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Quantifying the movement patterns of birds from ring recoveries

JACQUIE A. CLARK[1]*, KASPER THORUP[2] and DAVID A. STROUD[3]
[1]*BTO, The Nunnery, Thetford, Norfolk IP24 2PU, UK* [2]*Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark* [3]*Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY, UK*

Scientific bird ringing was initiated to study the movements of birds, particularly annual migrants. When a ringed bird is reported to the ringing scheme we have the location of that bird at two points in time – where and when it was ringed and where and when it was found. The collation of reports of ringed birds (recoveries) allows patterns of location change with time to be described. Different methods of presenting these simple data have been devised over the years; initially, the aim was to summarise our knowledge of where birds go. Quantitative inference about population behaviour from recovery data is complicated by several factors, particularly the differences in recovery probabilities between different regions. However, the power of ringing-data analysis is now being increased using statistical methods to correct for the expected geographical biases in recovery patterns. The quantitative interpretation of movement patterns of birds is essential for basing conservation policy on sound evidence. The continuation of large-scale ringing and recovery efforts, and the development of statistical tools for analysis and interpretation of the data at continental scales, are therefore vital for the conservation of migratory birds and to understand the impact and spread of disease.

Scientific bird ringing was started to try to understand the movements of wild birds and continues to provide vital information on migration and dispersal and on how these change and evolve in relation to environmental conditions. Ringing began in Denmark in 1899 when Hans Christian Cornelius Mortensen ringed 165 Starlings *Sturnus vulgaris* using individually numbered rings with a return address (Jespersen & Tåning 1950). This allowed anyone finding one of these birds to report which individual had been found, when and where it was found and what had happened to it. Other ringing schemes were established across Europe in the next few years and movement data accumulated rapidly.

As early as 1910, Thienemann, who had started scientific ringing at Vogelwarte Rossitten (now Rybachy) on the eastern Baltic in 1903, published details of movements of 35 White Storks *Ciconia ciconia* (Thienemann 1910). Nine years later, von Lucanus (1919) published a paper summarising the migration and movements of birds in Europe, using reports of ringed birds (recoveries), although he did not include any maps. He followed this in 1922 with a book – *Die Rätsel des Vogelzuges* ('The mystery of bird migration') – which again used recoveries from across Europe, for 127 species, and incorporated just four maps showing main migration routes (von Lucanus 1922). It also included data on flight, gathered from airships. The first 'migration atlas' – *Atlas des Vogelzugs* (Schüz & Weigold 1931) – consisted of a bound text and 150 loose-leaf pages of 262 maps, covering a wide range of species and using data from across Europe; about two-thirds of the pages of maps were devoted to non-passerines. Many atlases and papers describing the movements of birds have followed since, although most national atlases have been published in recent years, since statistical and mapping tools able to handle large amounts of data became available. Methods to display and interpret recovery data continue to be developed and are discussed below.

SUMMARISING RECOVERY DATA

Presenting spatial data using lines, dots and kernels

Perhaps the simplest way to depict movement data is to draw lines on a map connecting the ringing and finding sites of a bird (Fig 1a). This generally gives a good impression of the movements of birds, but one that is dependent to some extent on the map projection used (Gudmundsson & Alerstam 1998), and it suggests that an individual moved along a straight line, which is unlikely to be the case. In addition, it can be confusing when there are so many lines superimposed on each other that the underlying details are obscured (Fig 1b). To avoid this problem, dots may be

* Correspondence author
Email: jacquie.clark@bto.org

used instead of lines (Fig 2a). Dots are generally used for recoveries relating to one geographical area, *eg* a country or a ringing station, and show the locations of birds away from that area. Although the underlying map remains visible, the use of dots does not convey the impression of movement imparted by line maps. A combination of lines with dots is particularly helpful if the lines are printed in such a way that they do not obscure either the details of the map or the positions of the dots (Fig 2b).

A development which has helped us to understand and summarise the quantitative aspects of recovery data is the use of kernels to describe the spread of recoveries. Kernels can be fitted using the package *ks* written for the statistical program *R* (Duong 2007), and smoothed densities for the spatial pattern of recoveries can be estimated and shaded to show how recovery density varies spatially (Fig 3). This gives a further understanding of the distribution of a species or population, as shown by recoveries, as well as indicating key areas.

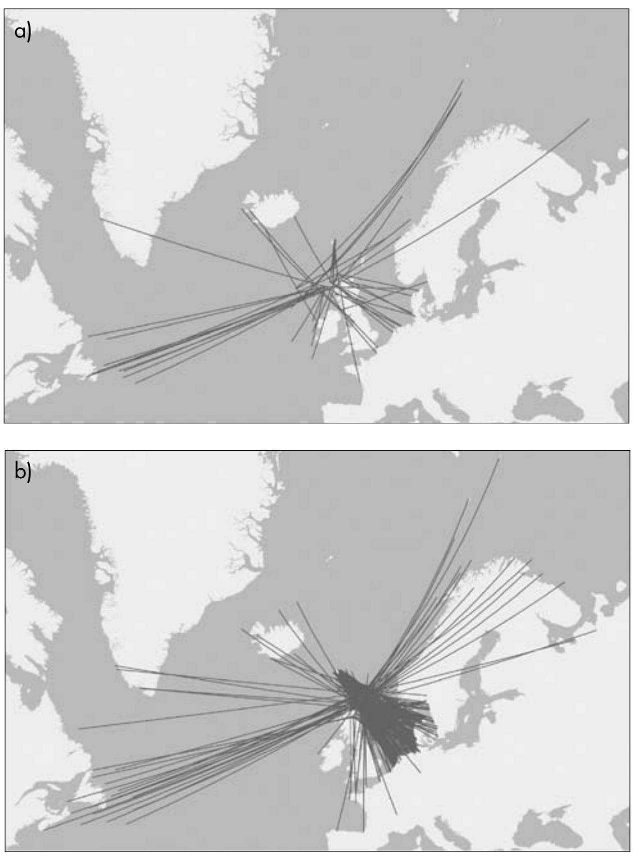

Figure 1. Movements of birds from recoveries indicated by lines on a map connecting ringing and finding places. (a) Movements of Fulmars *Fulmarus glacialis* between the northwest of Britain & Ireland and other countries (58 recoveries). (b) Movements of Fulmars between the north of Britain & Ireland and other countries (433 recoveries). Note that when there are a lot of similar data the map becomes obscured by the lines. Maps from Wernham *et al* (2002).

Presenting seasonal data

Simple line, dot, kernel or combination maps of all recoveries for a species from a particular area provide spatial but no temporal information. A series of maps may be drawn depicting movements at different times of year, but interpretation is simpler if temporal information can be provided on a single map. This can be done by calculating the mean positions of birds from a geographical area at

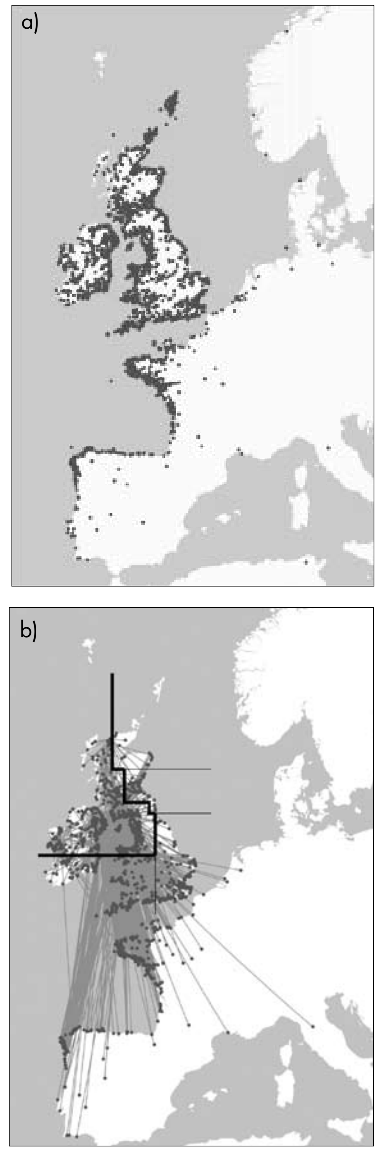

Figure 2. Movements of Cormorants *Phalacrocorax carbo* from recoveries of birds ringed at coastal colonies shown using dots alone and a combination of dots and lines. (a) Locations outside the breeding season of immature birds that were present in Britain & Ireland during the breeding season (5,601 recoveries). (b) Locations outside the breeding season, and movements of over 20 km between the breeding and non-breeding season, of Cormorants present in northwest Britain & Ireland during the breeding season. Maps from Wernham *et al* (2002).

different times of year. Perdeck (1977), building on work by himself (Perdeck 1967) and others (Doude van Troostwijk 1974, Imboden 1974), suggested three different formulae to calculate mean positions, with the third, the calculation of centres of gravity, describing both latitude and longitude and correcting for the differences in distance between degrees of longitude that occur with latitude. Monte Carlo simulation statistics can be used to look for differences between the mean positions of two groups of birds (Lokki & Saurola 1987). These methods have been used by recent migration atlases (*eg* Formula 2: Fransson & Pettersson 2001, Fransson *et al* 2008, Fransson & Hall-Karlsson 2008; Formula 3: Bakken *et al* 2003, 2006, Bønløkke *et al* 2006). Mean monthly positions have also been calculated by plotting latitude and longitude separately against the month of recovery, these can then be mapped and lines fitted to indicate a smoothed migration route (Hofer *et al* 2006, Atkinson *et al* 2007) (Fig 3).

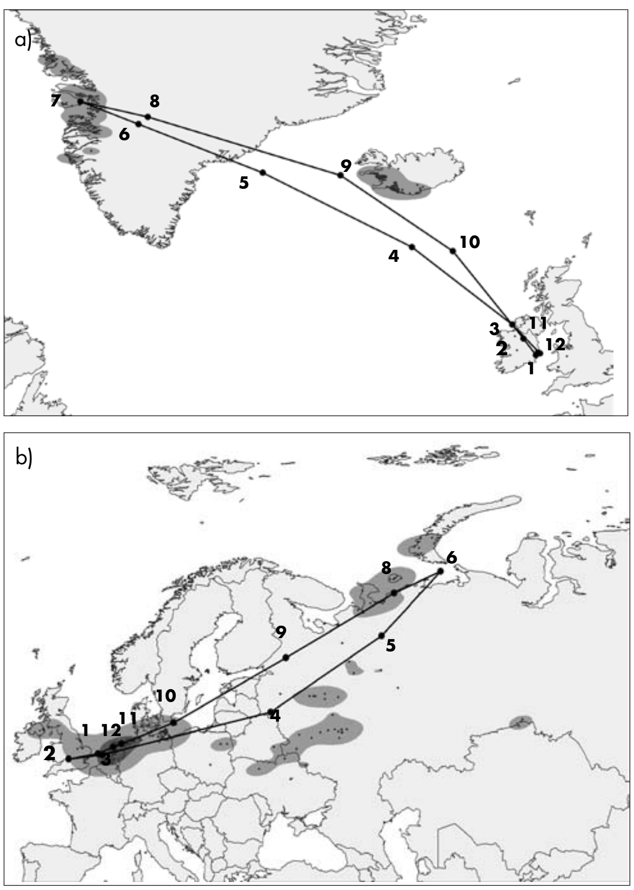

Figure 3. Maps showing recoveries between Britain & Ireland and other countries for White-fronted Geese *Anser albifrons* moving to (a) Greenland and (b) Russia. The small dots are the actual recoveries, the larger dots joined by lines indicate the average position by month and the kernels enclose 50% (light shading) and 95% (dark shading) of the recovery locations. Maps from Atkinson *et al* (2007).

Mean positions of recoveries and smoothed routes are a valuable aid to understanding migration, but describe only the average position of the population and may be unrealistic with respect to the location of individuals. For example, recoveries of birds migrating from Britain to Iceland in spring might have a mean position in the sea between Scotland and Iceland, as some have not yet left Scotland and others have already arrived in Iceland. Also, if there are populations which migrate in different directions (*eg* to Greenland and to Russia), then mean positions are only meaningful if the data from the different populations are separated (see below). Overall, combining mean positions and smoothed lines to provide temporal information with kernels superimposed over the underlying raw data to assist with interpretation of the data, probably provides the best summary of observed movements possible on a static map (Fig 3).

Describing and distinguishing directions of movement

The direction of movements of birds from an area are often, more or less, common to individuals over a large geographical range and thus provide simple summary measures of population behaviour; these may describe population movement better than just delimiting a goal

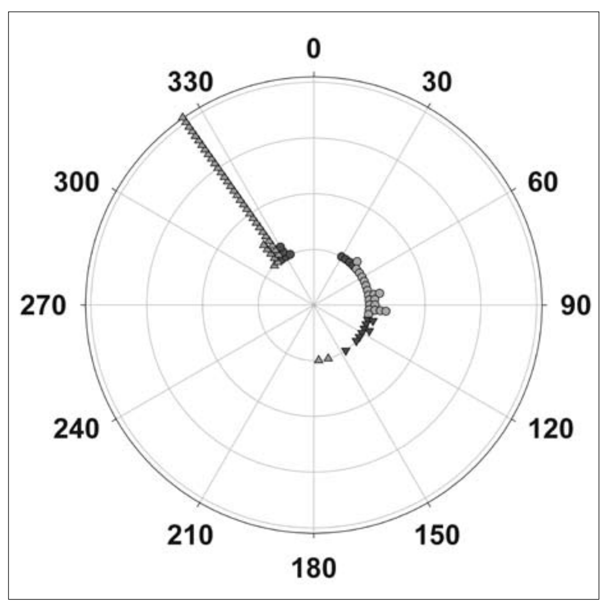

Figure 4. Compass diagram showing movements of White-fronted Geese to and from Britain & Ireland. The recoveries are grouped by direction of travel. Two major directional movements can be seen – one (circles) between 60 and 90 degrees representing birds migrating to Siberian breeding areas and one (triangles) at about 330 degrees due to birds moving to Iceland and onward to breeding areas in Greenland. Each symbol represents five recoveries. The groupings moving to the northwest and northeast are mapped in Fig 3.

area. Furthermore, migratory journeys may consist of several legs which are best described by the direction of each leg. Directional data can be described using a compass diagram illustrating the main directions of travel (Fig 4). Differences between groups of birds (*eg* sexes or age classes) can be tested using circular statistics (Fisher 1996). Where there is a spread of recoveries they can be grouped by direction of travel by plotting the distance of each recovery against the direction travelled; a smoothed curve can be fitted through the data (Hastie & Tibshirani 1990) to identify the turning-point minima (troughs between peaks) which can be used to place the recoveries into distinct groupings (Atkinson *et al* 2007, Fig 5). The statistical resampling technique of bootstrapping can be used as part of the analytical process to assess confidence in the turning points. Different groups of recoveries, defined by the turning points, can then be considered separately and mean positions calculated.

Using recovery data to describe migration

Recoveries have provided much of the information we have about the migration of birds. When inferring population behaviour from ringing data, a number of assumptions have to be made. Perhaps the most important is the assumption that ringed birds do not behave differently from unringed birds; it is also assumed that the birds ringed and recovered constitute a representative sample from a population. Assumptions about the probability of changes in recovery rates over space and time, and differences between age and sex classes, are more difficult to assess, as clear differences have been demonstrated (Perdeck 1977). For example, the number of recoveries of quarry species will vary both during a year (open and closed shooting seasons) and between years (if hunting regulations change). The number of recoveries also varies depending on the behaviour of finders, for example with more people taking walks on fine days. The method of recovery may also affect the pattern of distribution. Perdeck (1977) found that, if the breeding areas of Mallard *Anas platyrhynchos* and Teal *A. crecca* ringed between September and November in the Netherlands were described using birds reported as shot and birds found dead in May and June, the birds shot were found further east than the birds that were found dead. There may also be differences between different age groups and between the sexes: for example amongst Gannets *Morus bassanus* ringed in Britain & Ireland, juveniles winter further south than adults (Wernham *et al* 2002).

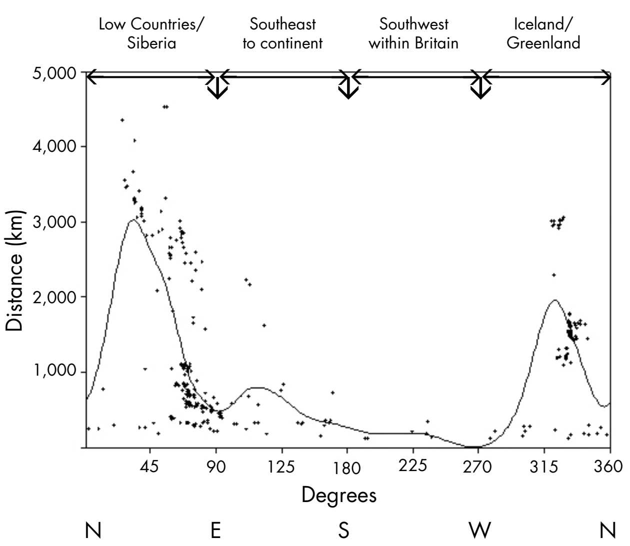

Figure 5. Distance and direction for ring recoveries from White-fronted Geese for birds either ringed or found in Britain & Ireland. Each point represents a report of a bird. A smoothed line is fitted to the data and turning points and different groupings of recoveries are indicated at the top of the graph.

The chance of a ringed bird being recovered is a product of the chance of an individual being found (encounter rate) and the chance of it being reported to the ringing scheme (reporting rate). It is clear that these rates will vary spatially (with fewer birds being reported from areas of sparse or no resident human population, or where few people visit), between species (large obvious birds are more likely to be found than small brown ones) and by finding circumstances (birds brought into a house by a cat or killed on the road are more likely to be found than those dying in undergrowth in a woodland). So although we have information on where some birds have moved to, we do not know if the lack of recoveries of that species in another area is because the birds do not occur there, or is due to ringed birds not being found, or to their being found but not reported (but see below). Recovery rates also vary temporally, because of changes both in ringing patterns and in reporting rates, which are currently falling, probably as a result of fewer people reporting birds (Robinson *et al* 2009). Recovery rates also vary on a shorter scale when certain activities, such as hunting, are restricted to certain times of the year. Although these caveats must be taken into account when using recoveries to describe migration, it should be remembered that much has been learnt from reports of ringed birds and that we will continue to improve our understanding of the movements of birds as we receive more recoveries, develop additional analytical tools and combine the data from recoveries and other techniques (Baillie *et al* 2009, Coiffait *et al* 2009, Fiedler 2009).

Understanding what data are missing

The methods of illustrating and analysing movements that are described above all use reports of ringed birds. They give information on where ringed birds have been found and reported, but do not tell us where ringed birds occur and have been found and not reported, or just not found; therefore, these methods rarely provide truly quantitative estimates of bird migration. The challenge for the future is to quantify the biases inherent in the ringing data, for example the strong spatial bias in recovery probability between different geographical regions. To estimate recovery probabilities, either some additional data have to be used, or some explicit assumptions have to be made about how the data were generated. Additional data can be in the form of other studies for comparison, or prior information on factors influencing recovery probability, such as human population density. Explicit assumptions could include that actual recoveries are an estimate of where recoveries could possibly come from, or that similar populations, species and age classes have the same chance of being recovered.

The way recoveries are interpreted is often based on comparisons with other species or age classes. For instance, we would infer intuitively that trans-Saharan migrants actually do winter in sub-Saharan Africa, despite the very limited number of recoveries there: in Europe during autumn there are many recoveries of Garden Warblers *Sylvia borin* but very few in winter; therefore, they must have gone to Africa. Fig 6a shows recoveries of Garden Warblers ringed in Denmark and recovered in autumn and winter. Of the 107 recoveries, only four occurred in winter and only two of these birds were found in Africa, with one autumn recovery in North Africa. Furthermore, Fig 6b shows that a small proportion of ringed Garden Warblers are recovered in winter compared to the proportion of Robins *Erithacus rubecula*, again indicating that Garden Warblers are unlikely to be in Europe in winter. Thorup & Conn (2009) estimated that 96% of Garden Warblers from Denmark wintered south of North Africa, but no Robins from Denmark wintered that far south. In addition they estimated that 64% of Blackcaps *Sylvia atricapilla* from Denmark and 100% of Thrush Nightingales *Luscinia luscinia* winter south of North Africa (Fig 6b).

Recent work (Korner-Nievergelt *et al*, submitted[4]) has identified four methods that, with the use of additional data, can provide the quantitative estimates of spatio-temporal biases in recovery probabilities that are needed to improve our understanding of bird migration based on ringing data.

- *Simple comparisons with other methods where spatio-temporal biases can be assumed to be small.* Variation in

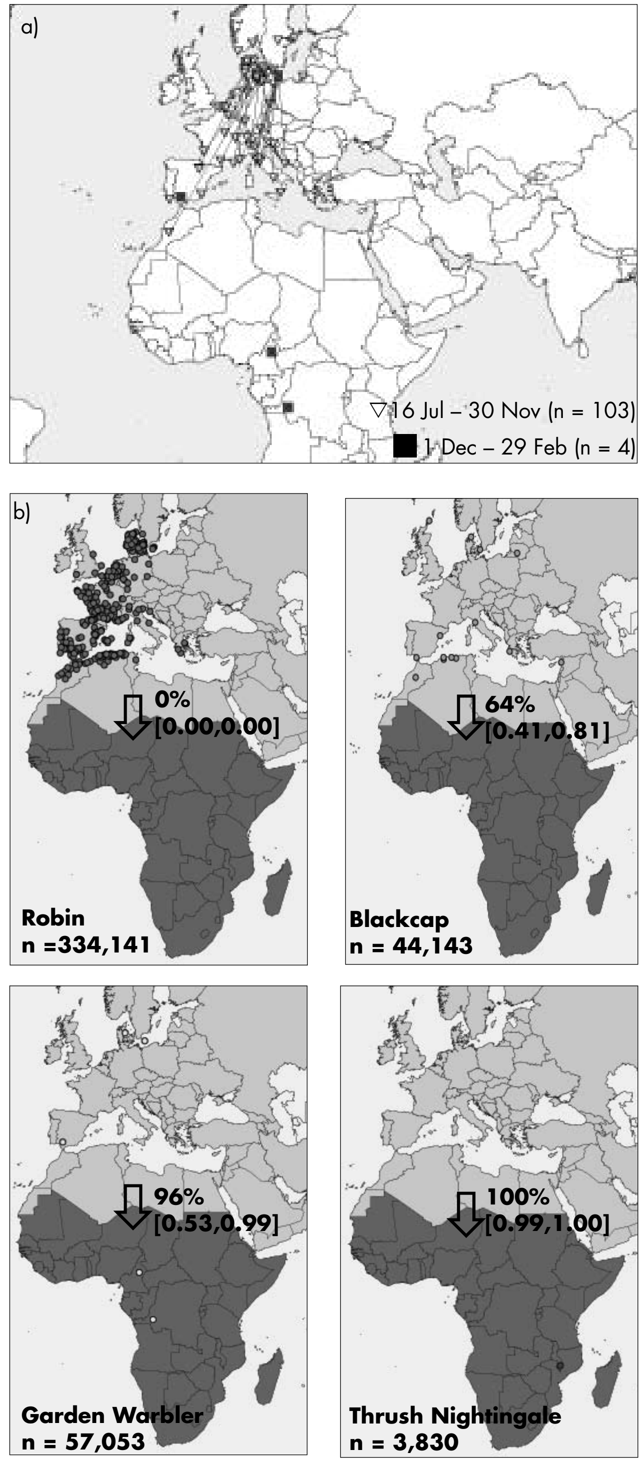

Figure 6. Spatial distribution of recoveries of small songbirds ringed in Denmark: (a) Garden Warblers recovered in autumn and winter and (b) four songbirds recovered in winter (December–February) only birds found dead are included. In (b) the estimated percentages of individuals of a species that winter south of North Africa (and associated confidence intervals) based on capture–mark–recapture models are shown. After Thorup & Conn (2009). Reproduced with kind permission of Springer Science and Business Media.

[4]**Korner-Nievergelt, F., Sauter, A., Atkinson, P.W., Guélat, J., Kania, W., Kéry, M., Köppen, U., Robinson, R.A., Schaub, M., Thorup, K., van der Jeugd, H. & van Noordwijk, A.** (submitted) *Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity.*

recovery probability can be assessed by combining extensive data from recoveries with intensive data on a small number of individuals using new techniques such as satellite telemetry, so that an assessment can be made of where recoveries would be expected, but have not been reported.
- *Modelling the underlying processes of creating recoveries, using external information.* For example, socio-economic factors, habitats and human population densities are thought to be important factors in creating heterogeneous recovery probabilities, which can then be corrected to control for the influence of these factors.
- *Estimating the distribution of possible recovery points.* All possible observations of birds can be generated, based on the spatial distribution of actual recoveries of the population being studied, and refined with other data, for example the distribution of observers. This can then be compared to the observed distribution of recoveries.
- *Using comparisons between different groups where certain assumptions can be made about equal recovery probability to make quantitative estimates.* The groups could be different species, populations, age classes or cohorts but, to be useful for estimation, there must be differences in recovery patterns between the groups. This kind of analysis requires the number of birds ringed to be known. In the case of small insectivorous birds, this technique has been used to derive estimates of migration rates (and associated confidence intervals) to certain areas even when there are no recoveries from these areas (Thorup & Conn 2009).

THE PRACTICAL VALUE OF RECOVERY DATA

The understanding of movement patterns and destinations of populations of wild birds is vital for conservation and underpins policy with respect to large or strategic issues such as the creation of protected areas, the development of land-use policies to benefit birds and the risks of wild birds spreading disease from one location to another. A coherent, evidence-based response to such issues requires a synthesis of data to allow overall patterns of movements in space and time to be understood.

International flyways and the potential spread of disease

Published flyway atlases for Anatidae (Scott & Rose 1996) and for waders (Delany *et al* 2009) have presented key site information from census data overlain on the best available information on the extent and location of migratory flyways. Yet this latter information has generally been derived qualitatively, and for many species (of duck in particular) ultimately derives from work, such as that of Isakov (1970), where early assessments have been repeatedly copied forwards by subsequent authors (see Stroud 2005). However, where contemporary analyses of ringing results have been assessed on a flyway basis, results have suggested that some ducks show much less population differentiation and more complex movement patterns than described by their traditionally accepted biogeographic populations (*eg* as presented by Scott & Rose 1996). For example, Guillemain *et al* (2005) showed that Teal ringed in the Camargue were found throughout the Mediterranean flyway (as defined by Scott & Rose 1996) as expected, but also throughout the northwest European flyway, where it had been assumed that they did not occur (Fig 7).

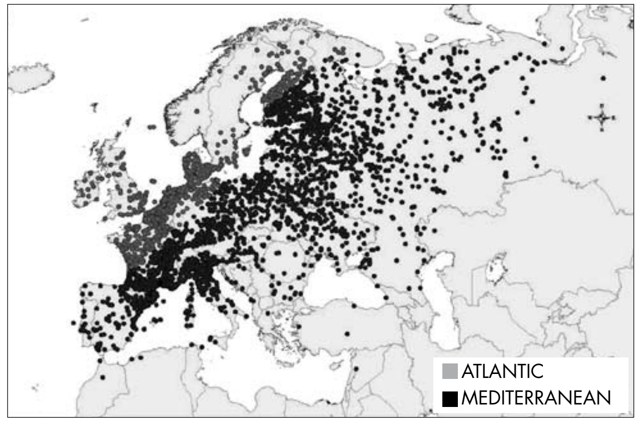

Figure 7. Analysis of recoveries of Teal *Anas crecca* ringed in the Camargue, France, showing little differentiation into the historically derived northwest European (grey dots) and Mediterranean (black dots) populations postulated for this species (Scott & Rose 1996). From Guillemain *et al* (2005). Reproduced from *Ibis* with kind permission of the British Ornithologists' Union.

The African–Eurasian Waterbird Agreement has highlighted the urgent need to integrate census data with data from ring recoveries in the next generation of flyway atlases. A wealth of data exists within ringing databanks, yet the scale of the task means that migration atlases to date have nearly exclusively been national in scale (in terms of source/destination of marked birds). Integrating these data at continental scales is a major challenge in terms of both the resources needed for such a project, and the practicalities of handling the large volumes of data that now exist.

Waterbirds as a group have been associated with the spread of highly pathogenic Avian Influenza (HPAI). A recent and innovative synthesis of recovery data in NW Europe has been the development of the Migration Mapping Tool (http://blx1.bto.org/ai-eu) for the specific task of providing inputs into risk assessments related to the spread of HPAI H5N1 of Asian lineage (Atkinson *et al* 2007). This computer program generates

– for specific species within defined regions – monthly locational 'centres of gravity' and other tabulated and mapped information, showing anticipated sources of birds using a site and their probable next destinations. Even though there remain major unknowns regarding the epidemiology of HPAI H5N1 in wild birds (Artois *et al* 2009, Hesterberg *et al* 2009), the tool has been a valuable means of allowing rapid, 'real-time' synthesis of ringing data to inform decision-makers in government about likely movement scenarios for wild birds in the event of outbreaks of HPAI H5N1.

Protection of important staging areas and stopover sites

A central element of nature conservation policy is the identification and subsequent protection or management of important sites. Over at least the last century, there has been a long development of legal frameworks that oblige or encourage the establishment of single protected areas as well as wide networks of sites at scales ranging from local to international (Holdgate 1999). Historically, survey and monitoring data on birds have played a particularly significant part in the identification of important areas requiring protection, but ringing data have, in general, not been used to their full potential for identifying areas in need of protection.

Short-term recovery data (resightings of colour-marked birds or recaptures of metal-ringed birds) can provide extremely valuable data for site assessment. The flux of birds using sites during migration periods means that the total numbers of birds using a site can be significantly greater than estimated from peak counts. Turnover (numbers of birds entering and leaving a site) can be assessed using mark and recapture (or resighting) of ringed birds using a site. In this case, recoveries within a site can provide information on the movements of a species, as they allow us to estimate how long birds remain at that site and the total number of individuals passing through in a given period. Smit & Piersma (1989) gave an early example from Sidi Moussa estuary, Morocco, where observations of marked Dunlins *Calidris alpina* showed that, over the spring migration period, the site was used by three times the peak count of birds present at any one time, demonstrating the international importance of the site for Dunlin which was not apparent from counts alone.

The Ramsar Convention explicitly encourages the use of such data on turnover, where they are available, in the interpretation of its quantitative Criteria 5 and 6 relating to waterbirds. There are relatively few high-quality data sets measuring turnover at sites, as collecting these data requires significant investments of ringing and subsequent resighting effort. Turnover has, however, been assessed at specific sites. For example Moser & Carrier (1983) found that, although there was a consistent count of around 400 Ringed Plover *Charadrius hiaticula* on the Solway Firth thoughout the spring passage in 1983, birds marked in an early catch were no longer present towards the end of the period. This suggests that these birds had moved on and that the population using the estuary was much larger than suggested by the peak count. More recently, Gillings *et al* (2009) using resightings of individually marked Knot *Calidris canutus* in Delaware Bay, USA, in spring 2004 estimated a stopover duration for individuals of 8–12 days, although the passage period was 28 days. This gave an estimate of 17,707 birds using the Bay, approximately 30% higher than the peak count of 13,315. These studies clearly show how ringing can inform conservation action by helping us to understand usage of sites, and providing information which is not available from counts alone. The development of improved analytical methods (Atkinson *et al* 2001, Frederiksen *et al* 2001, Schaub *et al* 2001, Choquet & Pradel 2007) is now allowing further analysis of data sets from around the world.

MAINTAINING RECOVERY DATA SETS FOR THE FUTURE

There are still major challenges to ensure that the analysis of data generated by ringing continues to develop and to influence the making and implementation of relevant conservation policy, as well as being available to the research community. These include:

- *Continuing to maintain the core infrastructure of national ringing schemes and relevant international cooperation mechanisms that are essential for the generation and collation of large numbers of recoveries.* It will be extremely challenging to maintain resources for this in times of economic recession, especially as national and international conservation policy moves away from traditional species-based orientations (eg Davidson & Stroud 2006). There will need to be sustained advocacy from those who appreciate the capacity of ringing data to address a wealth of questions central to current and future conservation issues.
- *The financial implications of unlocking the vast archive of ring recoveries so that more international analyses, reflecting the international movements of birds, can be undertaken.* In conjunction with this it is essential that new and innovative means of synthesising knowledge for researchers and decision-makers continue to be developed.
- *Given the already changing patterns of migration that are consequent upon the changing climate, there is a strong need for historical data and long, unbroken time series, such as ringing data, to investigate biological changes.* Furthermore,

analyses summarising movements must be updated frequently to reflect the changing world. This may mean developing systems which produce summaries of selected data that are automatically updated as recoveries are received (via on-line geographical information systems or similar technologies).

- *Better and more systematic analysis of recoveries, to give a more thorough assessment of distributional limits of populations and of the usage of individual sites.* This work should be integrated with relevant survey and census data. As ever, such work will need a high level of interpretation by species specialists who understand the biases inherent in combining multiple data sets, and thus needs to be undertaken on a cooperative, international basis.

Thus it is essential, particularly in the light of global climate change and the impact of disease within the food economy, that ringing schemes continue to maintain large ringing and recovery data sets. This will require continued commitment by public bodies to finance ringing schemes, because without such funding it will not be possible to maintain the contributions of the many volunteer ringers on whom the ringing and recovery data sets depend. It will also be essential to develop further sophisticated analyses of these data and improved methods of communication and data transfer. In Europe EURING (the European Union of Ringing Schemes) will continue to play a pivotal role in coordinating the efforts of the schemes, which work to common standards and maintain a high level of cooperation. In addition the EDB (EURING databank), which already holds recovery data from schemes across Europe in a standard format, will become an even more important repository of data. The future for ringing schemes and volunteer ringers will be challenging, but will also be exciting as we continue to collect and analyse the data that are essential for underpinning conservation action and understanding the spread of disease on a global scale.

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