringing totals per scheme are added; see [www.euring.org](http://www.euring.org)).

The Euring database contained 12,235 reencounters of 7,017 individuals of Common Nightingales (deadline: 17 September 2008). We selected all nightingales ringed as fully grown with known breeding area, i.e. birds that had been ringed during the breeding period, resulting in 5,899 reencounters of 3,532 individuals. We defined the breeding period to last from 5 May to 15 July because spring migration is normally completed by 3 May in central Europe (Amrhein et al. 2007; Zink 1973), and autumn migration can start in mid-July (Wernham et al. 2002). To separate different breeding populations within Europe, we plotted the 3,532 ringing locations and defined the populations based on the cluster pattern of the ringing locations. In this way, four different breeding areas with high ringing effort were distinguishable: W central Europe (including northern France, western Germany, Benelux states, Switzerland), E Europe (Austria, Hungary, Czech Republic, Slovakia and south-eastern Poland), S central Europe (Italy and Corsica) and NE central Europe (eastern Germany and western Poland, Fig. 1). Reencounters of birds whose place of ringing did not belong to one of these four breeding areas were discarded. This selection reduced the dataset to 5,045 reencounters of 2,856 individuals.

The reencounters were divided into two datasets. The first dataset (“breeding period data”) contained all live recaptures during the breeding period (as defined above) by a ringer in the same breeding area. The second dataset (“non-breeding period data”) contained all reencounters during the non-breeding period south of 45°N and with a minimum distance of 200 km from the place of ringing.



**Fig. 1** Place of ringing (symbols) and place of reencounter (end of line) of Common Nightingales (*Luscinia megarhynchos*) ringed during the breeding period (5 May–15 July) and reencountered during the non-breeding period (16 July–4 May). Sample sizes are 16 reencounters in WEST from birds ringed in W central Europe, 5 in WEST from birds ringed in NE central Europe, 4 in CENTRAL from birds ringed in S central Europe and 1 in each flyway from birds ringed in E Europe. Polygons give the breeding areas (based on the breeding period data, see text) of the four populations considered in the study. The non-breeding area south of 45°N was divided into three flyways, WEST, CENTRAL and EAST

This ensures that only migrating or wintering individuals are considered.

The breeding period dataset was used to estimate the total number of ringed nightingales per breeding area. It contained records of 1,229 individuals (23 in W central Europe, 254 in E Europe, 176 in S central Europe and 776 in NE central Europe) that were ringed and recaptured alive by a ringer in the same breeding area during the breeding period in subsequent years.

The non-breeding period dataset then served to estimate the non-breeding distribution of nightingales from each population. The potential area during non-breeding period spans from western Africa (17°W) to Ethiopia (about 40°E; Cramp 1988; Wisz et al. 2007). We assigned the reencounter locations to three flyways within the potential non-breeding area. Here, geographical criteria were used with two aims: (1) to minimise spatial heterogeneity of ring reencounter probability within the flyways, particularly in the Mediterranean where most of the non-breeding period

reencounter data were located, and (2) to assign birds to three geographically distinct flyways. Note, the term “flyway” here delineates geographical areas, i.e. it does not refer to biologically identified populations in contrast to its original definition (Boere and Stroud 2006). The flyway WEST included the Iberian Peninsula, north-western Africa and west Africa west of 5°W, CENTRAL included the Apennine Peninsula and a north–south band in central Africa, and EAST included the Balkan peninsula, the Middle East and Africa east of 18°E (Fig. 1). The non-breeding period dataset contained records of 28 individuals, 22 of them were found in WEST, 5 in CENTRAL and 1 in EAST. Reencounter probability presumably differed between flyways mainly due to differences in human population densities and socio-political factors (Korner-Nievergelt et al. 2010a). Such differences are reflected in our data by different finding circumstances of the reencounters. In WEST, 35% of the reencounters were due to hunting, 44% due to unknown reasons and only 7% due to ringing. In CENTRAL, 40% of the reencounters were due to ringing activity and 20% each due to collision and hunting. The only reencounter in EAST was due to hunting. Of the 28 reencounters during the non-breeding period, 14 had been made during the autumn migration (August–October), 3 in winter (December, January) and 11 during spring migration (March, April).

#### Estimating the proportions of birds using different flyways

We combined two probabilistic models to estimate for each of the four populations the proportions of birds using each of the three flyways. The first model (a) was a Cormack–Jolly–Seber model (CJS; Cormack 1964; Jolly 1965; Lebreton et al. 1992; Seber 1965) that was applied conditional on the first recapture on the breeding ground. It was used to estimate the number of ringed birds. Secondly (b), using a multinomial model (Thorup and Conn 2009), the proportions of birds from each population using each of the three flyways were estimated. The first model was fitted to the breeding period data, the second to the non-breeding period data. The two models were fitted simultaneously by Markov chain Monte Carlo (MCMC) simulations using WinBugs and its R interface R2WinBUGS (Sturtz et al. 2005) in R 2.10.1 (R Development Core Team 2009). The WinBugs code of the model is given in the Supporting information 4.

#### *Cormack–Jolly–Seber model (CJS) and estimation of the number of ringed individuals*

We used CJS models conditional on first recapture (note that the original CJS model is conditional on first capture)

to estimate the probability that an individual survived and returned to the breeding area in the following breeding season  $\Psi$  (hereafter called return probability; see Table 1 for definition of parameters), and the recapture probability  $p_B$  given a bird was present at the breeding area B. Because Euring data did not contain the number of ringed and released birds per breeding area  $N_B$ , we conditioned our model on the first recapture of an individual, i.e. all individuals were then at least in their second year. The number of individuals recaptured at least once ( $n_B$ ) was treated as the number of individuals “marked and released” in the model. The data were arranged in so-called m-arrays (Burnham 1987), including seven breeding seasons after the first recapture as capture occasions (Table 2). These m-arrays contained in the first row the numbers of firstly recaptured individuals after the release per capture occasion. The number of recaptured individuals at capture occasion 1 served then as the number of released individuals during occasion 1 (second row of the m-array). This row contained the number of firstly recaptured individuals after they were released at occasion 1. The sum of the individuals recaptured during occasion 2 was then used as the number of released birds during occasion 2 in row three and the m-array was completed accordingly (Table 2; for area-specific m arrays, see Supporting information 1). The CJS model was fitted using a multinomial likelihood for each row of the m-array. The cell probabilities were  $\pi_{Bij} = \Psi^{(j-i)} q_B^{(j-i-1)} p_B$  for  $j > i$  and  $\pi_{Bij} = 0$  for  $j \leq i$  where  $j$  was the recapture occasion (number of years after release),  $i$  was the release occasion in numbers of years after first recapture (0 for birds released at their first recapture), and  $q_B = 1 - p_B$ . For each breeding area B, a separate CJS model was fitted, but return probability  $\Psi$  was assumed to be equal in all four breeding areas, whereas recapture probability  $p_B$  was estimated separately for each breeding area. We assumed temporally constant return probability  $\Psi$  and recapture probabilities  $p_B$ . The assumption of constant return probability may be a reasonable approximation here because we restricted our data to individuals that have survived at least their first year of life and returned to the breeding site. Therefore, in our model, only adult survival (that we here call return probability) is estimated.

If we further assume that the return probability  $\Psi$  between first and second capture is the same as between the subsequent captures, and that the recapture probability  $p_B$  for the first capture equals the one during the subsequent capture occasions, an estimate of the unknown number of ringed birds  $N_B$  can be obtained. This estimate will be lower than the actual number of ringed birds because we assume that all individuals were ringed as adults, i.e. we ignore the proportion of first year birds that died during their first year. This proportion surmounts the proportion of

**Table 1** Description of the most important parameters and indices used

Name	Description
Parameters	
$\Psi$	Probability of return to the breeding area in the next year given a bird was alive and present in the breeding area this year
$p_B$	Recapture probability within the breeding area $B$ given a bird is present in the area $B$
$r_D$	Reencounter probability in the flyway $D$ during the non-breeding seasons in the course of the whole life of a bird given the bird uses flyway $D$
$m_{BD}$	Proportion of birds from breeding area $B$ using flyway $D$
$n_B$	The number of individuals recaptured at least once during the breeding season in breeding area $B$
$N_B$	Number of ringed birds in breeding area $B$ (but see exact definition in text)
$V_{BD}$	Number of reencounters of birds from breeding area $B$ in flyway $D$
Indices	
$B$	Breeding area: W central Europe, S central Europe, NE central Europe, E Europe
$D$	Flyway: WEST, CENTRAL, EAST

**Table 2** Structure of the m-array used to fit the conditional CJS model

Released	Year after first recapture							Not recaptured
	1	2	3	4	5	6	7	
$n_B$	$x_{01}$	$x_{02}$	$x_{03}$	$x_{04}$	$x_{05}$	$x_{06}$	$x_{07}$	$n_B - \sum_{j=1}^7 x_{0j}$
$x_{01}$	–	$x_{12}$	$x_{13}$	$x_{14}$	$x_{15}$	$x_{16}$	$x_{17}$	$x_{01} - \sum_{j=2}^7 x_{1j}$
$\sum_{i=0}^1 x_{i2}$	–	–	$x_{23}$	$x_{24}$	$x_{25}$	$x_{26}$	$x_{27}$	$\sum_{i=0}^1 x_{i2} - \sum_{j=3}^7 x_{2j}$
...	–	–	–	...	...	...	...	...
$\sum_{i=0}^5 x_{i6}$	–	–	–	–	–	–	$x_{67}$	$\sum_{i=0}^5 x_{i6} - x_{67}$

$n_B$  is the number of birds ringed in breeding area  $B$  recaptured at least once.  $x_{ij}$  is the number of recaptured birds released in year  $i$  after the first recapture and recaptured in year  $j$  after first recapture. The neutral notation  $x_{ij}$  instead the classical  $m_{ij}$  should indicate that the data contained, in contrast to typical m-arrays, only one release occasion

adults dying during a year (Grüll 1981). We further assume that the proportion of transients, i.e. birds which do not return to the capture area, is similar in all breeding areas (see “Discussion”).  $N_B$  is estimated by first estimating the probability that a ringed individual (of  $N_B$ ) is later recaptured at least once, i.e. that it is one of the  $n_B$  recaptured individuals. This probability equals one minus the probability that an individual is never recaptured ( $P(y > 0) = 1 - P(y = 0)$ , where  $y$  is the number of times an individual is captured). Assuming that each individual can potentially be recaptured during its whole life, e.g. no bird is released shortly before the end of the study period, the probability that an individual is never recaptured is

$$\begin{aligned}
 P(y = 0) &= (1 - \Psi) + \Psi(1 - p_B)(1 - \Psi) \\
 &+ \Psi^2(1 - p_B)^2(1 - \Psi) \\
 &+ \Psi^3(1 - p_B)^3(1 - \Psi) + \dots \\
 &+ \Psi^k(1 - p_B)^k(1 - \Psi)
 \end{aligned}$$

If  $k$  approaches infinity, this sum converges to  $\frac{1-\Psi}{1-\Psi(1-p_B)}$ .

It follows that the probability that an individual is recaptured at least once equals  $P(y > 0) = 1 - \frac{1-\Psi}{1-\Psi(1-p_B)}$

which is the proportion of birds ringed that is included in the Euring dataset  $\frac{n_B}{N_B}$ . Therefore, we used the estimated return probability  $\hat{\Psi}$  and recapture probability  $\hat{p}_B$  to obtain an estimate of the number of ringed birds:  $\hat{N}_B = \frac{n_B}{1 - \frac{1-\hat{\Psi}}{1-\hat{\Psi}(1-\hat{p}_B)}}$ .

We were not primarily interested in the number of ringed birds, but this estimate is fundamental to account for spatial variation in reencounter probability in the multinomial mark–reencounter model (see below). Ideally, for the multinomial mark–reencounter model, we would like to know the number of ringed birds during the time of reencounter exposure. Time of reencounter exposure in the multinomial mark–reencounter model is the sum of all non-breeding periods since the start of ringing. Therefore, we are interested in the total number of birds that were ringed and alive during the non-breeding seasons accumulated over the years, i.e. the total number of ringed birds that survived (at least) their post-fledging period. Our estimate  $\hat{N}_B$  from the CJS model assuming that all individuals have been ringed as adults does not correspond exactly, but it may be close to an estimate for the number of ringed birds

in which we are interested. Particularly, because juvenile survival after the post-fledging period may not substantially differ from adult survival (Grüebler and Naef-Daenzer 2008), and we restricted our non-breeding period data to birds that have been ringed as fully grown, i.e. after the post-fledging period. Further, a system-inherent characteristic of our model is that a bias in  $\hat{N}_B$  does not affect the estimates for the proportion of birds from breeding area B using flyway D ( $m_{BD}$ ) as long as the strength of bias is similar in all four populations (this is shown analytically in Supporting information 3).

#### *Multinomial mark–reencounter model to estimate population specific migration patterns*

We used a multinomial mark–reencounter model applied by Bauthian et al. (2007) and Thorup and Conn (2009) to estimate the proportion of birds using the different flyways,  $m_{BD}$ , based on the number of ringed birds per population and the number of reencounters in different flyways. Here, we used the estimated number of ringed birds  $\hat{N}_B$  from the CJS model described above. We implemented the multinomial mark–reencounter model in WinBugs as a sequence of Poisson models, similar to the “double-observer counts model” (Royle and Dorazio 2008). Thereby, the number of (observed) reencountered birds from breeding area B in flyway D ( $V_{BD}$ ) was modelled as a Poisson model:

$$V_{BD} \sim \text{Poisson}(m_{BD} * r_D * \hat{N}_B)$$

where  $m_{BD}$  was the proportion of birds from breeding area B using flyway D, and  $r_D$  was the probability that a bird was reencountered in flyway D at least once during or at the end of its life given it used this flyway. We assume that the same individual does not change flyway during its life.

The uncertainty of the estimated  $\hat{N}_B$  was projected to the multinomial mark–reencounter model using Bayesian methods. *Uniform* (0,1) distributions were used as priors for  $p_B$ ,  $\Psi$ , and  $r_D$ . The priors for  $m_{BD}$  were uniform priors as well, but they were constrained to sum to one for each breeding area B. Posterior distributions of the parameters were obtained from every 100th value of the last 50,000 sampled values of two Markov chains each of length 250,000. Convergence was assessed by the  $\hat{r}$  values (Brooks and Gelman 1998; values lower than 1.01 were accepted). The means and the 2.5 and 97.5% quantiles of the posterior distributions are presented.

#### Sensitivity to violation of model assumptions

We assumed that annual survival and recapture probability in the breeding season was equal for individuals from the same population. Furthermore, reencounter probability

during the non-breeding period was allowed to differ between the flyways, but is assumed to be similar for all individuals within a flyway independent of the origin of the individual. This is a key assumption of the multinomial mark–reencounter model, making the model parameters identifiable (see Korner-Nievergelt et al. 2010b). Finally, the total of the flyway areas is assumed to cover the whole non-breeding range for the four populations analysed.

We assessed the magnitude and directions of bias in the parameter estimates for four different types of violations of assumptions using simulated data: (1) violation of homogeneity of recapture probability  $p_B$  between individuals, (2) violation of homogeneity in return probability  $\Psi$  between individuals, (3) violation of independence of reencounter probability  $r_D$  from the origin of the birds (systematic differences in reencounter probabilities between the populations), and (4) violation of homogeneity of reencounter probability within a flyway (random variance between the individuals). Note that between-individual variance corresponds to between-time variance in our data, because individuals were pooled over many years. Therefore, simulations of between-individual variance will also show effects of heterogeneity over time.

We first simulated data that did not violate any model assumption (“perfect data”). The underlying values of the model parameters were taken from fitting a preliminary model to the Nightingale data in order to mimic a realistic scenario (Supporting information 2). Second, data were simulated based on recapture probabilities that differed between individuals, i.e. the individual recapture probability  $p_{Bi}$  was sampled from a *Beta*(2,9) distribution. The third sets of data were based on return probabilities that differed between individuals, i.e. individual return probabilities  $\Psi_i$  were sampled from a *Beta*(3,3) distribution. Fourth, reencounter probabilities in the flyways were divided by two for birds originating from S central Europe and doubled for birds originating from NE central Europe to obtain a positive correlation between reencounter probability and latitude of breeding area. This mimics, e.g., a situation where birds from northern breeding populations spend more time in the non-breeding area (due to shorter breeding time) and, therefore, have a higher probability of being reencountered there than birds from southern breeding areas (see “Discussion” for other sources of heterogeneity in reencounter probability). In the fifth simulation, reencounter probabilities in the flyways was halved for birds of the NE central European population and doubled for individuals from the S central European population to obtain a negative correlation between reencounter probability and latitude of breeding area. For the last (sixth) simulation, reencounter probabilities were drawn separately for each individual per flyway from beta-distributions with expected values of  $r_D$  (see Supporting information 2) and their 2.5% and 97.5%

**Table 3** Estimated number of ringed Common Nightingales (*Luscinia megarhynchos*) per population,  $N_B$ , and estimated proportion of birds per flyway,  $m_{BD}$ ; 95% credible intervals are in parentheses

Breeding area	Estimated $N_B$	Proportion (%) of birds per flyway		
		West	Central	East
W central Europe	1,035 (156–4,141)	64 (23–95)	18 (0–56)	18 (0–56)
S central Europe	1,220 (879–1,690)	2 (0–12)	90 (53–100)	8 (0–42)
NE central Europe	4,633 (4,057–5,293)	7 (0–33)	34 (0–97)	59 (0–97)
E Europe	1,448 (1,156–1,812)	6 (0–27)	49 (7–94)	48 (3–88)

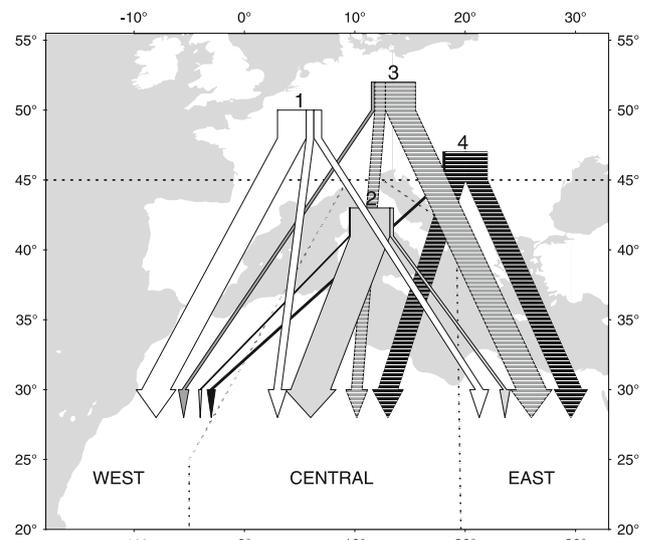
quantiles equal to  $r_D/10$  and  $10*r_D$ , respectively. This outputs data with reencounter probabilities differing up to a factor of 100 between individuals within the same flyway.

A total of 50,000 virtual birds per population were released in each simulation. These artificial large sample sizes enable us to measure bias with high precision. Each of the six simulations was repeated 20 times and our model was fitted to each  $6 \times 20 = 100$  datasets. For each dataset, the bias for every parameter estimates were calculated as the difference between the estimated and true parameter value and presented graphically. R codes for the simulations can be obtained from the authors.

**Results**

Reencounter data density during the non-breeding period was much higher in the flyway WEST than in CENTRAL or EAST (Fig. 1). Birds ringed north of the Alps, in W and NE central Europe, were exclusively found in the flyway WEST, whereas birds ringed at the Apennine Peninsula where exclusively found in the flyway CENTRAL (Fig. 1). The three individuals ringed in E Europe were reencountered one each in the three flyways.

The estimated recapture probability in the breeding areas  $\hat{p}_B$  was 0.11 (95% credible interval: 0.01–0.40) in W central Europe, 0.45 (0.34–0.58) in E Europe, 0.36 (0.21–0.57) in S central Europe, and 0.42 (0.35–0.51) in NE central Europe. The return probability, a product of annual survival and site fidelity,  $\hat{\psi}_B$  was 0.33 (0.29–0.37). From these parameters, we have got estimates for  $N_B$  between 1,035 in W central Europe and 4,633 in NE central Europe (Table 3). Reencounter probabilities during the non-breeding period were estimated to 0.0463 (0.0042–0.1838) in the flyway WEST, 0.0026 (0.0005–0.0067) in CENTRAL and 0.0004 (0–0.0022) in EAST. Consequently, the main part (around 64% as estimated in the model) from the W central European breeding population used the flyway WEST (Table 3; Fig. 2), whereas most of the birds from S central Europe (around 90%) used CENTRAL. Both these proportion estimates were significantly higher than for the other breeding populations (as deduced from the credible



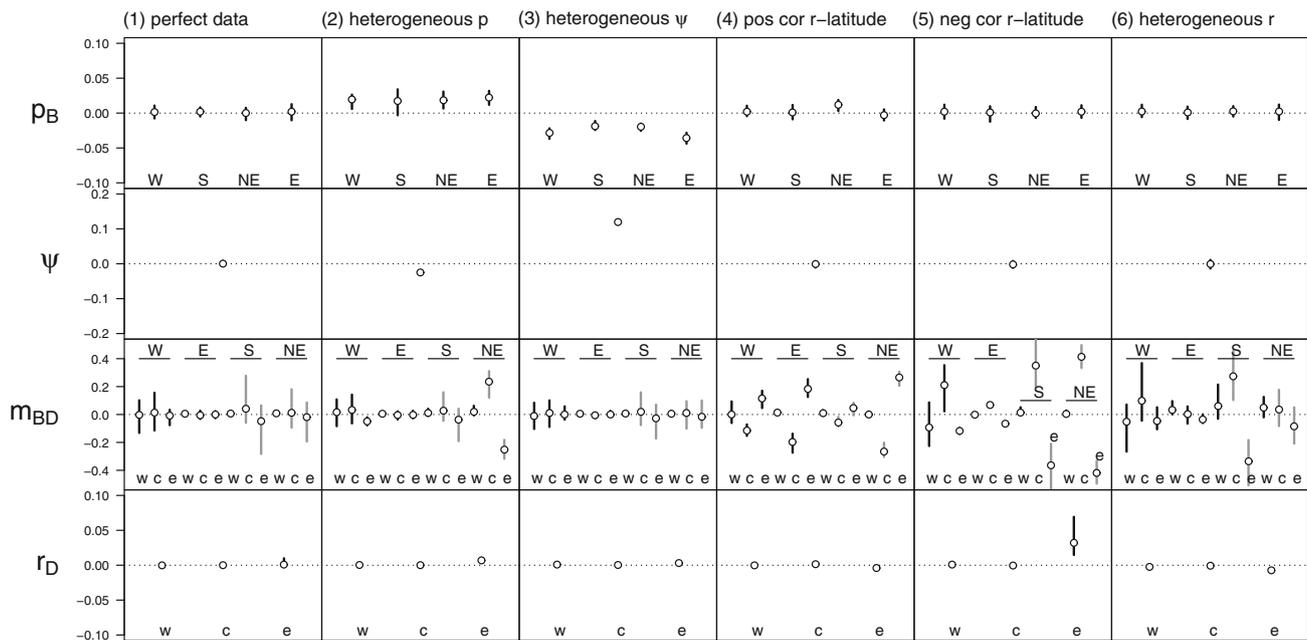
**Fig. 2** Estimated proportions of individuals of four different Common Nightingale breeding populations using three different flyways. Arrow widths indicate estimated proportions of birds migrating to the non-breeding area (values in Table 3). Estimates with high uncertainty (lower limit of the credible interval <0.1 and upper limit >0.9) are hatched white. Populations are: 1 W central Europe (white), 2 S central Europe (grey), 3 NE central Europe (dark grey) and 4 E Europe (black)

intervals in Table 3). For the E and NE breeding population, the proportion using the flyway WEST was lower than that using CENTRAL or EAST.

Sensitivity to violation of model assumptions

When breeding area recapture probability differed between individuals, recapture probability,  $p_B$ , was overestimated whereas return probability,  $\Psi$ , was underestimated (Fig. 3), and the estimates for the number of ringed birds per breeding population were biased (one over- and three underestimations). Further, the estimated proportions of birds from E Europe migrating to CENTRAL and EAST were seriously biased.

When return probability differed between individuals, recapture probabilities were underestimated, return probability were overestimated, and the numbers of ringed birds



**Fig. 3** Bias of the parameter estimates if the combined model is fitted (1) to data that do not violate any model assumption (“perfect data”), (2) to data that comprise heterogeneous recapture probabilities (“heterogeneous  $p$ ”), (3) to data with heterogeneous return probability (“heterogeneous  $\Psi$ ”), (4) to data with a positive correlation between reencounter probability and latitude of breeding area (“pos cor r-lat”), (5) to data with negative correlation between reencounter probability and latitude of breeding area (“neg cor r-lat”), and (6) to data that comprise heterogeneous reencounter probability.  $p_B$  = recapture probability in the breeding  $B$ , where  $B$  is either W central Europe (W), S central Europe (S), NE central Europe (NE) or E Europe (E),

constantly underestimated, whereas  $\hat{m}_{BD}$  were apparently unbiased (Fig. 3). A positive or negative correlation between reencounter probability and the latitude of the breeding populations did not affect the estimates of recapture probabilities, return rate and numbers of ringed birds. However, the estimates for the proportions of birds using the different flyways ( $\hat{m}_{BD}$ ) were biased, especially the proportion of birds from the breeding areas NE central and E Europe using CENTRAL and EAST (Fig. 3). Between-individual variance in reencounter probability within the flyways did not bias the parameter estimates except for the proportions of the NE central European breeding population using the flyways CENTRAL and EAST. In all simulations, the proportion of NE central European birds using CENTRAL was overestimated whereas the proportion using the flyway EAST was underestimated (Fig. 3).

## Discussion

Our results show that the non-breeding distribution of birds can be estimated from the Euring reencounter database.

$\Psi$  = return probability,  $m_{BD}$  = proportion of birds from breeding area  $B$  using flyway  $D$ , where  $D$  is either WEST ( $w$ ), CENTRAL ( $c$ ) or EAST ( $e$ ),  $r_D$  = reencounter probabilities in non-breeding area  $D$ ,  $N_B$  = number of ringed birds in breeding area  $B$ . The absolute bias is given for  $p$ ,  $\Psi$ ,  $m$  and  $r$ . For  $N$ , the bias is given in proportion of the true numbers. Circle mean of 20 simulations, vertical bars include 95%. The proportions of birds from breeding areas NE central Europe and E Europe towards CENTRAL and EAST are indicated in grey. These estimates seem to be particularly sensitive to violation of model assumptions

Euring reencounter data suffer from heterogeneous reencounter probability in space and time, a lack of information on the number of ringed birds, and often low numbers of reencounters (Bairlein 2001; Thorup and Conn 2009). However, ring reencounter data already exist from a wide geographic range of breeding populations. The 28 Common Nightingales reported from the non-breeding period are sufficient to draw inference about migratory connectivity at least for some flyway usages, whereas for others, e.g. NE central European and E central European birds migrating to CENTRAL and EAST, uncertainties in the estimates are high. This clearly indicates that ringing data collected over the last 100 years can be suitable to tackle some current topics in bird migration, e.g. migratory connectivity. Further, when, for one or more breeding populations, more detailed information from other tracking techniques becomes available, these data can be easily included in the proposed model by, e.g., informative prior distributions for  $m_{BD}$ . This clearly also reduces the uncertainty of the parameter estimates for those populations where no additional data are available, because reencounter probabilities in all flyways will be estimated more precisely.

In this study, we show that the drawback of heterogeneous ring reencounter probability and the lack of information on the numbers of ringed birds can be overcome by combining two mark–reencounter models: a CJS model (Cormack 1964; Jolly 1965; Seber 1965) that we conditioned on first recapture, and a multinomial mark–reencounter model (Bauthian et al. 2007; Thorup and Conn 2009). The combination of these two models is a new, and potentially promising, method for further ring reencounter analyses.

#### Methodical notes on the combined model

In both models, key assumptions have to be made so that the parameters of interests, which are the proportions of birds using the different flyways, are estimable. In the first sub-model (CJS model), this key assumptions are that recapture probabilities and return probability are constant over time and equal for all individuals. In the second sub-model (the multinomial mark–reencounter model), reencounter probabilities are assumed to be independent of the origin of the birds, i.e. equal for all birds within a flyway. This assumption is essential and cannot be relaxed without having further information. In contrast, the assumptions we made in the CJS model (constant and equal recapture and return probabilities) could be relaxed to some extent if temporal or between-individual variation was accounted for in the CJS model (as, e.g., by Pledger et al. 2003). However, the population size estimation from such models is problematic (Link 2003), and it may require several weeks of computer time to fit individual-based models which are necessary for modelling between-individual variation. Because return and recapture probability were not of primary interest in our study, we used a simpler model with reasonable run time, and assessed the effect of heterogeneity on the estimates for our parameters of interest using simulated data.

The effect of unaccounted heterogeneity on the parameter estimates depends on the focal parameter(s) with heterogeneity. Carothers (1973) has shown analytically that survival and population sizes are underestimated in mark–recapture models when heterogeneity in recapture probability is ignored. This bias might be negligible for survival but substantial for population size estimates (Carothers 1973; Gilbert 1973). Similarly, for our specific scenario, we found a bias of around only  $-2\%$  for the return probability (“survival”) estimate, but the number of ringed birds (“population size”) was underestimated by up to  $40\%$  if the model was fitted to simulated data with heterogeneous recapture probabilities. However, one of the four population estimates was also overestimated by  $10\%$  (Fig. 3). Various effects of unaccounted heterogeneous

return probability in mark–recapture models have been reported. Cormack (1972) concluded that heterogeneous return probability might be unimportant, whereas Pollock and Raveling (1982) and Nichols et al. (1982) found that such heterogeneity biased parameter estimates, and that this bias was either positive or negative. For our scenario, heterogeneous return probability produced a consistent underestimation of the numbers of ringed birds ( $N_B$ ), a substantial overestimation of return probability ( $\Psi$ ) but a negligible effect on the estimated population-specific proportion of birds using the different flyways ( $m_{BD}$ ). As the last is our parameter of interest, we conclude that heterogeneous return probability is of less concern for our study. However, heterogeneous recapture probability can lead to substantial bias in some of the estimated  $m_{BD}$ , namely the estimated proportions of birds from the E European population migrating to CENTRAL or EAST could comprise a large bias (Fig. 3). Nevertheless, the number of substantially biased  $\hat{m}_{BD}$  was low (2 out of 12). Heterogeneity of recapture probability could be caused by different habits of recording recaptures, e.g. between different ringers, or between ringing schemes. Therefore, it would be valuable to include a country effect of recapture probability to account for this heterogeneity in future studies, if computer capacity and data structure allows for it.

In many passerines, return probability changes with the age, e.g. in Common Nightingales about  $30\%$  of first year birds return to their natal breeding site, whereas around  $50\%$  of the adults return to the place where they had bred the preceding year (Glutz von Blotzheim and Bauer 1988; Grüll 1981). However, this age effect on return probability did not apply in our breeding period data, because we selected captures of birds in their second year and older, and age effect is negligible in the multinomial mark–reencounter model (see “Methods”). Consequently, we describe migratory connectivity of adults only.

Our estimates  $\hat{N}_B$  will be lower than the actual number of birds ringed (see “Methods”), as many individuals might not have survived their first few weeks. This expectation is confirmed when we compared our estimates for  $N_B$  with ranges of possible total numbers of birds ringed that we compiled from ringing schemes and ringers (Table 4). Our estimates are all near or below the minimal number of ringed birds during the breeding time. This underestimation of the number of ringed birds,  $N_B$ , could have, besides the age effect, a further reason. In many mark–recapture studies, a high proportion of birds ringed disappear after ringing independent of age. Those that are recaptured once have a higher capture probability than those that are never recaptured. Pradel et al. (1997) coined the term “transients” for the proportion of individuals that are never recaptured. The effect of transients can be taken

**Table 4** Information about the number of ringed fully grown Common Nightingales in the four breeding areas up to 2007 (if not otherwise indicated), compiled from personal communication with the ringing schemes and ringers

Population	Information on minimal numbers of ringed birds (after accounting for juvenile mortality)		Information on maximal number of ringed birds	
	Number of individuals in Euring data	Number of individuals ringed during breeding season	Annual ringing totals	Areas (schemes) without information
W central Europe	103	FR-PCA: 367 NLA: 909 <sup>a</sup>	DEH: 20,728 DER: 7,057 BLB: 11,059 <sup>b</sup> NLA: 5,377 <sup>c</sup> HES: 3,320	France except FR-PCA
S central Europe	602	–	–	Italy
NE central Europe	1,253	DEH: 8,685 <sup>d</sup>	DKC: 50 PLG: only a few <sup>e</sup>	–
E Europe	898	CZP: 2,141 <sup>f</sup> HGB: 7,434	CZP: 16,170 <sup>g</sup> HGB: 19,252 PLG: only a few <sup>e</sup>	Slovakia

For the sources of information, see Acknowledgements. *FR-PCA* Study area Petite Camargue Alsacienne (France), ringing schemes, *BLB* Belgium Bruxelles, *CZP* Czech Republic Praha (including former CSSR), *DEH* Germany Hiddensee, *DER* Germany Radolfzell, *HES* Switzerland Sempach, *HGB* Hungary Budapest, *NLA* Netherlands Arnhem, *PLG* Poland Gdansk

<sup>a</sup> Years 1991–2007

<sup>b</sup> Number of ringed birds up to 2007 but recoveries were reported to Euring database only up to the ringing year 1992

<sup>c</sup> Sum of the annual totals 1911–1990

<sup>d</sup> From 1977 onwards

<sup>e</sup> Only one reencounter up to 2009—no information about the number ringed

<sup>f</sup> From 1999 onwards

<sup>g</sup> Including former CSSR

into account when capture probability is modelled as dependent on whether it is the first or a subsequent capture of the individual (Pradel et al. 1997). This requires data on first captures, which are not available in Euring data. Therefore, we must accept that our estimate for  $N_B$  may be underestimated if such transients were present. An underestimation of  $N_B$  does not affect the estimates of the proportion of birds per breeding area using the flyway  $m_{BD}$  as long as the degree of underestimation of  $\hat{N}_B$  is similar in the four breeding areas (this is shown analytically in Supporting information 3). However, reencounter probabilities will be overestimated when  $N_B$  is underestimated. Consequently, when transients are present in the breeding period mark–recapture data, estimates for reencounter probabilities are higher than they actually might be, and estimates for the proportion of birds using the different flyways  $m_{BD}$  are only reliable when the proportion of transients is similar between the four breeding area datasets.

The key assumption made by the multinomial mark–reencounter model is that the reencounter probability during the non-breeding period did not depend on the origin of the individual. In nature, differences in reencounter probabilities between birds from different breeding areas might appear, for example, due to population-specific migration

phenology or the use of different stop-over sites along the flyway. For example, if birds from one population migrate in a non-stop flight to areas where reencounter probability is extremely low, whereas birds from another population at the same flyway stop-over for a longer time at sites with higher reencounter probabilities, the probability that a bird is reencountered is higher for the latter population than for the first. We tried to minimise such spatial heterogeneity in reencounter probabilities within the flyways by defining these in a sensible way. We focussed on the Mediterranean, because most data from the non-breeding period were recorded here, and we included political and topographic criteria, i.e. the three distinct flyways were defined by the Iberian Peninsula, the Apennines and the Balkans, to minimise within-flyway variance in reencounter probability compared to larger between-flyway variance. However, we cannot exclude between-individual or between-population differences in the use of stop-over sites. In our simulations, between-individual variance in reencounter probability did not affect the results, whereas between-population variance biased the estimated proportions of birds using the different flyways ( $\hat{m}_{BD}$ ). However, even though the between-population difference in reencounter probability was large (factor 4) in simulated data, the differences between the

estimated and true proportions of birds using the different flyways did not exceed 40% (Fig. 3).

#### Proportions of Nightingales from different breeding populations migrating along different flyways

We estimated the distribution pattern of Nightingales from four different European populations in three different flyways. The results quantitatively describe the preferred flyway a specific population uses and how much individuals from different breeding populations may mix up along the flyways.

Nightingales from the W central European breeding area clearly preferred the western flyway, only a small proportion may use the flyway CENTRAL and very few individuals may use the eastern flyway. Here, the wide credible interval of 0–55% indicates a good chance that the proportion of eastern flyway migrants is close to 0%. A similar pattern occurred for birds from S central Europe, where the majority should use the central flyway and only a few birds, probably close to zero, may migrate along the other two flyways. However, the pattern of a clear directional preference did not apply for individuals of both eastern breeding areas. Birds of eastern provenance may use the central and eastern flyway in similar proportions, but they definitely did not prefer the western flyway (Table 3; see also discussion of our simulation study). The general pattern of specific flyway use in relation to geographic origin of the focal individual could be explained by the avoidance of crossing large ecological barriers, the Alps and the Mediterranean Sea (Liechti et al. 1996; Bruderer and Liechti 1998).

Zink (1973) had already suggested that Nightingales from the eastern parts of the breeding area might show migration directions different from SW. Here, we present for the first time estimates of the proportions of Nightingales taking the eastern and western migration routes.

To conclude, the combined model presented here allows one to analyse spatial distribution of birds by taking into account the spatial variation in reencounter probabilities based on ring reencounter data with unknown numbers of ringed birds. The flexible Bayesian framework enables increased precision of the results by adding more information, such as from tracking single individuals (e.g. via prior information). Our model can be applied to each migrant species with a wide distribution range and therefore potentially population-specific migration patterns. Our approach allows the expressing of the information inherent in Euring ring reencounter data about population-specific migration patterns while spatial differences in ring reencounter probability are considered. The Euring database, for example, contains data from 87 species with more than 10,000 records (Baillie et al. 2007). These are clearly

candidates for statistical analyses of population-specific migration patterns as shown here.

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