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SPECIAL ISSUE. MODELLING DEMOGRAPHIC PROCESSES IN MARKED POPULATIONS: PROCEEDINGS OF THE EURING 2013 ANALYTICAL MEETING

Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives

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Summary

1. A major aim of bird ringing is to provide information about the migration and movements of bird populations. However, in comparison with demographic studies, little research has been devoted to improving quantitative inferences through large-scale spatial analyses. This represents a serious knowledge gap because robust information on geographical linkages of migratory populations throughout the annual cycle is necessary to understand the ecology and evolution of migrants and for the conservation and management of populations.

2. Here, we review recent developments and emerging opportunities for the quantitative study of movements of bird populations based on marked birds. Large-scale spatial analyses of ringing data need to account for spatio-temporal variation in re-encounter probability and the complexity of movement processes, including variability among individuals and populations in migration direction and distance.

3. We identify seven recent studies that used quantitative methods for large-scale spatial analyses of ringing and re-encounter data gathered by national ringing centres. In most cases, numbers ringed and recovered in a series of source and destination areas were used to derive estimates of the proportion of each source population travelling to each destination area. Where recovery data were sparse, precision was improved by incorporating information on re-encounter probabilities of similar species. When numbers ringed were not available, inferences could sometimes be drawn based on local recapture data from the source areas.

4. Studies to date illustrate that analyses of these large-scale ringing data sets can provide robust quantitative inferences. Further work is needed to develop these modelling approaches and to test their sensitivity to key assumptions using both real and simulated data. Data for all birds that were marked, not only those re-encountered, are often inaccessible and should be computerised in parallel with analytical developments. Further, there is great potential for the formal combination of re-encounter data with information from additional data sources such as counts and detailed movement data from radiotracking or data loggers. Because data from bird ringing operations cover long periods of time and exist in large quantities, they hold great promise for inferring spatio-temporal migration patterns, including changes in relation to climate, land use change and other environmental drivers.

Key-words: re-encounter probability, observer bias, spatial distribution, migration, bird ringing, bird banding, migratory connectivity

Introduction

Knowledge of the seasonal movement patterns of migratory bird populations is important for understanding all aspects of their ecology as well as for conservation planning. Our understanding of even basic migratory patterns for many species is still surprisingly poor. For example, we know the general breeding and wintering ranges for most migratory species, but we have a limited understanding of their migratory connectivity, the geographical linkages of populations between phases of the annual cycle. Effective conservation initiatives for migratory birds require knowledge of the spatiotemporal distributions of migratory populations (Webster *et al.* 2002; Norris 2005; Norris & Marra 2007). This information is necessary to address issues such as dependence on winter or stopover areas and meta-population dynamics. Further, our knowledge of and ability to predict the spatial distributions of specific populations throughout the year is important for management of

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Fig. 1. Recoveries of ducks (*Anas* and *Athya* combined) ringed in Denmark showing the potential for spread of avian influenza by these species. Ducks are the natural reservoir for low-pathogenic avian influenza. The lines connect the ringing and recovery locations.

contemporary topics for society such as disease spread involving avian vectors (Fig. 1). Further, it is increasingly clear that we cannot understand patterns of biodiversity without knowledge of seasonal changes in the distributions of migratory animals (Marra, Studds & Webster 2010).

Yet, movement is not easy to study. The seasonal distribution of migratory birds can be inferred indirectly from count data without individual recognition. However, without information about the movement of individuals, inference is limited to the species or meta-population level. Methods allowing individual recognition enable inferences regarding movement at the individual and population levels, information that is necessary for understanding migratory connectivity and population regulation.

Several different approaches have been used to follow individuals that move long distances. Individual recognition can be achieved using intrinsic markers, such as individual colour patterns (e.g. tail fin coloration in whales), or extrinsic markers, such as metal rings or transmitters. The way data are gathered also varies. Passive re-encounters include reporting of metal rings by the public and automatic relay of data via satellites, and active re-encounters include systematic searching for colour-ringed or radiomarked birds.

Ringing of birds was originally designed to enable tracking the movement of birds (Mortensen 1901; Greenwood 2009). Since the advent of ringing, more than 100 million birds have been ringed in Europe and more than 10 million of those have been re-encountered (EURING databank; www.euring.org). In North America, more than 70 million birds have been ringed and more than 4.5 million of those have been re-encountered (North American Bird Banding Laboratory, BBL; www. pwrc.usgs.gov/bbl). The extensive ringing of many species is illustrated by the numbers and distribution of re-encounters of Barn Swallows *Hirundo rustica* in the EURING databank (Fig. 2). Not surprisingly, there have been considerable changes over time in the number of birds of different groups ringed and re-encountered (Example in Fig. 3 from Denmark).

Ringing was invented more than 100 years ago, and it still has wide applications in both applied and basic science today not least because of the development of capture-mark-recapture analyses. New technologies allow detailed tracking of large-scale movements of individuals over long distances so one may ask why we still need large-scale ringing and reencounter data. There are two central reasons why such data remain highly valuable for understanding bird movement. First, historical changes in migration patterns cannot be acquired with new technology. As our globe is undergoing rapid changes, the need for long-term data has exploded. Ringing and re-encounter data can reveal important changes over time (Example in Fig. 4). Historical baseline data are essential for detection of changes and for analyses of the causes of those changes. Second, the broad coverage of species and individuals represented in existing ringing and re-encounter data bases is unlikely to be possible (or reasonable) to achieve with the new technologies in the near future given the cost and effort required to place and recover tracking devices on individuals (Fiedler 2009).

Traditionally, interpretation of ring re-encounters (recoveries of dead or recaptures/resightings of live ringed birds) has been qualitative. For example, in ring re-encounter atlases (e.g. Brewer *et al.* 2000; Wernham *et al.* 2002; Saurola, Valkama & Velmala 2013, see summary of European atlases on http:// www.euring.org/research/migration_atlases/index.html), encounter records are most often mapped without statistical analysis. Newer treatments use descriptive density functions such as kernel densities (e.g. Atkinson *et al.* 2007). However, it has long been recognised that unequal distribution of observers and variation in reporting rates impede the direct interpretation of the data (Perdeck 1977). Further, many of the ring recovery data have only limited information on each individual – often just one marking location and one re-encounter location.

Here, we first give an overview of methods used to describe long-distance migration patterns and their limitations, from unmarked birds, from birds marked with electronic markers and from ring recovery and resighting data. Second, we describe the challenges involved in inferring seasonal distributions and population movements of migrants from ringing and re-encounter records, describe how those challenges have been addressed and suggest future directions.

Approaches for studying movement patterns with unmarked birds

The study of movement in birds is long-standing, but many original approaches are still in use today. The earliest



Fig. 2. Re-encounters of Barn Swallows *Hir*undo rustica in the EURING databank. (a) Ringing locations of birds recovered dead, (b) ringing locations of birds recovered alive, (c) finding locations of birds recovered dead and (d) finding locations of birds recovered alive. Increasing symbol sizes show 1–10, 11–100, 101–1000, 1001–10 000 and 10 001–100 000 records.

approaches involved observing and counting birds. Even simple observational data can contain information on movements based on seasonal changes in abundance due to movement. Abundance can be estimated at breeding, staging and wintering areas with count data, or more directly at passage sites using radar (e.g. Bruderer 1997; Felix, Diehl & Ruth 2008; Buler et al. 2012), auditory (e.g. Wimmer et al. 2013; Smith, Paton & McWilliams 2014) or infrared observations (e.g. Liechti, Bruderer & Parroth 1995). Current methods for the analysis of winter or breeding population counts typically rely on simple presentations of such counts, on niche modelling based on checklist data (Wisz, Walther & Rahbek 2007) or on occupancy or point count models (MacKenzie et al. 2002; Royle 2004). Nevertheless, complex migration patterns are unlikely to be described well by niche modelling, which mainly deals with potential distributions. As an example, an analysis of the distribution of the Aquatic Warbler Acrocephalus paludicola based on niche modelling indicated equal suitability in eastern and western regions of Africa, which is contradicted by observations (Walther et al. 2007). Further, distribution and population models during the non-breeding and breeding period do not provide information about the migratory connectivity of populations, the linkage between breeding and non-breeding areas of different portions of the populations.

Direct observations of migrating individuals, for example observed with tracking radar, can elucidate mechanisms of migration and migration strategy (e.g. Horvitz *et al.* 2014). However, because the provenance and destination of unmarked individuals is unknown, interpretation of such data is limited by the lack of information about migratory connectivity.

When present, geographical variation in morphology or in distribution of parasites can be used to infer movement patterns. Gratto-Trevor *et al.* (2012) used bill length to link migratory Semi-palmated Sandpipers *Calidris pusilla* to three breeding populations that were known to differ in bill length. Pettersson *et al.* (1990) identified different routes during fall and spring for European Robins *Erithacus rubecula* based on various morphological measurements taken at different places during migration and winter. Fallon, Fleischer & Graves (2006) attempted to identify wintering areas based on blood parasites in Black-throated Blue Warblers *Dendroica caerulescens.* However, they found that species of blood parasites within North America were too widespread to provide site-specific information.

Genetic markers such as mitochondrial DNA (mtDNA) can provide information about the population a migrant is coming from (e.g. Kelly, Ruegg & Smith 2005; Lopes *et al.* 2013).



Fig. 3. Temporal distribution of recoveries of several ecological/taxonomic groups ringed in Denmark. The number of birds recovered reflects changes in the number ringed as well as changes in recovery causes. (a) Number of recoveries per decade for each group (primary axis) and in total (secondary axis). (b) Changes in recovery causes for two of the groups, raptors and songbirds, over time. Proportion of the numbers ringed recovered for each category indicated (primary axes) and total number ringed (secondary axes).

However, inferring migratory connectivity from genetic markers requires that the genetic structure of the populations under study is known. Often, the spatial resolution of the location information is low. Therefore, genetic markers have been used in combination with other methods such as ring re-encounters and morphology (Lopes, Marques & Wennerberg 2006) or stable isotopes (Rundel *et al.* 2013).

The chemical composition of inert tissues such as toenails or feathers provides information about the location of the animal during the time when the tissue was grown. Feathers grown during the winter retain the chemical signature of the wintering area when they are collected during the breeding season and vice versa. Stable isotopes (e.g. carbon $\delta 13$ C, nitrogen $\delta 15$ N, hydrogen $\delta 2$ H; e.g. Hobson *et al.* 2009; Hénaux *et al.* 2012; García-Pérez & Hobson 2014; Knick *et al.* 2014) and trace elements (Szép *et al.* 2003; Coiffait *et al.* 2009) have been used for this purpose. Often, such chemical markers provide a measure of which individuals have experienced similar environmental conditions (e.g. precipitation levels from carbon $\delta 13$ C), but the site-specific information has low resolution (e.g. Pain *et al.* 2004; Rocque *et al.* 2006; Farmer, Cade & Torres-Dowdall 2008; Kelly *et al.* 2008; Reichlin *et al.* 2013).

There may be scope for combining these techniques to improve inference. For example, chemical markers have been combined with morphology to infer movement patterns. Rushing *et al.* (2014) increased precision of Wood Thrush *Hylocichla mustilena* assignments from stable isotopes by including geographical variation in wing length.

Tracking movement with electronic markers

New technologies such as satellite-based radiotelemetry and archival data loggers have shown great promise in revealing the migration patterns of individuals with high spatiotemporal resolution (Robinson et al. 2010), and such data can also be analysed within a capture-mark-recapture framework (Schwarz 2009). Satellite-based radiotelemetry enables almost unbiased spatiotemporal tracking of individuals globally with high spatial precision from a few kilometres to a few metres for tags equipped with GPS. Advances in technology mean the tags can be fitted to increasingly smaller species. Satellite transmitters are now light enough to be carried by species as small as Common Cuckoos Cuculus canorus (average mass: 110-130 g). Therefore, approximately 60% of all bird species can be tracked by satellite (Bridge et al. 2011). Archival light-level loggers (geolocators) are lighter and can now be used to track the movement of even smaller species (<20 g), including many passerines (e.g. Stutchbury et al. 2009; Bächler et al. 2010; McKinnon, Fraser & Stutchbury 2013). Geolocation relies on light levels in combination with a clock enabling estimation of





Fig. 4. Recoveries of Barn Swallows *Hirundo rustica* ringed in Scandinavia (green, SC) and Finland (red, SF) showing pronounced differences in number of recoveries between West and East Europe and between Europe and sub-Saharan Africa. (a) Geographic locations, (b) temporal and (c) latitudinal distribution of recoveries. [Correction added on 16 December 2014, after first online publication: clarification of part labels added to figure caption.]

day length and time of midday from the timing of sunset and sunset (Lisovski *et al.* 2012). However, the geolocation devices currently available have considerably lower spatial resolution than satellite tracking devices (errors of more than 100 km are common, with much lower precision near the equinox; Fudickar, Wikelski & Partecke 2012) and log the data on the device so that the bird must be recaptured with the device intact for data retrieval.

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Furthermore, individuals followed are often not sampled randomly. Data from geolocators, for example, only include birds that survive, successfully return to the marking site and are recaptured so that the data can be recovered from the device. Satellite data may also be biased because these relatively large devices may influence behaviour compared to non-tagged birds. In general, each technology often includes a different (non-random) sample of birds. At least at the present stage, the different data types complement rather than replace each other.

Tracking birds with traditional metal rings or visible markers

Bird ringing schemes operate in many countries, in several cases having existed for over 100 years. Birds are captured as chicks or full-grown individuals and marked using metal rings carrying a unique serial number and a return address. Ringers return details of all birds marked and of encounters with marked birds to the appropriate ringing centre (usually one per country). Bird ringing schemes encompass a wide range of research projects and ringing activities, so while individual projects often follow very specific protocols, there is no overarching sampling strategy. Recaptures by ringers away from the original ringing location provide one source of information on movements. Historically, many local recaptures at the site where the bird was ringed were not reported to ringing centres, with only 'interesting' or unusual records reported (e.g. longevity), which limits their value for quantitative analyses. Many records of movements are obtained when birds are found, usually dead, by members of the public. Such records are more likely to occur when the cause of death is one associated with man, such as birds shot by hunters or those flying into windows. Excluding local recaptures, only a few percentage of birds carrying only metal rings are subsequently recovered. Some birds carry additional individually identifiable marks that can be read in the field, such as colour rings, wing tags and neck collars. These marks may generate substantial numbers of resightings both from carefully designed research programmes and from less systematic observations from birdwatchers. The extent to which such colour mark resightings are held by national ringing centres is variable. All of these factors lead to substantial spatial and temporal heterogeneity in reencounter rates that need to be taken into account during analysis.

Challenges for analysing movement from ringing data

The individual marking of birds has resulted in an impressive increase in our understanding of the movements of birds. In fact, ringing has arguably generated more knowledge about bird biology than any other method. The development of capture–mark–recapture analyses has increased the usability of ringing and re-encounter data tremendously (Lebreton *et al.* 1992). Only more recently has the focus on multi-state and state-space models allowed for estimation of movement

parameters together with demographic parameters (Schwarz, Schweigert & Arnason 1993; Schwarz & Ganter 1995; Patterson *et al.* 2007; McCrea *et al.* 2010), although the idea of using multi-state models for estimating movement rates came up much earlier (Arnason 1972). The lack of rigorous protocols for most traditional, large-scale ringing operations makes the resulting data less suitable for analyses with standard methods, and efforts have generally been directed towards strict field protocols that would create data suitable for mark–recapture models at a local scale (e.g. Constant Ringing Effort Sites; Robinson, Julliard & Saracco 2009). However, these approaches are focussed on demographic analysis and do not help with extracting information on movements from the heterogeneous collection of large-scale ringing and re-encounter data.

Ringing and re-encounter data are generally well suited to provide spatiotemporal information such as transition probabilities among sites under a state-space capture–mark–recapture (CMR) framework (Hestbeck, Nichols & Malecki 1991; Schwarz, Schweigert & Arnason 1993; Kendall, Conn & Hines 2006; Gimenez *et al.* 2007; Patterson *et al.* 2007). Many studies deal with movement rates (transition probabilities). In general, these rely on a substantial number of recaptures or resightings of birds moving (i.e. changing state) including of the same individuals, which ring recoveries only rarely provide. Typically, such studies focus on a few sites, often involving intensive and systematic resighting or recapturing efforts at relatively small geographical scales (e.g. Arnason & Cam 2004).

There are two major challenges with large-scale (typically continent-wide or intercontinental) spatial analyses of ringing and re-encounter data. The first is considerable spatiotemporal variation in re-encounter probability; the second is a high degree of complexity of the movement processes such as variation among individuals and separate periods within the annual cycle. Furthermore, the ringing databanks include data collected for many varying purposes, which complicates the separation of true movement patterns from the underlying data gathering processes. Thus, data from targeted studies on specific questions and data from general ringing activities are all combined in large data bases such as those held by EURING and BBL. The problems associated with the variation in reencounter probability differ markedly between the recoveries of metal rings of dead birds reported largely by members of the public and those associated with recaptures and resightings of live birds. In general, recoveries that result from public reporting of non-game species and hunters reporting game species are likely to be less heterogeneous than data sets comprising a mixture of public reports and recaptures and resightings due to targeted mark reading efforts of local-scale research projects. On the other hand, potential issues are in many cases better known and less random for the recaptures and resightings relating directly to such targeted projects (e.g. Frederiksen & Bregnballe 2000).

Re-encounter probabilities often show marked geographical variation within species. This is primarily related to human factors influencing reporting probability such as population density (e.g. very low at sea or in deserts), but also socio-eco-

nomic and political factors influence reporting probability. For Palearctic-African migrants, there is typically a large-scale difference between Africa and Europe as well as between East and West Europe (Fig. 5) attributable to human factors (Thorup & Conn 2009; Korner-Nievergelt *et al.* 2010a; Korner-Nievergelt, Liechti & Hahn 2012b). Re-encounter probabilities differ markedly among finding circumstances, and these in turn are often related to human activities such as hunting (Wernham *et al.* 2002). Geographical factors unrelated to human factors such as temperature affecting decay rate, birds being



Fig. 5. Changes over time in recovery locations of White Storks *Ciconia ciconia* ringed in Denmark during 1908–1969 (green) and 1970–2002 (black), indicating a change of flyway use. However, potential changes over time in recovery probability among areas have not been taken into account. (a) Geographic locations of recoveries; (b-c) directions from ringing to recovery sites. [Correction added on 16 December 2014, after first online publication: clarification of part labels added to figure caption.]

more difficult to find in some habitats and habitat-specific mortality rates also influence re-encounter probabilities (Wernham *et al.* 2002).

Re-encounter probabilities of course differ among species. Several intrinsic ecological factors such as size and habitat use will affect how easily a bird is found or observed. For example, Robinson, Grantham & Clark (2009) found different trends in re-encounter probability between ecological grouped species. Seasonal variation in re-encounter probabilities is less well known but can occur due to changes in behaviour and/or habitats. Many more songbird migrants are re-encountered during migration than during breeding (e.g. Bønløkke *et al.* 2006) either due to increased capture efforts during migration or possibly due to higher mortality during migration (Sillett & Holmes 2002).

Although information on first encounters of birds that are marked but not subsequently re-encountered is important for most quantitative approaches, the data are not computerised to the same degree as histories of birds that were re-encountered. Only a few European ringing schemes have computerised most of their first encounter (=ringing) data, for example Helsinki, Finland with more than 7 million ringed birds since 1974 and Hiddensee (eastern Germany) with 4 million ringed birds since 1977. Most ringing centres are now computerising all encounter data, including first encounters and local recaptures, but these data sets rarely extend before 2000. This is less of a problem in North America where all ringing and reencounter data are computerised from 1960 to the present, along with most data from 1955 to 1960. However, prior to 1955, only the re-encounter data were computerised, with ringing data for birds that were not re-encountered only available in paper format.

Historically, annual totals of birds ringed in each country in Europe are usually available, separated into adults and chicks (see http://www.euring.org/edb/index.html). These data may facilitate some modelling of the spatial distribution of recoveries, provided that countries are suitable geographical units and the analysis can focus on birds marked as chicks (which were obviously ringed in the nesting season). This may be possible for some gulls, seabirds and raptors. However, in most cases analyses need to include re-encounters of birds marked as fully grown, and here there is usually insufficient information on season and location of ringing to provide the data that would be needed for a robust analysis (e.g. separating likely breeding birds from those caught on passage). However, the availability of computerised first encounter data is improving rapidly, and we anticipate that many quantitative analyses of these long-term data will be possible over the next decade.

Ways to estimate spatiotemporal variation in re-encounter probability

Korner-Nievergelt *et al.* (2010a) outline four ways to address the major issue of spatiotemporal variation in re-encounter probabilities: (i) comparison with other methods such as reward rings or satellite tracking, (ii) using external covariates of re-encounter probability such as socio-economic factors, (iii) comparing re-encounters with all possible re-encounter locations and (iv) capture–mark–recapture analyses assuming equal re-encounter probabilities among different groups, for example species, populations or age classes, within the same geographical area and/or time period.

Comparing re-encounter probability of standard rings with reward rings has been used to assess reporting probability in many studies (e.g. Conroy & Blandin 1984), but it does not necessarily account for geographical variation in recovery probability. Ring re-encounter rates have been compared to other detection methods that do not have the spatiotemporal biases inherent in ringing data. Ring recoveries were compared to satellite telemetry tracking data for three raptor species (Strandberg, Klaassen & Thorup 2009) and to geolocator data for Red-backed Shrike Lanius collurio (Korner-Nievergelt et al. 2012a). These studies both identified a temporal bias for later southward migration timing estimates from ring reencounter location data as compared to tracking data, possibly caused by increased re-encounter probabilities of aberrant or sick birds staying behind or migrating later. Such bias could potentially be modelled as a latent state (e.g. sick versus healthy) that affects migration rate and re-encounter probability rather than as a general increase in re-encounter probability, but this has not been attempted so far. A number of other studies have supplemented movement analyses using molecular or geolocator data with ring re-encounter data without assessing biases in re-encounter probabilities (Boulet, Gibbs & Hobson 2006; Lopes, Marques and Wennerberg 2006; Procházka et al. 2008; Ryder, Fox & Marra 2011; Van Wilgenburg & Hobson 2011). No study has yet presented an integrated analysis, which would extend inference from both methods while accounting for re-encounter probabilities.

Royle & Dubovsky (2001) incorporated spatial autocorrelation in estimation of observer heterogeneity. In such models, external covariates such as human density could potentially be included as predictors for re-encounter probability. Such predictors would help estimating re-encounter probability for regions with fewer or no re-encounters. But, to our knowledge, this has not been done yet.

Comparing actual observation with a set of all possible observations (e.g. all nest boxes in an area or all observations of all species similar to the study species) can be used to estimate observer heterogeneity. However, such methods have only been used on relatively small-scale studies (e.g. nest-box studies; Winkler *et al.* 2005). For large-scale studies, the distribution of all ring re-encounters or of a selection according to finding circumstances might potentially be used, but no studies have attempted such use.

Most studies that have dealt with the variation in re-encounter probability have used variation in movement rates (seasonal transition probabilities or spatiotemporal distributions) among groups based on an assumption of equal re-encounter probabilities among groups. Table 1 provides an overview of studies of movement patterns from large-scale ringing data that have dealt with variation in re-encounter probabilities explicitly.

many wintering CMR = captur	areas). The key chall ə-mark-recapture. M	enges are aspects of the study the study the maximum likelihood. N =	hat were difficult to solve or cc north, S = south, E = east, W	uld only be solved suboptimally through 1 / = west, C = central	key assumptions. See text for a more	detailed discussion of the studies.
Group/species	Marking areas	Re-encounter areas	Data	Key assumption (s)	Key Challenges	Reference
1; Woodcock	6; regions of France	2; Scandinavian and Russian flyways	Marking and re-encounter	Flyway-specific recovery probability equal among birds ringed in different regions	Estimates of uncertainty using CMR (ML method)	Bauthian <i>et al.</i> (2007)
7; songbird species	1; Denmark	2; Europe/N Africa or sub-Saharan Africa	Marking and recovery; annual totals	Survival and area-specific recovery probabilities equal among species	Estimates of uncertainty using CMR (ML method)	Thorup & Conn (2009)
			Marking and recovery; summed totals	Area-specific recovery probability equal among species	Estimates of uncertainty using CMR (ML method). Model only estimable with a non- moving reference species included	Thorup & Conn (2009)
3; duck species	1; Lake Sempach	2; < or >200 km from ringing	Marking and re-encounter (both recovery and resighting); annual totals	Parameters constant within species only. Re-encounter probabilities proportional among species	Survival estimates generally biased and with very low precision. Model only estimable with a non-moving reference species included	Korner-Nievergelt et al. (2009)
1; Common nightingale	4; WC, SC, NEC, E Europe	3; W, Central and E flyway to sub-Saharan Africa	Re-encounter only (both recovery and recapture); unknown number of birds ringed	Equal return probabilities among areas	Heterogeneous return probability not affecting movement estimates	K orner-Nievergelt, Liechti & Hahn (2012b)
l; European robin	4; Sweden, Denmark, Germany, Switzerland	4; N Europe, C Europe, Mediterranean, N Africa	Marking and recovery; monthly totals	Region-specific recovery probability equal among different groups	Low sample size for some groups; non-homogeneous recovery probability within the (large) regions	K orner-Nievergelt, Liechti & Thorup (2014); this volume
3; Common, Roseate and Caspian terns	3; E, C, and W North America	4; E South America, W South America, Mexico and Central America, S United States and Caribbean	Marking and re-encounter (recovery or recapture/ resight); capture histories	Region-specific recapture and recovery probability equal among species	Low precision of migratory connectivity from western regions where fewer birds were marked	Cohen et al. (2014); this volume

Table 1. Large-scale studies estimating proportional distribution of birds among areas taking heterogeneity in detection probabilities into account and including areas with little or no ringing efforts (as, e.g., in

Capture–mark–recapture analyses assuming equal re-encounter probabilities among different groups

If the number of groups of birds (e.g. marked in different areas) with differences in migration behaviour is equal to or greater than the number of re-encounter areas, movement parameters (transition probabilities or group-specific proportions of birds being in different areas at different times) are identifiable even if no additional information on observer effort is available (Kania & Busse 1987; Kendall, Conn & Hines 2006). Despite the potential of using this information, originally proposed by Busse & Kania (1977) and Kania & Busse (1987) as the division coefficient, few studies have used this method for estimation of proportions of populations migrating to different areas. The division coefficient originally presented as a system of linear equations can be formulated as a product multinomial model with a multinomial model for each vector of re-encounters of birds from group g in different areas $\mathbf{R}g$, that is, a total of G multinomial models with G being the number of groups (Korner-Nievergelt et al. 2010b):

 $\mathbf{R}_{g} \sim \mathrm{Multinom}(\mathbf{p}_{g}, N_{g})$

$\mathbf{p}_g = (r_A m_{gA}, r_B m_{gB}, \dots, r_K m_{gK}, q_g)$

 N_g is the number of ringed birds in group g, r_k is the probability that a ringed bird being in area k is re-encountered there, K is the total number of areas and m_{gk} is the proportion of birds from group g that migrated to area k, and q_g is the probability that a ringed bird is never found again. In the case of independent model parameters (no constraints, no covariates), the model parameters are identifiable if the number of groups G is equal to or higher than the number of areas K, and if the proportions of birds migrating to the different areas, m_{gk} , differ among the groups. An implicit, essential assumption made by the model is that the areaspecific re-encounter probability does not differ between the groups, that is, all individuals that migrate to k have the same re-encounter probability independent of where they came from. In addition, the method requires that the number of marked birds N_{σ} is known.

For example, assuming equal re-encounter probability within each of two flyways for Woodcocks *Scolopax rusticola* ringed in different regions of France during winter, Bauthian *et al.* (2007) estimated ring re-encounter probabilities in various breeding areas together with proportions of the region-specific winter populations that breed in the different breeding areas. These authors provided estimates of uncertainty using a maximum likelihood method.

Thorup & Conn (2009) extended this analysis to a group of migrant songbird species and estimated the proportions of birds of each species moving from Europe/North Africa to sub-Saharan Africa. Two modelling formulations were used. In the first, annual recovery probabilities were modelled assuming constant survival and recovery probabilities among species. In the second, lifetime recovery probability was modelled, and the assumption of constant survival rates could be relaxed. However, constant recovery probabilities are still assumed, and differences between species in causes of mortality could result in different reporting rates.

Korner-Nievergelt *et al.* (2009) used a similar approach for three duck species, combining recovery and recapture data, and assuming only that parameters were constant within and re-encounter probabilities proportional among species. Survival estimates were, however, generally biased and with very low precision, and the models in reality were comparable to those assuming constant survival rates among species.

Both Thorup & Conn (2009) and Korner-Nievergelt *et al.* (2009) used a 'reference' species to increase precision. In both cases, the reference species was a species whose migration rate could be assumed to be zero. In general, parameter estimates become more precise when differences in movement rates are high (Thorup & Conn 2009; Korner-Nievergelt *et al.* 2010a).

Cohen *et al.* (2014) modelled long-distance migratory connectivity of three tern species. They built on Thorup & Conn (2009) and Korner-Nievergelt *et al.* (2009) using 'reference' species, where the linkages to some areas can be assumed to be zero, and assumed equal re-encounter probabilities within separate geographical areas among the three closely related species modelled together. Further, they incorporated ring reencounters of live and dead birds and estimated both recapture and recovery probabilities (Kendall, Conn & Hines 2006). 'Observer effort' covariates were built for re-encounter probabilities derived from re-encounters of additional species occurring within the same habitat and spatiotemporal re-encounter regions.

Interestingly, none of these studies have explicitly addressed the potential problematic assumption of homogeneous re-encounter probability within regions (but see Korner-Nievergelt, Liechti & Hahn 2012b). Because species with different distributions are unlikely to be equally distributed within regions, this assumption becomes crucial. Thus, the specification of large re-encounter regions could lead to bias. For example, re-encounter probabilities are unlikely to be equal in North Africa and Europe, and when combining these, as in the study by Thorup & Conn (2009), the estimated proportions of species staying north of Sahara are likely biased for those predominantly staying in the north compared to those moving south. The best solution may be to define the regions as small as possible, depending on the scale of study. For large-scale studies, the country level (or state/province for large countries) is probably sufficient. The smaller the regions, the higher the number of parameters that have to be estimated, resulting in more data hungry models (Lebreton & Pradel 2002). This may be compensated by including covariates for the model parameters. Defining countries or states/provinces as regions would, for example, allow one to use human population density as a covariate for re-encounter probability.

None of these methods explore the possibilities of inferring movement from the temporal variation in re-encounters within a species or group. Recently, Korner-Nievergelt, Liechti & Thorup (2014) added a second dimension, season, to the product multinomial model described above. To model the number of re-encounters per area and season, the probability vector was modified for two seasons:

$\mathbf{p}_{g} = (S_{1}r_{A1}m_{gA1}, S_{1}r_{B1}m_{gB1}, \dots, S_{1}r_{K1}m_{gK1}, S_{2}r_{A2}m_{gA2}, S_{2}r_{B2}m_{gB2}, \dots, S_{2}r_{K2}m_{gK2}, q_{g}),$

where S_i is the probability that a bird dies during season *i*. In this way, differences in the distribution between the different groups of birds become larger and therefore, the model parameters better estimable. In this model, the location of a bird does not depend on where it was the time period before. As a consequence, it is not necessary to have birds released in every region to obtain precise estimates.

For mark–re-encounter models developed for the aquatic environment (e.g. Sibert *et al.* 1999), the spatial variation in reencounter probability is most often closely related to known commercial fishing or resighting efforts, which is less likely to be the case in terrestrial environments. For much of the EUR-ING data, only the re-encounter data have been computerised. Korner-Nievergelt, Liechti & Hahn (2012b) circumvented this problem in an analysis of Common Nightingale *Luscinia megarhynchos* recoveries on flyways, by estimating the num-



Fig. 6. Information from different data sources and different species can be combined in an integrated two-level model, as shown in the example for six hypothetical species. The first level constitutes the movement model: the latent state variable Z¹(X¹) describes the movement pattern of species j with respect to explanatory variables X^J. This movement pattern is observed by three methods A, B and C. Such methods could be marking and re-encountering individuals, tracking by geolocators or stable isotope analyses. This produces a maximum of $6 \times 3 = 18$ data sets. When analysing these 18 data sets in one integrated model, information about the observation processes is exchanged among the species and information about the movement process is combined over the three data sets obtained by the different methods for the same species. This allows us, for example, to extrapolate results from a small population that was tracked by geolocators to a much larger population of individuals that were ringed. See Box 1 for a simplified (one species only) specific example of an integrated model.

bers of birds marked using recaptures within breeding sites. There were three rather strong assumptions: (i) no spatial variation in probability of recaptures within breeding sites, (ii) homogeneity in breeding area return probability and (iii) homogeneity in re-encounter probability within the flyways. The assumption of equal probability of recaptures among sites may be problematic for larger more complex data sets. While the computerisation of ringing data may be more of a practical issue than an analytical problem, the enormous amount of data involved means that the importance of computerising the data must be seriously considered.

Future directions

In general, the analysis of seasonal movement at the species and population level from ringing data is restricted by a limited number of re-encounters, and thus, single-species analyses would only work without restrictive and unrealistic assumptions for a few common species, such as the European Robin (Korner-Nievergelt, Liechti & Thorup 2014). However, models built on realistic assumptions for a few species with larger numbers of re-encounters can potentially be extended to include other species with few re-encounters assuming similarity in estimated parameters. Given the many ways, spatiotemporal variation in re-encounter probabilities can be estimated and the freedom a Bayesian framework provides, a way forward might be to combine information from different data sources, methods and species (Fig. 6). In Box 1 we present an example of a model for the integration of ring re-encounter data with known and unknown number of ringed birds and stable isotope data to estimate population-level proportions of birds migrating to different areas. To our knowledge, such a model has not yet been applied. Including many species in a combined model framework would potentially allow mapping of ring re-encounter probabilities in space and time for different species for use as a reference for future studies. In this case, the main problem becomes the complexity of movement processes and how to deal with the expansive parameter space given the often limited data.

A valuable step would be to identify data sets (single- or multi-species) that contain clear information on re-encounter probability. Such data sets should meet the model assumptions as closely as possible, that is, it should be possible to divide these data sets into groups of individuals with a homogeneous behaviour in relation to survival, migration and re-encounter probability. Such data sets exist from standardised ringing programmes, from ringing schemes that have computerised a large amount of the ringing data or from populations for which migration has been measured additionally with other techniques (such as satellite transmitters). In some cases, it may be possible to use annual marking totals directly. For example, in some species only certain age classes are ringed at certain times of the year (typically young in the nest), and in others they are only catchable at certain times of the year (e.g. this is true for swift species). Such approaches might circumvent some of the issues with missing marking data.

Box 1.

Here, we give a simplified example of an integrated model (for one species) that allows combining the information in qualitatively different data sets about the proportion of birds from population g (1, 2, ..., G) migrating to different areas k (A, B, ..., K). The biological process (on the population level) can be formulated as a Dirichlet distribution for each population, with m_{gk} being the proportion of population g migrating to area k. Within one population g, these proportions sum up to 1.

 $m_{gk} \sim \text{Dirichlet}(\mathbf{a}_g)$

We add three observation processes, (1) for the ring re-encounters with known number of ringed birds, (2) for the ring re-encounters with unknown number of ringed birds and (3) for the stable isotopes.

Observation model 1: See text for a description of this model and its assumptions and requirements.

$$\mathbf{R}_{g} \sim \text{Multinom}(\mathbf{p}_{g}, N_{g})$$

$$\mathbf{p}_{g} = (r_{A}m_{gA}, r_{B}m_{gB}, \ldots, r_{K}m_{gK}, q_{g})$$

Observation model 2: Based on area-specific re-encounter probabilities r_k and the proportions m_{gk} , we can formulate an expected distribution of the re-encounters among the different areas and build a multinomial model for the re-encounters \mathbf{R}^*_g with unknown number of ringed birds. This model makes the same assumptions as the one above.

$$\mathbf{R}_{g}^{*} \sim \text{Multinom}(\mathbf{p}_{g}^{*}, \sum \mathbf{R}_{g}^{*})$$
$$\mathbf{p}_{g}^{*} = (r_{A}m_{gA}, r_{B}m_{gB}, \dots, r_{K}m_{gK}) / \sum (r_{A}m_{gA}, r_{B}m_{gB}, \dots, r_{K}m_{gK})$$

Observation model 3: Let y_i be a measured stable isotope of individual *i* that belongs to group g_i . When we assume that the y_i of all individuals that migrated to the same area k are normally distributed with a mean and a variance that is defined by the climatic condition of the area k, a normal mixture model can be formulated for the y_i of each breeding population g.

$$y_i \sim \operatorname{Norm}(\mu(k_i), \sigma(k_i))$$

$$k_i \sim \text{Categorical}(m_{g[i]A}, m_{g[i]B}, \ldots, m_{g[i]K})$$

Bayesian methods allow us to use informative priors for $\mu(k_i)$, $\sigma(k_i)$. Maps of stable isotopes published by, for example, Hobson *et al.* (2012) provide information about area-specific means and variances of different stable isotopes.

As explained above, and emphasised also by other authors (e.g. Norris, Wunder & Boulet 2006), ring re-encounter data complement other data sources such as observations or tracking by modern technological devices. Therefore, combining information from different data sources, species and methods provides a key to extracting information such as migratory connectivity that is needed to understand migration ecology from ring re-encounters.

Good practice would dictate that scientists evaluate existing ringing and re-encounter data before planning a study on migratory connectivity using expensive and often also more invasive techniques. It is the plan for EURING to compile all ringing and re-encounter data into a pan-European ringing atlas (http://www.euring.org/research/migration_atlases/index. html). The degree to which interpretation will build on traditional, qualitative methods or will be extended to more advanced analytical methods is largely a matter of (i) the computerisation of marking data and (ii) the state of methodological development of inference from the ringing data. In the western hemisphere, an Atlas of Migratory Connectivity for the Birds of North America is in preparation. It will include maps of ring re-encounters across seasons and modelled estimates for migratory connectivity as well as connectivity information from other sources (e.g. stable isotopes, satellite transmitters).

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Data accessibility

All data shown in Figures are archived in the EURING databank (www.euring. org) and published in the following sources:

Bønløkke J, Madsen JJ, Thorup K, Pedersen KT, Bjerrum M, Rahbek C (2006). Dansk Trækfugleatlas. [The Danish Bird Migration Atlas]. Rhodos, Humlebæk, Denmark: fig. 1,3,4,5

Bakken V, Runde O, Tjorve E (2006) Norsk Ringmerkings Atlas (Volum 2 Duer-Spurvefugler) [Norwegian Bird Ringing Atlas (Volume 2 Pigeons-Passerines)]. Stavanger, Stavanger Museum: fig. 4.

Fransson T, Hall-Karlsson S, Larsson P (2008) Svensk ringmärkningsatlas (Volym 3 Tättingar) [Swedish Bird Ringing Atlas (Volume 3 Passerines)]. Stockholm: fig. 4.

www.EURING.org: fig. 2.

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