



Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity

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Ring re-encounter data, in particular ring recoveries, have made a large contribution to our understanding of bird movements. However, almost every study based on ring re-encounter data has struggled with the bias caused by unequal observer distribution. Re-encounter probabilities are strongly heterogeneous in space and over time. If this heterogeneity can be measured or at least controlled for, the enormous number of ring re-encounter data collected can be used effectively to answer many questions. Here, we review four different approaches to account for heterogeneity in observer distribution in spatial analyses of ring re-encounter data. The first approach is to measure re-encounter probability directly. We suggest that variation in ring re-encounter probability could be estimated by combining data whose re-encounter probabilities are close to one (radio or satellite telemetry) with data whose re-encounter probabilities are low (ring re-encounter data). The second approach is to measure the spatial variation in re-encounter probabilities using environmental covariates. It should be possible to identify powerful predictors for ring re-encounter probabilities. A third approach consists of the comparison of the actual observations with all possible observations using randomization techniques. We encourage combining such randomisations with ring re-encounter models that we discuss as a fourth approach. Ring re-encounter models are based on the comparison of groups with equal re-encounter probabilities. Together these four approaches could improve our understanding of bird movements considerably. We discuss their advantages and limitations and give directions for future research.

Animal movements are studied in many species and locations. At several scales they are important elements of a species' life history. However, especially at the larger scales needed for the study of seasonal migration, there are still many gaps in our knowledge about the numbers of animals moving, because observers are often unevenly distributed in space and time. Estimating which number of individuals from what species is moving when and to where is essential for many fundamental ecological questions. Apart from the influence of animal movements on the population dynamics, the potential role of birds as vectors for transmitting emerging diseases, such as avian influenza, has invigorated research into bird movements (Gauthier-Clerc et al. 2007).

It is well known that the relationship between an observation and the behaviour of the animal studied is nearly always complex. A bird that dies in a nest-box is likely to be found, whereas the same bird dying in the same

forest but outside of the nest-box has a much lower chance of being recovered. Similarly, a bird dying in Africa is much less likely to be found and reported than a similar bird dying somewhere in Europe. Thus our observations are always a result of two different processes: 1) the biological process we want to study, in our case the movement of animals and 2) the observation process in which the spatio-temporal distribution of observer effort is the main variable. In fact, the observation process often can explain more variation in our data than the biological process (Fig. 1). Consequently, if we do not explicitly consider the observation process, our estimates of the biological process are likely to be biased (Perdeck 1977, Royle et al. 2005, Patterson et al. 2007, Doligez and Pärt 2008). This paper results from a workshop where we discussed several recent methods that account for the observation process in analyses of spatial patterns in ring re-encounter data.

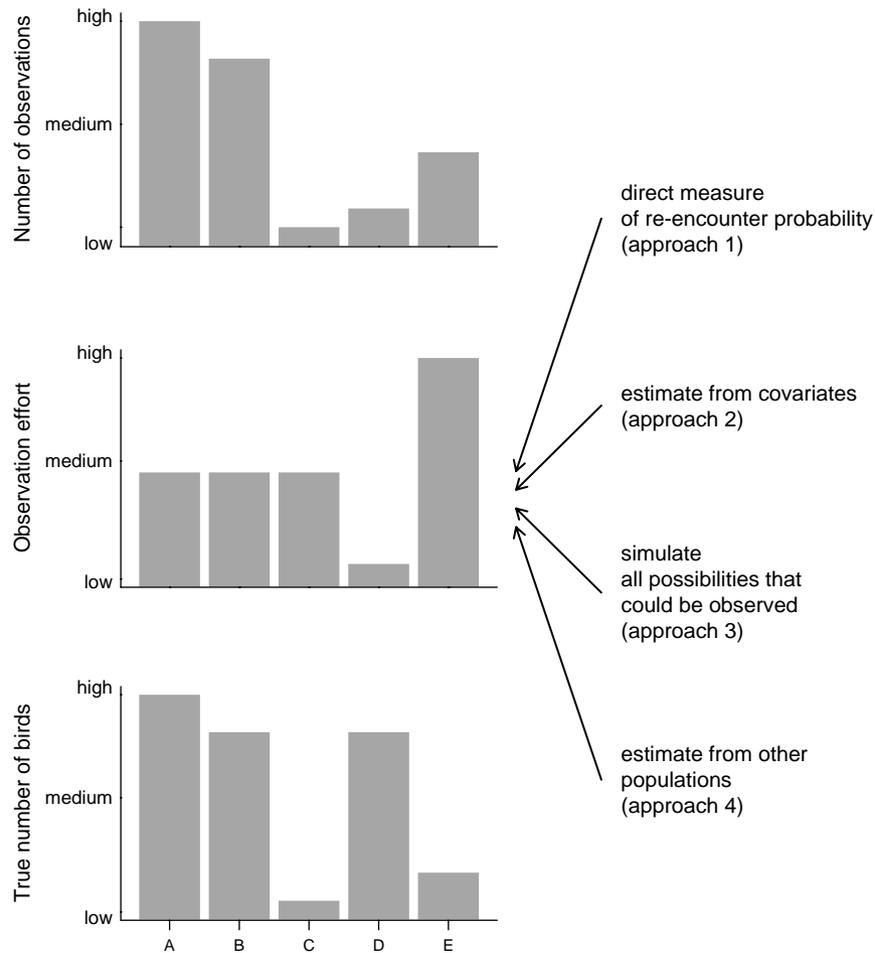


Figure 1. Distribution of observations, observation effort and the (unknown) true bird distribution in areas A to E. The unknown true bird distribution is proportional to the ratio of the number of observations and the observation effort. Observation effort can be estimated or accounted for using one of the four approaches discussed in this article.

The challenge can also be expressed in a different way: we would like to know to what extent the absence of a record is caused by the genuine absence of the organisms studied. Or put in a more quantitative way: we want to know how the unknown observer distribution influences our observed distribution of bird re-encounters. We would like to make the transition from the absence of evidence to collating evidence for an absence. Several methods discussed in this paper take this approach. A first one is the direct measurement of re-encounter probability (approach 1). A second method is to model re-encounter probability for an area with known bird density using covariates from human behaviour and environmental factors. Re-encounter probability can then be predicted for other areas and the comparison with the actual re-encounter densities gives information about bird density (approach 2). A third method is to construct a full description of all possible observations and to compare the observations actually made with this description of the pattern that is expected in principle (approach 3). In the last approach, information on re-encounter probability can be extracted from mark-recapture data if several groups of birds with similar properties are compared (approach 4). We finish with a synthesis and a discussion of the perspective of these methods.

Definitions

To begin, we will discuss some technical terms because these terms are not used consistently in the literature, and we will give the definitions used in this article. For notation we mainly follow the recommendations given by Thomson et al. (2009). 1) *Observer bias*. Systematic error in the conclusion drawn from ring re-encounter data caused by temporally or spatially inhomogeneous re-encounter probabilities. 2) *Reporting probability* is the probability that the relevant information (i.e. ring number) of a resighting or a finding of a marked animal is reported to the bird ringing centre. Unfortunately, Thomson et al. (2009) could not give an unanimous recommendation concerning the use of “reporting probability”. Our definition differs from the one given by Seber (1970), who defined reporting probability as the probability that a dead bird is found and reported, which is the product of finding probability and reporting probability in our notation. Here, we call this product re-encounter probability. Much of the confusion stems from the different contexts in different studies. With hunted species, it is the reporting process where variation occurs, while with birds dying from natural causes the finding of dead birds is the variance producing factor. 3) *Re-encounter probability* is the product of the finding

probability and the reporting probability, where the *finding probability* is the probability that a marked animal or its mark is found or resighted by an observer given the animal is alive or its dead body is still detectable. Re-encounter probability is expressed with reference to a specific time period that is typically defined by the study design. Therefore, re-encounter probability is used in different ways. Rarely, it is used as defined here. More often re-encounter probability is not independent from survival probability because the bird has a chance to die and its body can disappear during the reference time period. There are many different ways in which survival and re-encounter probability can be confounded. This depends on the finding circumstances (life resightings, recaptures or recoveries of dead birds), the study species (a species can be long-lived or short-lived) and study design (specific model, time periods considered). In almost every case re-encounter probability will interact with survival probability. For future work, we recommend defining exactly what re-encounter probability includes. 4) *Migration rate* (as defined in the mark-re-encounter framework) is the proportion of birds moving from one area to another within a given time interval. If this time interval is short (e.g. one week, one month) migration rate is interpreted as the probability that an individual moves within the time interval considered. If the time interval becomes long (i.e. at least one breeding cycle), the migration rate describes the bird distribution (e.g. proportions of birds from different breeding areas wintering in different winter areas) rather than the dynamic bird movement. Theoretically, there is a continuum between dynamic migration rate (proportion of birds moving within a short time interval) and static bird distribution (proportion of a bird group present in different areas) depending on the length of time interval the migration rate refers to.

Approach 1. Direct measurement of re-encounter probability

Several studies have assessed reporting probability in hunted species. A common method is to compare recovery probabilities of standard rings with those of reward rings for hunted species (e.g. Bellrose 1955, Tomlinson 1968, Henny and Burnham 1976, Reeves 1979, Conroy and Blandin 1984, Nichols et al. 1991). Furthermore, questionnaires and active surveys of hunters can provide information on reporting probabilities (Geis and Atwood 1961, Martinson 1966, Martinson and McCann 1966). However, these methods require an enormous effort and they do not give information about reporting probabilities for non-hunted species. For non-hunted species, it might be possible to assess variation in reporting probability by mapping re-encounters together with political boundaries and important habitat features (Fig. 2). If countries explain a high percentage of variation in re-encounter density this might be caused by different reporting probabilities among countries.

Measuring finding probability is difficult. It might be possible in experiments where reporting probability equals one, for example in studies where re-encounters are made by the investigators (e.g. Prosser et al. 2008). However, even

in such studies, it is difficult to estimate finding probability if one cannot rule out emigration from the study area or if finding rate varies within the study area. One approach to assess the effect of finding probability is to compare re-encounter data with data obtained by methods that presumably have a finding probability equal to one, e.g. radio or satellite telemetry. Bächler and Schaub (2007), for example, estimated stopover duration by Cormack-Jolly-Seber (CJS) models based on resightings and recaptures of marked birds and compared these with estimates obtained from telemetry data of the same birds. The authors found that estimated stopover duration based on telemetry data is twice as long as the same estimate based on resightings and recapture of marked birds. This shows that finding probabilities influence conclusions drawn from re-encounter data even if these conclusions are drawn with methods accounting for finding probability such as CJS models. This problem is more serious when the average finding rate is low. Nonetheless, this study indicates that combining information from ringing and telemetry studies might give important insights in the mechanisms of re-encounter process.

Even though the described approaches are the most straight-forward to deal with observer bias, they have two major drawbacks: 1) an enormous logistical effort is required, and 2) most of them can not be applied retrospectively, as would be required to analyse the large amount of re-encounter data stored by most national ringing schemes. It would be exciting to distribute a very large number of dead and marked birds in different countries and subsequently measure recovery rate. We do not know of any such experiment.

The use of recent technological advances in tracking methods (satellite telemetry, GPS-loggers, day-time loggers) appears more promising. These methods now allow researchers to follow some individuals in detail throughout their live (e.g. Croxall et al. 2005, Stutchbury et al. 2009). If the same individuals are simultaneously radio tracked and visually resighted, a finding probability for the resightings can be measured directly (e.g. Bächler and Schaub 2007). Such situations are, however, rare. Nevertheless, to combine ring re-encounter and tracking data helps to assess possible bias in ring re-encounter data (e.g., Kenward 1993, Strandberg et al. 2009). Furthermore, such a combination can improve conclusions, because tracked individuals give us detailed information on a few individuals, while ring re-encounters provide coarse information on many individuals and thereby a variance measure.

Approach 2. Assessing geographic patterns in re-encounter probability using environmental and socio-demographic covariates

Ring re-encounter data give us the location of an individual at two or more points in time. There are many ways to model the occurrence of such events in space. Some of these include bivariate kernel density estimation (Duong 2007), geostatistical methods (Ripley 1981, Webster and Oliver 2007), habitat suitability modelling

using generalised linear/additive models (McCullagh and Nelder 1989, Guisan and Zimmermann 2000, Wood 2006) or other recently developed techniques (Guisan and Thuiller 2005, Elith et al. 2006). If such models are applied to ring re-encounter data, a spatially explicit matrix of weights is required beforehand, which corrects the observed events for differences in re-encounter probabilities.

Some properties of the re-encounter locations influence re-encounter probability and thus can be used to reduce the variance caused by heterogeneity in observer distribution. Predictive spatial models of re-encounter probability could be established using environmental and socio-demographic covariates. Probability of re-encounter will depend on a number of factors (Payevsky 1973). The primary determinant will be human activity, which may vary with socio-political systems (Fig. 2) or simply human population density (Fig. 3). Other factors include body size (large birds are much more often found than small ones), species ecology (those occurring in dense vegetation will be less likely to be found than species of open habitat) and rate of decay (for dead animals, corpses will remain detectable longer in boreal/temperate areas than in tropical regions). The finding circumstance will also introduce bias, e.g. the distribution of hunted individuals will differ markedly from those resighted alive or found by ornithologists while ringing birds. Spatial re-encounter probability models could be established using large datasets containing several species,

such as the combined data set of several ringing schemes with known numbers of ringed birds.

Recently developed hierarchical modelling and estimation techniques enable one to potentially model the biological and observation processes separately (e.g. Royle and Dorazio 2008). Thus, the number of birds reported is expressed as the result of a hierarchy of processes: firstly, the underlying movement process generates the ‘true’ number of individuals available to be recovered, a subset of these (determined by some model of observer behaviour) are then subsequently found and reported. The recent implementation of Bayesian methods, through Markov chain Monte Carlo (Brooks 2003) or sequential importance sampling (Newman et al. 2006), now mean that fitting such complex models, which were deemed too computationally demanding only few years ago, can now be practically considered. For example Royle and Dubovsky (2001) used a spatial binomial random effects model to estimate a map of recovery probabilities for mallards *Anas platyrhynchos*. This gave harvest managers a much clearer picture of regional variation in hunting pressure. Such hierarchical spatial models are a promising tool for separating re-encounter probability from true bird distribution.

The applicability of spatial models to predict re-encounter probability should be tested for a variety of species. Using well described situations, e.g. areas where bird surveys are conducted repeatedly important covariates

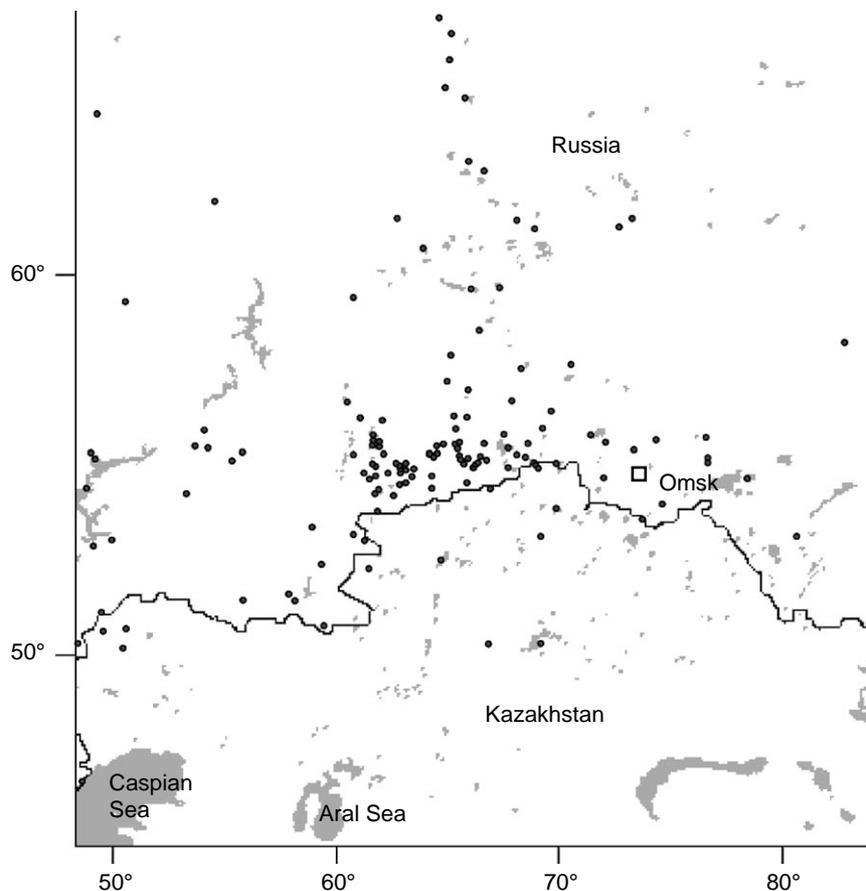


Figure 2. Re-encounters of pochards *Aythya ferina* (dots) ringed in Switzerland in the Russian-Kazakhstan region. The line indicates the border between Russia and Kazakhstan. Lakes are in grey. Recovery density in Russia is higher than in Kazakhstan although the density of lakes is about equal. The figure is taken from Hofer et al. (2006).

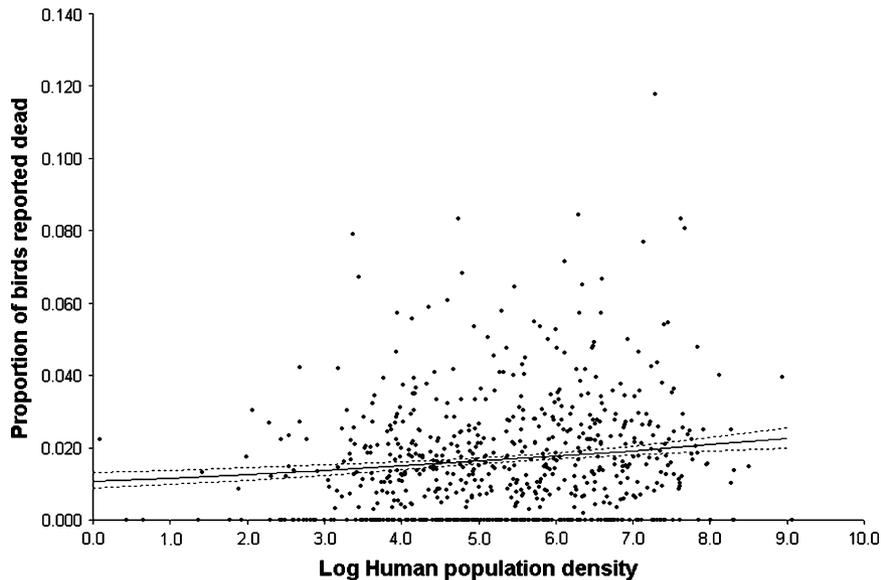


Figure 3. Proportion of British breeding blackbirds *Turdus merula* ringed between 1990–2000 and subsequently found dead (to 2008) according to (log) human population density in the area of ringing. Solid line represents binomial GLM ($\beta = 0.084 \pm 0.017$, $\chi^2 = 23.30$, $P < 0.001$), dashed lines 95% confidence interval. Each point ($n = 695$) is a ten-km square of the national grid; squares where fewer than 30 Blackbirds are ringed were excluded. Most British breeding Blackbirds are recovered < 5 km from the ringing location and mean life expectancy is 3 years.

(e.g. availability of wetlands, information about hunting regimes per region, gross domestic product) could be identified. The measurement of these covariates should then be prioritised in future studies or the information could be collected retrospectively (where possible). For some situations, it might be worth exploring the usefulness of geostatistical modelling techniques (Diggle and Tawn 1998, Guisan and Thuiller 2005, Elith et al. 2006) for identifying regions with suitable habitats but low re-encounter probabilities.

Approach 3. Describing the set of all possible observations

Another way to deal with heterogeneity in re-encounter probability is to describe the set of all possible observations based on the spatial distribution of known re-encounter locations. Then, the comparison of the actual observations with all possible observations gives information about bird behaviour.

Sometimes this can be done literally, for example in a study of dispersal where all possible observations are obtained by connecting all known sites of birth to all known sites of breeding, and then the distributions of all possible dispersal distances is compared with the distribution of the observed dispersal distances in order to infer bird behaviour (e.g. Winkler et al. 2005).

One example of explicit construction of the set of all possible observations was given by van Noordwijk (1984) who showed that the possible observations starting from one nest-site could differ substantially from the possible observations from a different nest site. Assuming random resettlement lead to substantial correlations between the distances dispersed by fathers and sons, simply because sons

are born in the nests where the fathers breed. This idea was later extended to measure dispersal as distance-dependent recruitment rates (van Noordwijk 2006). This method is based on a description of all potential observations by describing the average numbers of nestlings ringed in each distance class from the points where ringed or unringed birds recruited into the population. The ratio of the observed movements per distance class over the average number ringed previously in that distance class gives a recruitment rate, expressed as the number of adults recruited per nestling ringed. To conclude, comparing the observed re-encounter distribution with the observer distribution (i.e. all possible observations) eliminates a large part of the variation caused by heterogeneity in observer distribution.

This approach has only been used in small scale situations with well known habitat structures such as the locations of nest-boxes. The applicability to ring re-encounter data on larger scales should be tested. The key to the solution will be to find a good measure of observer distribution. If it is not possible to obtain observer distribution directly, it could be done approximately, for example when studying migration based on recoveries of dead birds, where the recovery sites of other populations of the same species or the recovery sites of other species can be taken as evidence of the presence of an observer at that place at that moment. For example, the relative re-encounter ratio concept (see approach 4) estimates observer distribution based on a larger set of re-encounters from bird groups with similar re-encounter probability as the bird group of interest. The estimated re-encounter probability itself could serve as an approximation of observer distribution. It might be valuable to combine both methods, i.e. describing all possible observations within a model that estimates re-encounter probability such as a multi-state model (approach 4), in

order to gain more precise results. We are not aware of any such study.

Approach 4. Comparing groups of birds with equal re-encounter probabilities

One can also deal with spatio-temporal heterogeneity in re-encounter probabilities by comparing the data from different groups of birds making certain simplifying assumptions. Imagine that birds originating from different groups (e.g. local populations, sexes, migration waves, eventually species) use different discrete locations for spending, e.g., the non-breeding period. Our goal is to know which proportion of birds moves to which area (i.e. migratory connectivity, Webster et al. 2002).

For example, ringed swallows *Hirundo rustica* are re-encountered across sub Saharan Africa; Dutch swallows in the western part, Swedish swallows in the centre, and Finnish swallows in the eastern part of the continent (Fig. 4). Assuming that there are no intrinsic differences in the likelihood of a marked swallow from these different breeding areas to be recorded in Africa then the occurrence of records of Dutch swallows, but not of Swedish or Finnish swallows, conveys information on the absence of Swedish and Finnish swallows, and *vice versa*. Of course, we can say nothing about the presence of swallows (Finnish or otherwise) where no swallows have been recorded, but the proportion of Finnish and Dutch swallows wintering in different areas of Africa can be compared relatively, using *relative re-encounter ratio* (Kania 2006, Rivalan et al. 2007). Sometimes it may be possible to obtain estimates of absolute proportion of birds per area and area specific re-encounter probabilities using the *division coefficient concept* (Busse and Kania 1977) or analogously, *multi-state mark-recapture/recovery models* (e.g. Schwarz 1993, Bauthian et al. 2007, Thorup and Conn 2009). All these approaches require data on different groups of birds to be analysed simultaneously and also require all groups to have certain parameters in common, in this case, re-encounter probabilities, while others (e.g. distribution among destination locations) can be different.

The *relative re-encounter ratio concept* was initially developed to analyse long-term changes in the proportion of a population moving to a specific destination area (Kania 2006, called *relative recovery rate* there). These relative measurement of change is a ratio of re-encounter probabilities (ratio of the ratios of re-encounter numbers to number of ringed birds for the group of interest and a reference group; see details in Kania 2006). Rivalan et al. (2007) integrated the *relative re-encounter ratio* into a ring recovery model (as developed by Brownie et al. 1985) in order to estimate temporal changes in migration strategies of blackbirds *Turdus merula* and redwings *T. iliacus*.

An approach that has widely been used to estimate proportions of birds moving from and to different areas within a given time interval constitute *multi-state models* as described by Arnason (1972) for recapture data and further developed by Schwarz (1993) for recovery data. These models require that birds are released in different areas, that data is stratified into short time intervals (at maximum one breeding cycle), and often some constraints

on the movement pattern are needed in order to obtain precise estimates (Arnason 1972, see also review in Lebreton and Pradel 2002).

If the interest is in the proportions of birds migrating to different destination areas, special types of multi-state models are needed, and it is essential to include more than one group of birds having the same re-encounter probability in shared destination areas. To analyse such data Busse and Kania (1977, see also Kania and Busse 1987) related the numbers of ringed birds per group and the numbers of re-encountered birds per group and per destination area in a system of linear equations. The least-square solution of this equation system enables one to estimate area-specific re-encounter probabilities and the proportions of birds from each group in each destination area. This method, called *division coefficient concept*, is equivalent to a type of multi-state model applied by Bauthian et al. (2007) and Thorup and Conn (2009). For a comparison of this type of multi-state model with the division coefficient method see Korner-Nievergelt et al. (2010). In the division coefficient method and in the multi-state models applied by Bauthian et al. (2007) and Thorup and Conn (2009) time intervals considered are large (at minimum one breeding cycle). These methods require that the proportion of birds moving towards each area differs between the bird groups and that the birds from different groups experience the same re-encounter probability given they are in the same destination area. If the data do not meet these requirements (called extrinsic factors) parameters may not be estimable (Thorup and Conn 2009). When applying the division coefficient method it is further required that some birds from each group are re-encountered in each area. Otherwise the equation system cannot be solved. This requirement might be less important if maximum likelihood or Bayesian methods are used for parameter estimation though partial lack of re-encounter data may result in low precision. An evaluation of bias and precision showed that precision increases with increasing difference of the proportion of birds migrating to different destination areas between groups, and with decreasing differences in re-encounter probability between the destination areas (Korner-Nievergelt et al. 2010). This study also introduced a bootstrap procedure to estimate uncertainty of the estimated division coefficient.

While the division coefficient can be calculated on standard software (or even by hand), multi-state models require specialised software and at least basic knowledge in statistical modelling. An advantage of any type of multi-state models is that they are based on the maximum likelihood concept or on Bayesian theory and, therefore, no bootstrapping is needed to produce estimates of precision. Furthermore, additional parameters such as survival probabilities can be estimated. However, if multistate models have many parameters and are complex, parameters might be redundant and therefore not identifiable (for details see Catchpole and Morgan 1997, Gimenez et al. 2009), quite apart from requiring large quantities of data to estimate the parameters efficiently.

Often, multi-state models need to be formulated carefully before they can be applied to data in order to find a parameterisation or specific constraints that allow separate estimates of the parameters of interest. Thorup and Conn



Figure 4. Re-encounters of barn swallows *Hirundo rustica* ringed in Finland (black triangles), Sweden (white rectangles) and the Netherlands (grey circles). Finnish data were kindly provided by Jari Valkama (Ringing Centre, Finnish Mus. of Nat. Hist.), the Swedish by Thord Fransson (Bird Ringing Centre, Swedish Mus. of Nat. Hist.), and the Dutch by Vogeltrekstation.

(2009) were able to obtain estimates of the proportion of several passerines that migrate to sub-Saharan Africa by including one reference species with extreme migration behaviour, i.e. no migration to sub-Saharan Africa. Furthermore, correlates of re-encounter probabilities such as population density, socio-economic or game harvest statistics, can be included in the model.

It may also be possible to create more complex multi-state mark-re-encounter models that include, for example, several re-encounter areas, or that combine recoveries with live recaptures (Gauthier and Lebreton 2008). In all of these cases it will be useful to check the identifiability of the model parameters using the methods described in detail in Catchpole and Morgan (1997), Catchpole et al. (2001) and Gimenez et al. (2003). In addition, or as a valuable alternative, we recommend conducting simulations to study estimability, bias and precision (e.g. Calvert et al. 2009, Schaub 2009).

The methods described in this section all require that at least the number of birds ringed and the time of ringing is known. Additional characteristics of the bird, such as age, sex, or breeding status, will improve model estimates when such heterogeneity is accounted for in the constructed model (Pledger et al. 2003). Unfortunately, this information is not available from all ringing schemes in the past. The EU of Ring Schemes (EURING, www.euring.org) is working towards this goal; we can only emphasize that collecting this type of data will be an enormous asset for future ring re-encounter analyses.

Key to the parameter identifiability when using ratio of re-encounter probabilities, the division coefficient method and multi-state models is the inclusion of several groups of birds for which similar re-encounter probabilities can be assumed. This assumption is difficult to meet because re-encounter probability is influenced by many sometimes unexpected factors such as the address on the ring (Sales 1973). Therefore, basic knowledge about the re-encounter and survival probabilities of different groups of birds should be established in order to facilitate finding groups that can be included in the same model. Given this knowledge, these methods have a large potential for the analysis of ring re-encounter data correcting for heterogeneity in re-encounter probability.

Ideally, groups (populations of one species, similar species) with equal re-encounter probability should be determined independent of the multi-state model framework. The possibility of determining such groups based on similarities in their behaviour and in their relation between environmental variables and re-encounter density seems to be worth exploring.

Discussion

In this essay we presented four different approaches that have been used to correct for observer bias produced by heterogeneous re-encounter probability in the analyses of ring re-encounter data: direct measurement of re-encounter probability, using covariates as surrogate for re-encounter probability, simulating observer distribution, and group comparison. We will give now a short synthesis and discuss perspectives.

The approaches described in this review use different sources of information to account for observer bias in ring re-encounter analyses. For the spatial models (approach 2) information from covariates is used to predict re-encounter probability. When describing the set of all possible observations (approach 3), the observed distribution of recoveries is compared with the distribution of observers or an approximation such as the number of ringed birds in a specific area. When information about re-encounter probability is estimated by comparing groups (approach 4), the assumption of a common re-encounter probability for the different groups or populations has to be made. This assumption, however, is much weaker than the required assumption that there is no spatial variation in re-encounter probability when conclusions are drawn from ring re-encounters without accounting for this variation in re-encounter probability.

Comparing results from analyses estimating re-encounter probability based on the re-encounter data with those using external information such as predictors for re-encounter probabilities might give valuable insights into the reliability of both methods. The combination of two or more approaches described in this review might be promising. Thomson et al. (2003) give an example of a combination of approach 1 (direct measure of re-encounter probability) and approach 2 (spatial covariate for re-encounter probability): using data on breeding bird densities and ringing locations, they quantified the spatial distribution of re-encounter probability as a function of distance from the ringing locations. The conclusions about natal dispersal in the pied flycatcher *Ficedula hypoleuca* changed drastically when the fact that close to ringing sites the observation probability is much higher than further away was taken into account (Thomson et al. 2003).

Developing a mark-re-encounter model that allows for separate estimates of finding and reporting probability might help to increase the precision of the estimates of re-encounter probability, because the two sub-processes (finding and reporting) of the observation process can be modelled each in its own way (Newman et al. 2006, Patterson et al. 2007). Such hierarchical models could be improved if for both parameters (finding probability and reporting probability) informative covariates are available. Such covariates could be habitat and population density for finding probability and country or gross domestic product for reporting probability.

Flexible and powerful software that have become recently available make further developments of mark-re-encounter models possible. In particular, Bayesian methods, naturally allow adding random factors and correlation structures to the model (for a worked out example see Calvert et al. 2009), or formulating individually based state-space models allowing for including individual covariates (e.g. Royle and Dubovsky 2001, Gimenez et al. 2007, review by Patterson et al. 2007, and book by Royle and Dorazio 2008). For example, Royle and Dubovsky (2001) showed how to model re-encounter probability as a spatially correlated random variable. The next step is now to include this structure of re-encounter probability into multi-state models, and to explore the identifiability and performance of parameter estimation in such hierarchical models. Furthermore, the combination of different sources

of information within one model might be promising. Royle and Rubenstein (2004) showed how to combine, in a Bayesian framework, information from stable isotopes and population density at wintering places. Satellite tracking data, census data and biometrical data are possible sources of information that might be combined with re-encounter data in the future. Such combined analyses have the potential to increase the value of the conclusions we can draw from ring re-encounter analyses. The flexibility and extension possibilities of mark-recapture models are overwhelming due to powerful software and modelling methodology. However, we think that, at the moment, profound knowledge about the mechanisms of what renders a parameter estimable and unbiased is missing. Therefore, we would appreciate further research on the identifiability of the parameters in the basic multi-state mark-recapture models. Finally, a catalogue of mark re-encounter models including descriptions of estimability of parameters and bias and precision of estimates would be helpful to ornithologists.

In summary, different new methods to measure the observation process have been developed recently and are waiting to be explored, and the problem of heterogeneity in observation effort perhaps does not seem so daunting anymore. However, not only will new models need to be developed and tested, but these sometimes complex models will also need to be useable for biologists rather than for statisticians only. We therefore encourage publication of not only the model details, but also of program code. In addition, literature is required with “cookbook” guidelines for the use of these models. However, biologists also need to further educate themselves so that they can better understand and apply these methods. Together these developments promise a much better insight in the quantitative description and understanding of animal movements.

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