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Estimating avian dispersal distances from data on ringed birds

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ABSTRACT *Data from birds ringed as chicks and recaptured during subsequent breeding seasons provide information on avian natal dispersal distances. However, national patterns of ring reports are influenced by recapture rates as well as by dispersal rates. While an extensive methodology has been developed to study survival rates using models that correct for recapture rates, the same is not true for dispersal. Here, we present such a method, showing how corrections for spatial heterogeneity in recapture rate can be built into estimates of dispersal rates if detailed atlas data and ringing totals can be combined with extensive data on birds ringed as chicks and recaptured as breeding adults. We show how the method can be implemented in the software package SURVIV (White, 1992).*

1 Introduction

Key biological processes, such as survival and dispersal, can be studied by ringing birds to make them individually identifiable. The fate of most ringed individuals remains unknown however, and the pattern of recaptures is governed not only by the biological processes themselves but also by the distribution and activities of ringers. Over recent decades there have been extensive developments in methods that contend with such nuisance variables when estimating survival (Lebreton *et al.*, 1992; Lebreton & North, 1993; North & Nichols, 1995; Baillie *et al.*, 1999), but this has not been mirrored by developments in the analysis of dispersal (Manly & Chatterjee, 1993). Just as temporal variation in recapture rate may impinge on the

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estimation of survival, so spatial variation in recapture rates could impinge on the estimation of dispersal. An analytical approach that can correct for such things would clearly be of value, and our objective here is to present one. We show how spatial heterogeneity in recapture rates can be corrected for by combining the data on birds ringed as chicks and recaptured as breeding adults with extensive atlas data and ringing totals. We illustrate the method using preliminary data on Pied flycatchers from the Netherlands, where abundant, detailed ringing data and atlas data (SOVON, 1987) are available with a level of detail found in few other countries.

2 Methods

A series of concentric circles can be drawn around the point at which a bird is ringed in the nest (Fig. 1). These circles enclose bands of distances a bird may disperse between fledging and breeding. This dispersal distance is, however, usually unknown because most ringed birds disappear without ever being encountered again. Despite this, we aim here to estimate the probabilities of birds moving to each particular distance band using information on the numbers of recaptures observed.

The probability of a bird being recaptured in each band is, however, influenced not only by the probability of moving to the band, but by the relative probability of a bird in that band being caught. If we know the numbers of breeding adults being caught and ringed in a band and we have an estimate of the relative numbers present in the band, a correction for relative recapture probability can be built into the model. The numbers ringed are available directly from national ringing data, and the relative numbers present are available from atlas data (SOVON, 1987). These atlas data do not give us the absolute number of birds present, but rather the relative numbers. We know for example that there are twice as many birds counted in one distance band compared with another, even though we do not know how many are actually present. Consequently, when using these data to correct for relative capture rates, we may know that a bird in one band has twice the chance of being caught as one in another band, but we do not know the absolute capture rate in either band. We show here that correction for relative capture rates are sufficient and that estimation of absolute capture rates is not required.

Formalizing the algebra, the expected number (N_i) of recaptures breeding within a specified distance band i, equals the total number recruiting across all bands (M) multiplied by the probability of a recruiting bird moving to distance band i (P_i) multiplied by the capture probability in distance band i (C_i):

$$N_i = M \times P_i \times C_i$$

where M is unknown and C_i is unknown. C_i is the number of ringed birds recaptured in band i divided by the number of ringed birds present, but it could also be estimated if we knew how many unringed birds were present in distance band i and how many of these were caught and ringed. We know how many birds are ringed in band i (this is accessible directly from ringing data), but we do not know exactly how many are present; we do however have an index of abundance from atlas data, which provide relative, though not absolute, abundance.[1] We can indeed also work with relative capture rates, and:

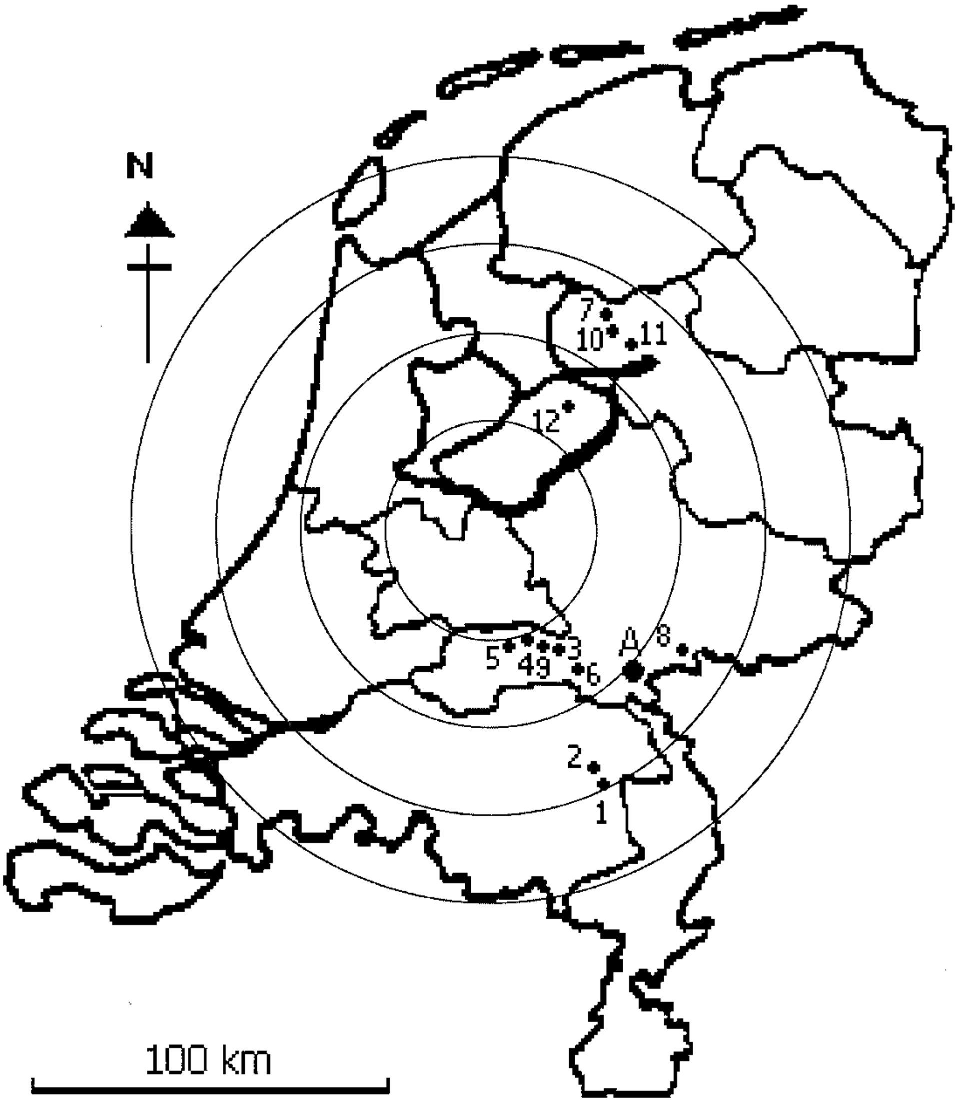

FIG. 1. Map showing how distance bands around the point of ringing may be established. The precise regions covered by each of these bands will of course differ among individual birds depending on the exact location at which each bird is ringed. Relative capture rate for each band can be estimated by combining ringing totals with atlas counts.

$$C_i = K_i(\Sigma N_i)/M$$

where K_i is the ratio of the band-specific capture rate to the population capture rate $(\Sigma N_i)/M$.

So

$$\begin{aligned} N_i &= M \times P_i \times K_i \times (\Sigma N_i)/M \\ &= P_i \times K_i \times (\Sigma N_i) \end{aligned}$$

Here, K_i is still unknown and is specific to each band i. By using the band-specific information that we do have (numbers of breeding adults caught and ringed, R_i,

TABLE 1. Worked example using preliminary data from Dutch Pied Flycatchers

Distance band	No. recaptures	No. adults ringed	No. adults counted	P_i	95%CI
0–5 km	812	488.63	56.13	0.15	0.13–0.17
5–10 km	131	510.52	392.03	0.16	0.13–0.19
10–50 km	137	1747.22	4438.80	0.56	0.50–0.61
50–100 km	21	1907.90	7337.36	0.13	0.08–0.18

and the sum of the counts from each atlas square within the band, D_i), we can replace the band-specific K_i with a general unknown constant common to all bands. We combine the band-specific R_i and D_i across all birds ringed as chicks to produce a single measure of K_i:

$$K_i = (R_i/D_i)k$$

where R_i = number of breeding adults ringed in band i, D_i = total abundance of birds across all atlas squares in band i, and k is still unknown at this stage, but unlike K_i it is not specific to each band. It is an average of D_i/R_i across all bands, weighted for the proportions of birds moving to each band, and it too can thus be formulated in terms of the R_i and D_i that we know, and the P_i that we want to estimate i.e.:

$$k = 1/\Sigma(P_i R_i/D_i)$$

The final model thus has one set of parameters P_i which yield the probabilities of birds recruiting at each distance band, and a further series of terms that are known in advance.

$$N_i = (P_i(R_i/D_i)\Sigma N_i)/\Sigma(P_i R_i/D_i)$$

The parameters P_i have a unit sum constraint, so the last P_i can be expressed as one minus the rest, and when this is applied, the parameters may be estimated. Unlike other methods (Manly & Chatterjee, 1993), the model contains no parameters for the estimation of capture rate or survival rate.

The method is based on live recapture data and does not currently use information from birds recovered dead. There is nothing comparable to the atlas data for indexing the size of the pool of dead birds and nothing comparable to ringing totals for indexing the number of these which are reported. There are well established methods that can estimate reporting rates of dead birds and these could be set in the necessary spatial context, but this would involve the incorporation of substantially more parameters, including survival rates, into an otherwise simple model.

This method has been applied to preliminary data for the pied flycatcher *Ficedula hypoleuca*, and we use these data here to illustrate the implementation of the method using the SURVIV software. The data used and the resulting parameter estimates are shown in Table 1. Input code for fitting this model in SURVIV is shown in Appendix A. These preliminary results indicate that dispersal may be greater than previously thought. If we were to infer dispersal directly from the raw pattern of recaptures, we would greatly underestimate dispersal. This is because the number of recaptures close to the nest is inflated by capture rates that are much higher than at greater distances. These results will be presented in full once the implementation of the method has been further developed and tested.

Although the model incorporates externally measured information on numbers ringed and breeding density, the parameter estimates prove to be very robust to errors in these. Because only relative breeding density, not absolute density, is used, an error of x% in the counts leads to no change in the dispersal estimates or their standard errors, even when x is very large. Because the numbers ringed can be extracted directly from ringing data, they are essentially known without error, but in any case again because we are estimating only relative capture rates, an error of x% in the totals leads to no change in the dispersal estimates or their standard errors.

This method does not assume that dispersal takes place isotropically. It does indeed produce a general probability that a bird will move to a particular distance band, but in practice the factors dictating the distance moved will be numerous and complex and will include the physical geography and the presence of a suitable habitat—not least the presence of dry land. These factors naturally vary between the numerous sites where birds are ringed. The models produce an overall estimate of the distributions of dispersal distances, averaged across all the numerous locations where birds are ringed, acknowledging that the dispersal patterns are the product of many factors and may involve many indirect paths.

Future priorities with this work will involve integrating the programs for data processing and model fitting into a single piece of software, and the application of this method to data from a wide range of species.

Note

1. Strictly speaking, the atlas counts not only the unringed birds, but also the very small proportions of ringed birds. These proportions are negligible, but even if they were to become large, the estimates of relative abundance in each band would be unaffected unless the proportions of ringed birds differed between bands.

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Appendix A. Input code used to fit these dispersal models in the SURVIV software package

(available from http://www.mbr-pwrc.usgs.gov/software/survive.html)

```
/* SURVIV input file for the estimation of dispersal distance
distributions */

PROC TITLE Dispersal distances;

PROC MODEL NPAR=3 /* Although there are here four biological */
                  /* parameters, there is a unit-sum constraint */
                  /* and the last can be defined in terms of */
                  /* the others - see first INLINE statement */;
COHORT = 1101; /* Total recaptures across all four distance bands */
INLINE S4=1-S(1)-S(2)-S(3);
INLINE RT1=488.63/56.13; /* Dividing numbers of birds ringed in a */
INLINE RT2=510.52/392.03; /* distance band by numbers atlassed, to */
INLINE RT3=1747.22/4438.80; /* give band-specific relative capture */
INLINE RT4=1907.90/7337.36; /* rate */
INLINE DENOM=S(1)*RT1+S(2)*RT2+S(3)*RT3+S4*RT4; /* reciprocal of k */
812:S(1)*RT1/DENOM;
131:S(2)*RT2/DENOM;
137:S(3)*RT3/DENOM;

LABELS;
    S(1)=P(moving 0-5km);
    S(2)=P(moving 5-10km);
    S(3)=P(moving 10-50km);

PROC ESTIMATE;
 INITIAL;
    ALL=0.2;

PROC STOP;
```

S4 (P moving 50-100km) has been chosen arbitrarily as the parameter expressed as 1-(the sum of the others). Confidence intervals can be produced for S4 by choosing one of the others instead.