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The EURING Data Bank – a critical tool for continental-scale studies of marked birds

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ABSTRACT
The European Union for Bird Ringing (EURING) coordinates bird ringing at a continental scale and operates the EURING Data Bank (EDB) to facilitate large-scale analyses of movements and demography. The EDB contains over 10 million individual encounter records which are summarised on a publicly available website, the EDB index. EURING welcomes applications to analyse these data. Ring-recovery data from the EDB contribute to research on many ecological issues, particularly migration and movements, hunting, mortality causes, disease transmission, population dynamics and dispersal. Recent developments will facilitate the incorporation of comprehensive sets of first-encounter records and local recaptures which are essential for robust quantitative studies of population dynamics and movements. Furthermore, the recent inclusion of fields for moult, measurements and weights within the EURING code will facilitate novel research at a European scale. We expect increasing use of the EDB for quantitative studies of avian demography and movements with high applied value. Wherever possible, this research should also incorporate complementary ecological information. EURING's immediate priority is the production of a European Migration Atlas that would provide an up-to-date synthesis of the movements of European bird populations, with many direct implications for their conservation.

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Studies of marked individuals form an essential part of pure and applied research in avian biology, particularly with respect to migration, movements and population dynamics. Furthermore, there is an increasing realisation that large-scale analyses of ecological data, supported by online data gathering, integrated database technologies and novel statistical and computational approaches can offer powerful new insights into the ecology of birds and other organisms. Thus the application of concepts such as big data (Schimel 2011, Hampton *et al* 2013), hierarchical modelling (Kéry & Schaub 2012), integrated population modelling (Robinson *et al* 2014) and machine-learning techniques (Fink *et al* 2010) offer many exciting opportunities for studies of marked birds to advance our knowledge of avian ecology over the coming decade. Linked to the development of these large-scale analytical approaches there is an increasing move towards the provision of open data that will allow analysts to combine data from a wide range of different sources quickly and easily (Reichman *et al* 2011, Michener & Jones 2012).

It is evident that many of the processes that determine the distributions, abundances and movement patterns of birds operate across political boundaries, and therefore studies covering groups of countries, continents or flyways are needed. From its inception, bird ringing has always addressed movements across political boundaries. The resulting need for a common language to support standardised data gathering, quality control and data exchange necessitated close cooperation between institutions that use bird ringing as a tool for avian science. Thus the European Union for Bird Ringing (EURING) was founded in 1963. Today, almost all European countries are represented in the EURING community through some 40 ringing centres, usually one per country. EURING provides guidelines and standards for bird ringing, maintains a standard code for the computerisation and exchange of mark–reencounter data and operates a multi-language website (www.ring.ac) for the reporting of ring recoveries. It facilitates communication between schemes, ringers and members of the public through the internet and other media, undertakes analyses of mark–reencounter data at a European scale and coordinates a network of over 500 Constant Effort Sites throughout Europe (Eglington *et al* 2015, Johnston *et al* 2016). It also promotes the development of statistical and computing methods for the analysis of

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mark–reencounter data, particularly through the influential series of EURING analytical meetings that bring together leading statisticians and ecologists working on this topic (Francis *et al* 2014). Last, but certainly not least, it runs the EURING Data Bank (EDB). This unique set of mark–reencounter data on European birds recently reached the milestone of 10 million encounter records and is at the disposal of the scientific and conservation communities.

The EURING Data Bank

Terminology used for mark–reencounter data

Here, first-encounter records refer to the initial encounter with an individual when it was first ringed. Recoveries comprise all dead (including sick and dying) encounters, many of which are from members of the public, live recaptures away from the ringing place (nearly all by qualified ringers), and live resightings away from the ringing place (mainly by ringers and other birdwatchers). Live recoveries include both recaptures and resightings away from the ringing place, normally with a threshold of 5 km, although there is some variation with respect to particular species and ringing centres (Table 1). Depending on context, the term 'recoveries' may refer to both a finding record and the original ringing record. Local recaptures and local resightings are those below the relevant distance threshold. All record types comprising ringing records, dead recoveries, recaptures and resightings are referred to as mark–reencounter data. An encounter history comprises all encounters of a particular individual. Following the normal convention, reencounter data based on live recaptures and resightings only are referred to as capture–recapture data.

Historical development of ringing in Europe

Scientific bird ringing began in Denmark in 1889 when H.C.C. Mortensen attached metal rings to Starlings *Sturnus vulgaris* in order to study their migration. Each ring carried a return address and a unique number – vital items required for identifying the individual and reporting the information about subsequent encounters. There are now some 40 formally constituted ringing schemes in Europe, several having achieved their first century. Studies of migration necessarily involve communication between ringers in one country and finders in another. In 1966, only three years after it was founded, EURING published a Code Manual which, for the first time, defined a coding scheme for recording information about ring-reencounter histories (Anon 1966). Technology limited the information held for each recovery (both ringing and finding information) to one 80-column punch card. At that time, most schemes did not have access to computers and the future power of information technology could not be foreseen. It is thus to the great credit of the code's authors that they provided such a firm foundation for subsequent developments. The code was revised in 1979, but still with the 80-character limitation (Mead *et al* 1979). Computerisation of current and historical recovery information was enhanced in 1982 by grants from the European Community coordinated through EURING. Thanks to this and other inputs, we now have access to ring recoveries dating back half a century before the development of digital computers.

In 1977, with support from the Netherlands Institute of Ecology, the EURING Data Bank (EDB) was founded. It aspired to hold all ring-recovery data for birds ringed or recovered in Europe so as to make them available for research. Initially, technology limited the scope of the Data Bank, with data transfers relying on low-capacity floppy disks sent through the post and very limited processing power, making data manipulation and analysis difficult.

In 2000, a major revision of the code was published, with the character constraint being increased from 80 to 255 per record (Speek *et al* 2001). At the same time, the ringing and reencounter information were split into separate records for each encounter, giving vastly increased capability to record relevant information and avoiding the duplication of first-encounter data. This new format is better suited to recording comprehensive sets of encounter histories, including the many records of marked individuals that are not subsequently reencountered. Space was reserved for data on measurements and moult – recognising that ringing data could now be used to address many research questions in addition to the description of migration routes and basic analyses of demographic rates.

The EDB was reorganised in 2005 and moved to the British Trust for Ornithology (BTO) in the UK. All records are now stored in an ORACLE database which facilitates rapid and effective data access, presentation and analysis. The EURING web site became the gateway to the EDB for researchers in search of data and also made the EDB more prominent and accessible.

In 2010 an extension of the 2000 exchange code was released, called the 2000+ code (du Feu *et al* 2010). This defined, for the first time, morphometric and moult variables and contained all the fields required for data exchange between schemes during recovery processing. Codes for some fields (Scheme, Place, Species, Finding Circumstances) are now available

Table 1. EURING Data Bank holdings by ringing scheme and 20-year period. Numbers of recovery records held by the EDB in June 2015. This includes all birds recovered dead or injured together with recaptures and resightings more than 10 km from the original ringing location. Initial ringing records and live recaptures close to the ringing location are excluded. These figures should be interpreted in relation to differing data management and submission practices between schemes (see text). Additional data may exist in the files of individual schemes or individual ringers, but may not have been submitted or computerised. In addition to the records summarised here the EDB holds some local recaptures for schemes marked [a] and some first-encounter data for birds with no reencounters for schemes marked [b]. Where appropriate, data from defunct schemes are included with those from the scheme currently covering the relevant country.

Scheme code	Country	Ringing centre	1900–19	1920–39	1940–59	1960–79	1980–99	2000 onwards	Total	Percent
BGS[a,b]	Bulgaria	Sofia						45	45	0.00
BLB	Belgium	Brussels		4222	13 106	49 048	48 817	46 187	161 380	4.07
BYM[b]	Belarus	Minsk						39	39	0.00
CIJ	Channel Islands	Jersey		1	402	3713	3841	7326	15 283	0.39
CYC	Cyprus	Nicosia					2	17	19	0.00
CZP[a]	Czech Republic	Praha	163	1122	7133	13 775	27 348	25 415	74 956	1.89
DEH[a]	Germany	Hiddensee				35 100	100 928	166 932	302 960	7.63
DER	Germany	Radolfzell	33	4566	9648	21 474	13 091	39 522	88 334	2.23
DEW[a]	Germany	Wilhelmshaven	4	9642	15 282	48 727	42 833	65 588	182 076	4.59
DKC	Denmark	Copenhagen	579	8425	10 737	58 883	52 871	16 784	148 279	3.74
ESA	Spain	San Sebastián			458	798	223	894	2373	0.06
ESI	Spain	Madrid			38	4129	23 474	30 215	57 856	1.46
ETM	Estonia	Matsalu				1143	3499	8840	13 482	0.34
FRP	France	Paris		19	210	2294	9361	16 094	27 978	0.70
GBT	Britain and Ireland	Thetford	2069	10 404	46 235	234 249	260 687	167 971	721 615	18.18
GRA	Greece	Athens					184	134	318	0.01
HES	Switzerland	Sempach	22	1781	6096	19 145	19 000	30 720	76 764	1.93
HGB	Hungary	Budapest	531	1501	1062	1250	11 564	25 240	41 148	1.04
HRZ	Croatia	Zagreb	33	93	988	1505	2269	11 479	16 367	0.41
IAB[a]	Italy	Bologna		277	734	7718	11 854	13 747	34 330	0.87
ILT[b]	Israel	Tel Aviv				108	230	509	847	0.02
ISR	Iceland	Reykjavik		1	7	81	190	172	451	0.01
LIK	Lithuania	Kaunas	227	86	326	4187	20 895	13 147	38 868	0.98
LVR	Latvia	Riga		255	919	7056	5888	311	14 429	0.36
MLV[a,b]	Malta	Valetta					7975	14 798	22 593	0.56
NAW	USA and Canada	Washington		3	5	105	164	107	384	0.01
NLA[a,b]	Netherlands	Arnhem	193	1329	6325	77 573	293 066	495 930	874 416	22.03
NOS[a]	Norway	Stavanger		72	951	2110	15 777	8049	26 959	0.68
PLG[a]	Poland	Gdańsk		406	366	6218	73 557	79 864	160 411	4.04
POL	Portugal	Lisbon					1498	908	2406	0.06
RSB[a]	Serbia	Belgrade					81	1174	1255	0.03
RUM	Russian Federation	Moscow		1834	7125	9348	10 364	1738	30 409	0.77
SFH[a]	Finland	Helsinki	242	2766	4231	83 519	227 580	337 082	655 420	16.52
SKB[a]	Slovakia	Bratislava				53	524	1825	2402	0.06
SVS	Sweden	Stockholm	57	5524	17 720	47 525	54 774	44 388	169 988	4.28
TUA	Turkey	Ankara					23	313	336	0.01
UKK	Ukraine	Kiev					60	1305	1365	0.03
Total			4153	54 329	150 104	740 834	1 344 312	1 674 809	3 968 541	
Percent			0.10	1.37	3.78	18.67	33.87	42.20		100.00

from interactive tables on the EURING website (Appendix), rather than being incorporated in the text of the code manual. The release of the 2000+ code realised the far-sighted vision of the authors of the 1966 code – and much more besides.

Current content

A full description of the contents of the EDB is provided by the EDB Index (du Feu *et al* 2016; Appendix) which is available online and is updated as new data are received. This includes summaries of numbers of dead and live recoveries by species and time period. It also provides maps showing the distributions of ringing and finding places of birds recovered dead and alive for each species (Figure 1). This information allows potential analysts to assess whether the data are likely to be suitable to address a specific research question. The figures presented in the online EDB index need careful interpretation, due to variation in the submission practices of different schemes, largely driven by differences in data-management practices and the extent of computerisation. Some 14 schemes submit data for all reencounters of ringed birds, at least for more recent years, while two have recently started to include ringing records for birds with no subsequent reencounters (Table 1). Most schemes submit data for all ringed birds found dead and those live recoveries beyond a certain distance from the point of ringing (see www.euring.org/data-and-codes/reportable-recovery-definitions for details). Although most records are relatively recent, a few are over 100 years old. For some species, there are

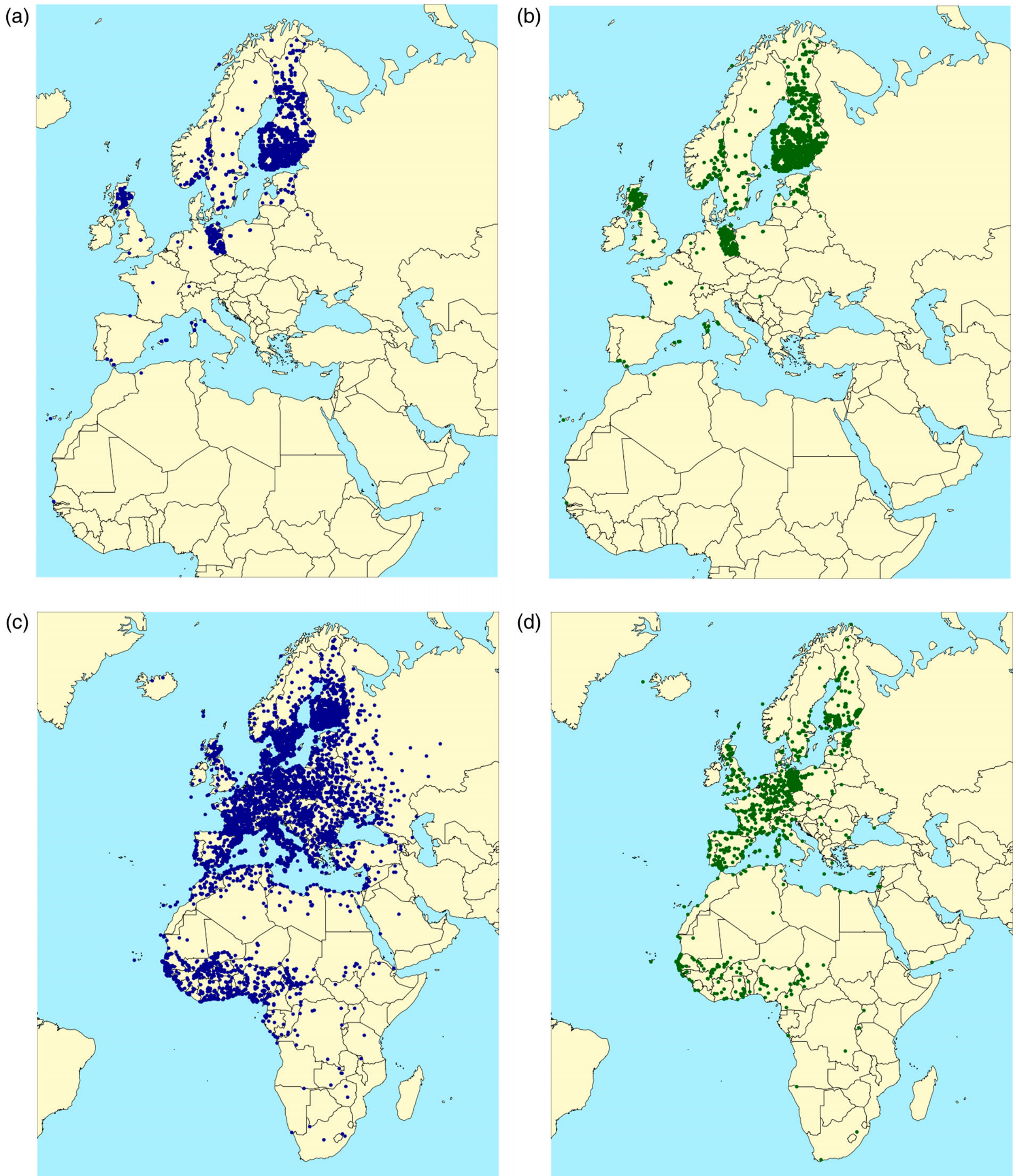

Figure 1. Distribution of ringing and recovery locations for Ospreys *Pandion haliaetus* ringed by European Ringing Schemes and recovered either dead or alive: (a) ringing locations of birds recovered dead; (b) ringing locations of birds recovered alive; (c) finding locations of birds recovered dead; (d) finding locations of birds recovered alive. Redrawn from du Feu *et al* (2016).

sufficient older records to enable analyses of long-term temporal changes in recovery and movement patterns (Fiedler 2001, Ambrosini *et al* 2011, Calladine *et al* 2012).

Here we provide a brief summary of the information available. Our latest analysis (June 2015) indicated that the EDB contains over ten million encounter records contributed by 37 ringing schemes. If we consider conventional recovery records, as defined above, the Data Bank contained 3 968 522 recoveries (Table 1). Eight schemes (Brussels, Hiddensee, Wilhelmshaven, Thetford, Arnhem, Gdansk, Helsinki and Stockholm) each contributed over 4% of the total and between them these schemes supplied 81.3% of all recovery records. Only 0.1% of these records are from before 1920, with 94.7% being since 1960 and 42.2% since the turn of the century (Table 1).

Eight species groups (ducks, raptors, gulls, owls, titmice, hirundines, *Acrocephalus* warblers, thrushes and finches) each contributed over 4% of individual birds recorded and between them these groups comprise over 55.7% of such records in the EDB (Table 2). The representation of different species groups within the EDB is due to a range of factors including species abundances and distributions, ease of capture, recovery probabilities, research priorities and the distribution and interests of volunteer ringers and professional ecologists. A high proportion of bird ringing is dependent on the efforts of highly trained volunteers, and thus tends to focus on small birds that can be captured in at least reasonable numbers using mist nets. This high representation of small passerines will become even more pronounced as more first-capture data and local recaptures are added to the EDB. In contrast, larger species such as ducks and gulls are ringed in much smaller numbers but have relatively high reencounter rates. For analyses of movements and survival that depend on reencounter records, the information content of the records for these larger species may be relatively high while, as information on measurements and moult is increasingly incorporated, the information on small birds, with large numbers of first captures and local recaptures, will become more prominent.

Table 2. EURING Data Bank holdings by species group. Number of records of individual birds held within the EDB in June 2015. Here one individual counts only once, regardless of the number of reencounters. The figures include local recaptures, but not individuals that were captured only once.

Species group	Number of individuals	Percentage of individuals
Swans	95 563	1.8
Geese	58 779	1.1
Ducks	291 887	5.4
Game birds cranes and bustards	14 503	0.3
Petrels storm petrels and shearwaters	31 024	0.6
Gannets and pelicans	5639	0.1
Cormorants	46 955	0.9
Herons	25 822	0.5
Storks	47 469	0.9
Ibises spoonbills and flamingos	10 902	0.2
Divers and grebes	2817	0.1
Raptors	264 041	4.9
Rails crakes and coots	98 127	1.8
Oystercatchers stilts coursers etc	184 250	3.4
Plovers	26 469	0.5
Snipe sandpipers phalaropes	112 149	2.1
Skuas	3252	0.1
Auks	30 984	0.6
Terns	58 402	1.1
Gulls	665 553	12.3
Doves and pigeons	43 456	0.8
Owls	334 781	6.2
Swifts	17 621	0.3
Kingfishers	11 851	0.2
Woodpeckers	22 480	0.4
Other non-passerines	3762	0.1
Shrikes	7701	0.1
Corvids	91 839	1.7
Crests	34 649	0.6
Penduline Tit	10 142	0.2
Titmice	563 422	10.4
Parrotbills	22 562	0.4
Larks pipits and wagtails	42 733	0.8
Hirundines	167 707	3.1
Long-tailed Tit	37 666	0.7
Phylloscopus warblers	136 614	2.5
Sylvia warblers	194 988	3.6
Acrocephalus warblers	313 707	5.8
Other warblers	43 065	0.8
Nuthatches and creepers	21 992	0.4
Wren	28 997	0.5
Starlings	98 581	1.8
Dipper	12 848	0.2
Thrushes	233 431	4.3
Flycatchers	56 795	1.0
Chats and wheatears	212 773	3.9
Accentors	51 794	1.0
Sparrows	71 055	1.3
Finches	347 823	6.4
Buntings	92 870	1.7
Other passerines	8243	0.1
Total	5 412 535	100.0

Data-provision services

Potential analysts are advised to use the initial enquiry form on the EURING website (www.euring.org/data-and-codes/edb-application-procedure) in order to establish the number of records available, to refine the request and to agree the charge. EURING endeavours to keep these charges as low as possible, but they are necessary to cover the basic running costs of the EDB, which receives no external funding. After the initial enquiry has been completed, a formal request can be made using the relevant form available from the same web page. This is sent, automatically, to all schemes who are thereby invited to agree to the release their data. It most cases this procedure is straightforward and once agreements have been obtained and the charge paid, data are supplied promptly. The process from submitting a formal request to receipt of the data can normally be completed in under a month. Data are supplied in a standard format defined in the EURING exchange code (du Feu *et al* 2010). Requests relating to particular species, areas, times or other selection criteria can be accommodated readily.

Future plans

The EDB was created to promote research into bird movements, demography and conservation using ring-recovery data on a European or flyway scale. The scope of possible research is being enhanced through the inclusion of records of birds which have been ringed but never reencountered, of local recaptures and of data on morphometrics and moult. The total number of records in the latter category is small, as yet, but is expected to increase rapidly in the near future. This will enable a wider range of studies into avian life histories, population processes, morphometrics and moult than has been possible to date. Some of the results together with ideas for novel future research are outlined in subsequent sections of this review.

Research based on large-scale studies of marked birds

Describing migration routes

The traditional and most widely understood aim of bird ringing is the description of migration routes. Understanding the spatiotemporal structure of bird movements is a prerequisite for species conservation as well as for understanding the drivers and consequences of migration. Ring-recovery atlases provide overviews of bird movements in space and time as shown by ring recoveries, sometimes also supplemented by other material such as counts or tracking data. Some 13 comprehensive national ring-recovery atlases have been published for European countries, ten in the last decade. Recent additions to the list include Croatia, Faroes, Finland, Hungary, Italy and Germany (Csörgő *et al* 2009, Spina & Volponi 2009, Kralj *et al* 2013, Bairlein *et al* 2014, Valkama *et al* 2014). Building on this basic knowledge of bird movements derived from ring recoveries, recent developments of loggers and transmitters facilitate the collection of information about individuals at much higher spatial and temporal resolutions (Fiedler 2009, Bridge *et al* 2011). Numerous studies have used ring-recovery data to describe patterns of connectivity between areas used by particular bird species, and also to document different migration routes of subpopulations, age or sex classes (*eg* Mason & Allsop 2009, Reichlin *et al* 2009, Liker & Nagy 2009, Kylin *et al* 2011, Ambrosini *et al* 2014). For example, Calladine *et al* (2012) used records from the EDB to describe the passage and wintering areas of different breeding populations of Short-eared Owls *Asio flammeus* (Figure 2). There is also increasing evidence of changes in migration routes over time, as Ambrosini *et al* (2011) showed for Barn Swallow *Hirundo rustica* and Calladine *et al* (2012) for Short-eared Owl.

Mortality causes

Dead recoveries are stored with the information about the reported cause of death whenever this information is provided by the finder. This typically provides information on conspicuous causes of death related to human activities such as hunting, oil pollution and mortality in fishing nets. Natural causes such as starvation or disease can only rarely be assessed adequately by finders, for example as part of specific studies. Although the finder's assessment of the reason that a bird died may not always be correct, data on reported causes of death allow some useful insights into mortality patterns (Hüppop & Hüppop 2002). Such analyses have been used to document geographical and temporal variation in the hunting of migratory birds across Europe (McCulloch *et al* 1992; Figure 3) and to relate variation in the demographic rates of seabirds to differences in exposure to oiling (Votier *et al* 2008).

A major problem is that the probability of finding a dead individual depends on the mortality cause, and therefore the frequency of mortality causes related to humans (*eg* hunting, traffic accidents, electrocution) is usually overestimated within the raw data. Schaub & Pradel (2004) developed a probabilistic model which provides unbiased estimates of mortality proportions based on recoveries of marked individuals. They applied their model to recovery data for Swiss White Storks *Ciconia ciconia* and found that about 35% of individuals died due to the collisions with power lines. Once cause-specific mortality probabilities and their temporal variations are known, hypotheses about whether a specific mortality cause is additive to the remaining (natural) mortality, or is (partially) compensated by lowering of other mortality causes through density-dependent population processes, can be tested (Schaub & Lebreton 2004, Servanty *et al* 2010). Such an assessment is often important for the management of populations, in particular for setting hunting bags. The degree of compensation of hunting mortality has been a key research focus for the regulation of the hunting of Mallard *Anas platyrhynchos* and other duck species in the USA (Burnham & Anderson 1984, Nichols *et al* 2007) and there is an urgent need to apply such approaches within a European context (Elmberg *et al* 2006).

Disease transmission

Birds are vectors for a multitude of pathogens, ranging from those that are mainly interesting for understanding host–pathogen interactions or

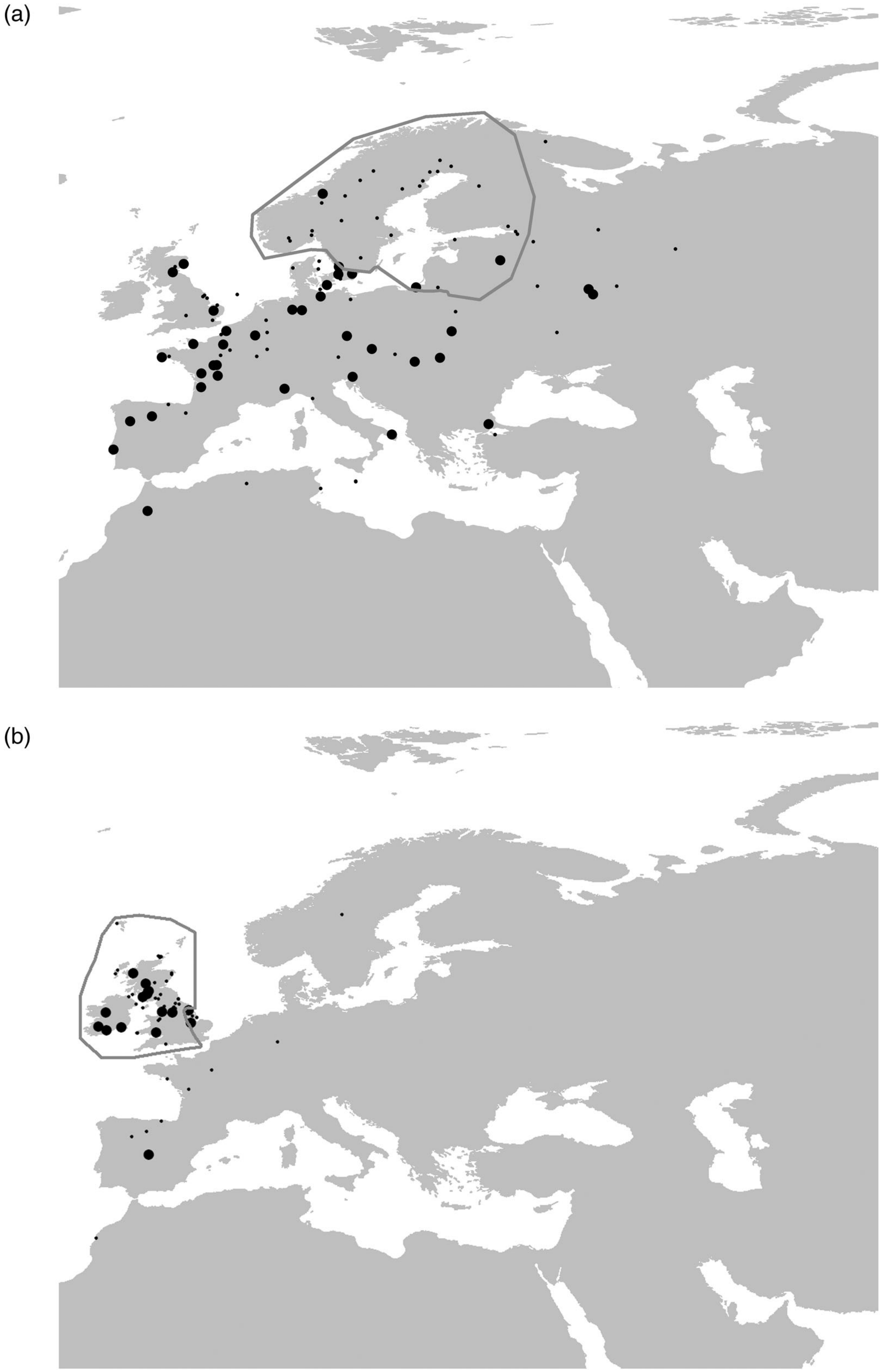

Figure 2. Recovery locations of Short-eared Owls *Asio flammeus* with natal/breeding areas in (a) the Boreal region and (b) the Insular Atlantic region. Regions are outlined; large dots show recoveries in winter, small dots in passage periods. Redrawn from Calladine *et al* (2012).

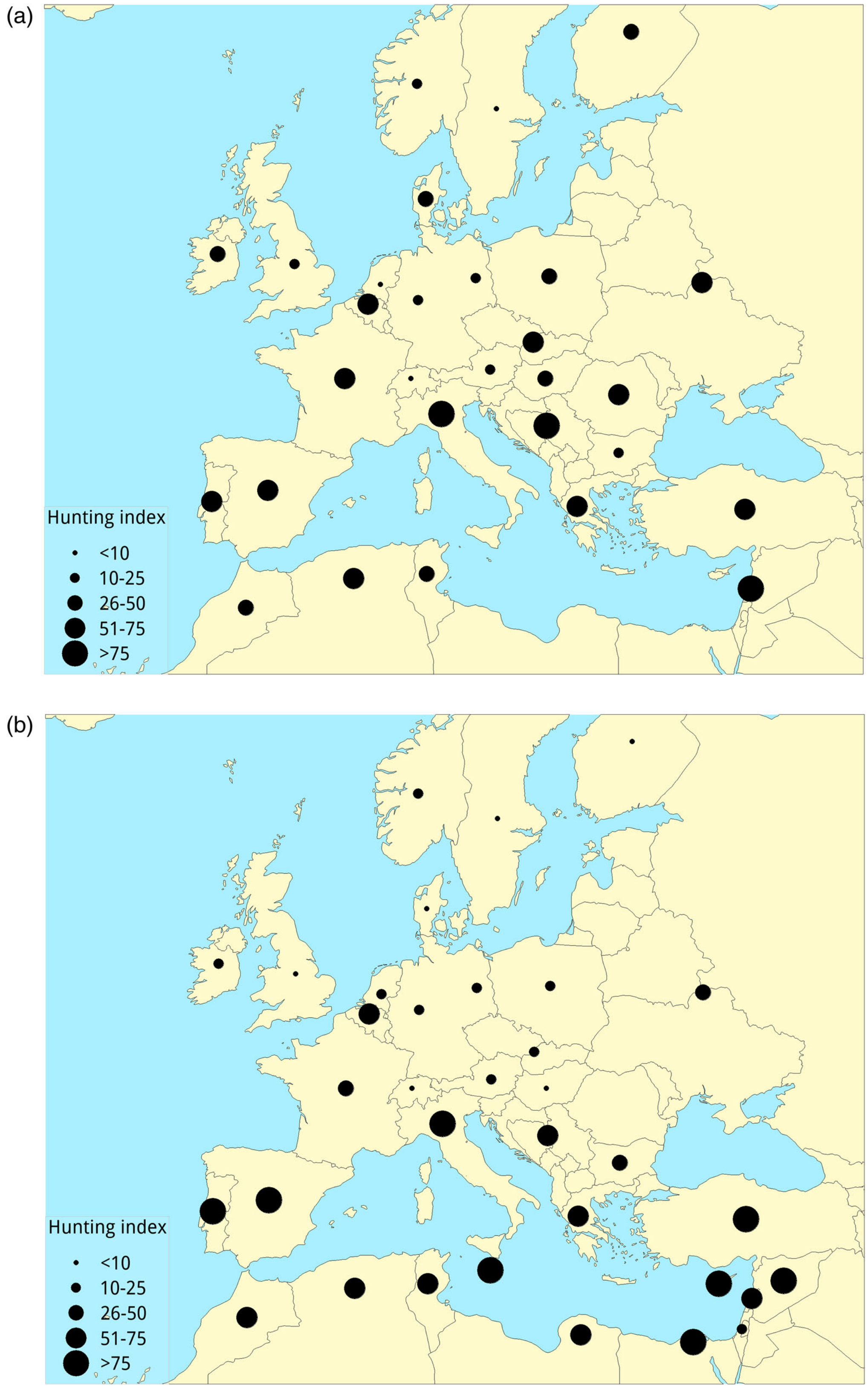

Figure 3. Geographical variation in hunting indices (a measure of the relative proportion of recoveries attributable to hunting) for (a) raptors and (b) passerines, in the pre-1980 period. Redrawn from McCulloch *et al* (1992).

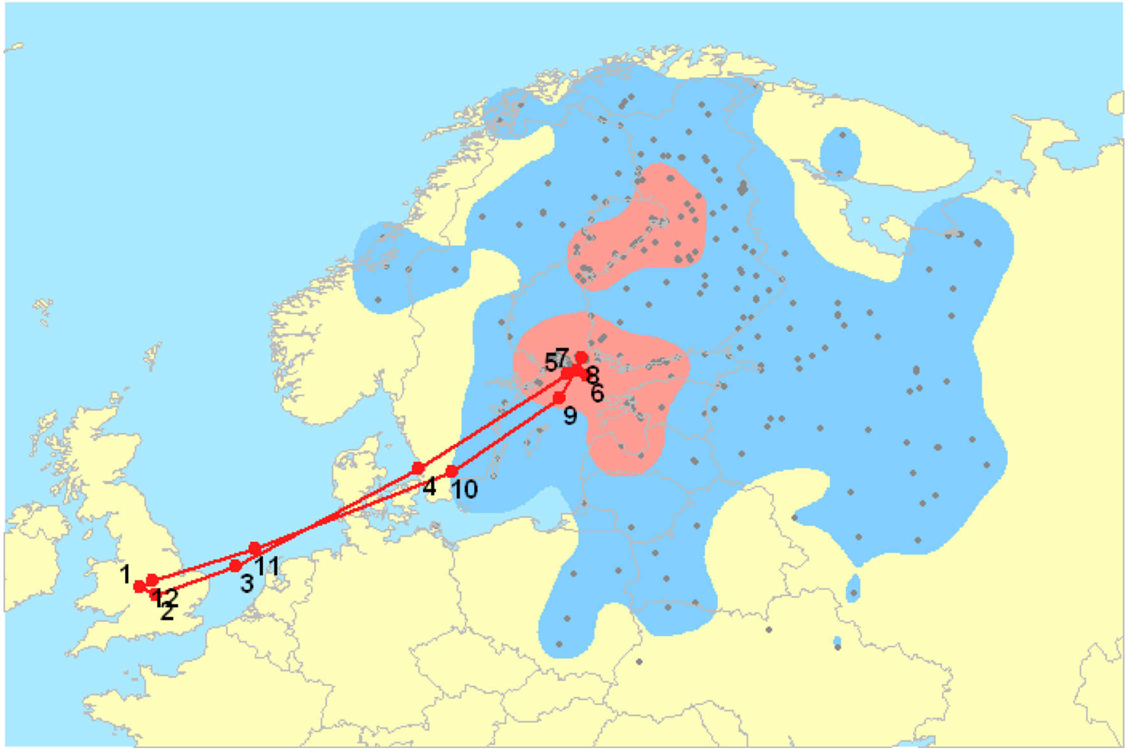

Figure 4. Movements of Tufted Ducks *Aythya fuligula* between the Baltic region and Britain and Ireland as shown by the Migration Mapping Tool. Coloured kernels indicate the main concentrations of recoveries (50% of all recoveries in red, 95% in blue). The average migration route is shown by a line with numbers indicating the average location in each month. This is one of nine flyways identified for Tufted Ducks occurring in Britain and Ireland. From Atkinson *et al* (2007).

epidemiological mechanisms (Hochachka & Dhondt 2006) to those of direct significance for the health of humans or livestock (Globig *et al* 2009a). Since few other vertebrate hosts are as mobile as migrating birds, the latter may play an important role in long-distance transmission of some diseases. While case studies can be undertaken using tracking and geo-logging devices to follow the migration routes of individual birds, at present such measures cannot fully replace the long-term ring-recovery data sets covering large areas and many species (Fiedler 2009).

In the context of highly pathogenic avian influenza virus H5N1, EURING, together with BTO and Wetlands International, and with financial support from DG Environment of the European Commission, developed a 'Migration Mapping Tool' as a mechanism for policymakers and others to assess migratory connectivity of waterbirds and the consequent potential for disease transmission between various parts of Europe, North Africa and the Middle East (Atkinson *et al* 2007; Figure 4). When, in February 2006, H5N1 reached the northeastern German island of Rügen, and shortly afterwards the southern German side of Lake Constance, existing ring-recovery data allowed the identification of the main origins of wintering waterbirds using this area. By combining this information with genetic data on the virus, it could be shown that two independent influx events happened at almost the same time (Globig *et al* 2009b). These findings provide an important illustration of the way that an epidemic involving this particular pathogen may develop.

Dispersal

Dispersal is often defined as the movement of an individual between its location of birth and the place of first breeding (natal dispersal) and between subsequent breeding locations (breeding dispersal; Greenwood & Harvey 1982); it is an important individual behaviour affecting the spatial structure of populations and their dynamics, as well as gene flow. Dispersal studies typically focus either on the distribution of distances moved or on the probability of conducting a dispersal movement. Either way, such studies are possible only if individuals can be followed, and ringing has been used widely for this purpose (Bennetts *et al* 2001). For example, Paradis *et al* (1998) compared dispersal distances of 75 European bird species based on recoveries of ringed individuals from Britain and Ireland. They found that interspecific differences in

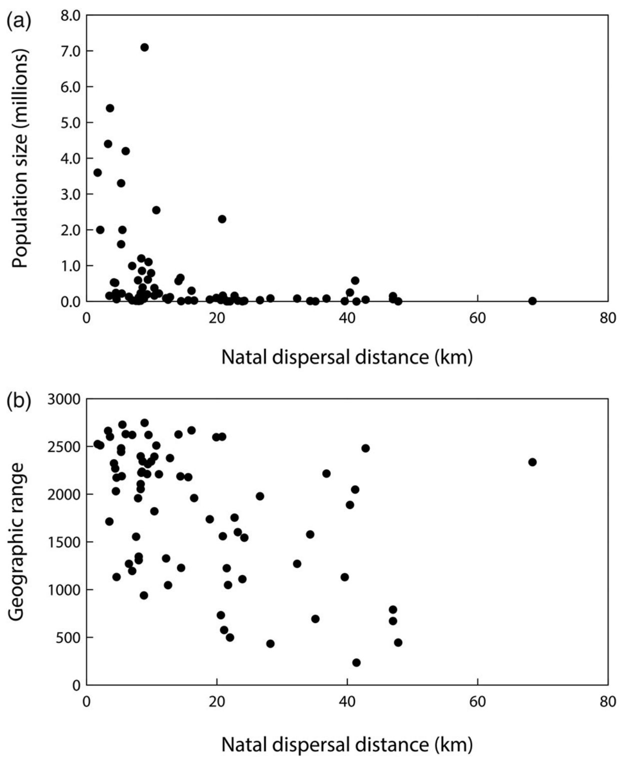

Figure 5. Relationships of (a) population size and (b) range size (number of occupied 10-km squares in Britain) with mean natal dispersal, estimated from ring recoveries for 75 British bird species (population size: r = -0.794, P < 0.001; range size: r = -0.601, P < 0.001: both after controlling for phylogeny). Redrawn from Paradis *et al* (1998).

dispersal patterns were related to species ecology. Both natal and breeding dispersal were lower among abundant species and among species with large geographic ranges (Figure 5), while migratory species showed greater dispersal than residents. Wetland species showed greater breeding dispersal than others, presumably reflecting the relatively patchy nature of wetland habitats.

Live recaptures or resightings of marked individuals sampled at different locations have been used to estimate dispersal probabilities between these locations by means of multistate capture–recapture models (Blums *et al* 2003, Schaub & Von Hirschheydt 2009). This provides a more precise approach than one based on dead recoveries but is generally limited to smaller spatial scales. A general limitation of using mark–recapture/resighting data for studying dispersal is imperfect detection: dispersal can be inferred only from some individuals, and these individuals are unlikely to be a random sample. If not corrected for, this typically results in a bias towards small dispersal distances and in an underestimation of dispersal probabilities, as individuals dispersing to locations that are not included in the study remain undetected. Promising approaches to reduce potential biases are the calculation of distance-related recruitment rates (van Noordwijk 2011) and the inclusion of spatial information in capture–recapture models (Schaub & Royle 2014). Thus, ring-recovery data and mark–recapture data offer complementary advantages and disadvantages for the study of dispersal. Ring-recovery data provide relatively crude dispersal distributions but can be applied to many species and are not constrained by sampling being restricted to particular locations. In contrast, mark–recapture data can provide much more detailed assessments but inference is normally limited to specific sampling locations and such studies are available for fewer species.

Survival, recruitment and breeding propensity

Survival, age at first breeding as a component of recruitment and breeding propensity are usually studied with ringed individuals, since individual identification is crucial for measuring these variables. The master data sources are dead recoveries of marked individuals and capture–recapture data. The main challenge in all these analyses is that observations are imperfect. Marked individuals that are still alive may not be seen and not all dead individuals are found. Therefore, statistical models that contain nuisance parameters such as the probability that a dead marked bird is found and reported or the probability that a marked individual is captured/sighted alive have to be used to analyse the data. There has been tremendous progress in the development of statistical methods for estimating demographic parameters from such data (Brownie *et al* 1985, Lebreton *et al* 1992, Williams *et al* 2002). User-friendly software is available which has resulted in wide use of these methods in demographic studies of birds (*eg* White & Burnham 1999). A website (www.phidot.org) providing links to software, discussion groups and future workshops is also available.

Although many demographic studies use capture–recapture data or ring recoveries collected by the researchers themselves, the use of data from the EDB and similar continental or national data sets have been particularly important for the study of long time series (*eg* Altwegg *et al* 2006, Robinson 2010) or for analyses at large spatial scales (Siriwardena *et al* 1998). Many of these studies reveal relationships with environmental factors that are likely to drive large-scale population changes (Figure 6; Altwegg *et al* 2006). In Britain, national ring-recovery data sets have made an important contribution to explaining the demographic causes of population changes amongst a range of widespread species such as Lapwing *Vanellus vanellus*,

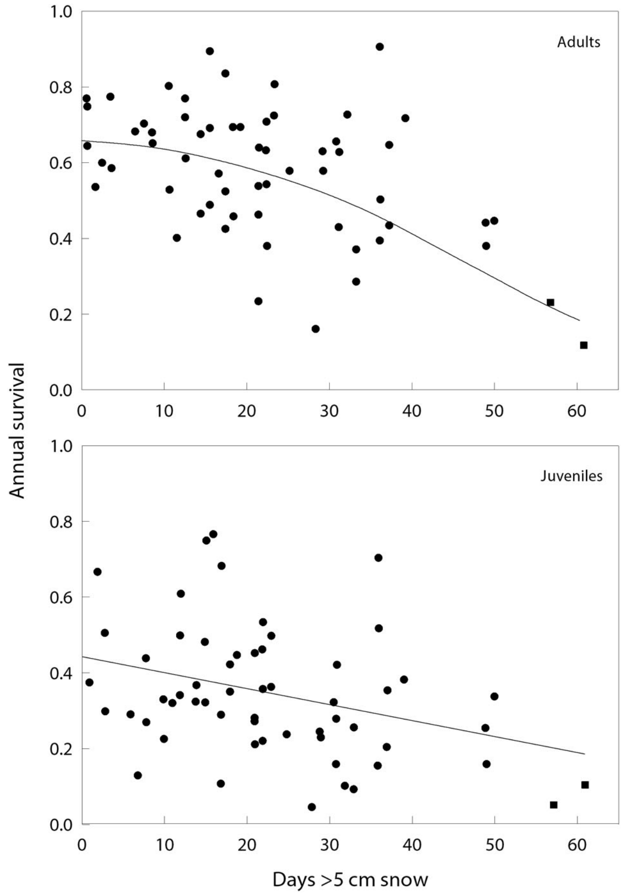

Figure 6. Survival of adult and juvenile Barn Owls *Tyto alba* in Switzerland, estimated from large-scale recapture/recovery data, in relation to the severity of winter weather. The two most extreme winters led to population crashes and are indicated with square symbols. Redrawn from Altwegg *et al* (2006).

Song Thrush *Turdus philomelos* and Blackbird *T. merula* (Peach *et al* 1994, Robinson *et al* 2004, 2012). More recently, the explanatory power of such analyses has been further improved through the use of integrated population models (Robinson *et al* 2012, 2014). Use of such data from the EDB itself has been seriously limited by the lack of information on cohort sizes of ringed samples, which is required to avoid an unrealistic assumption of constant ring-reporting rates. In the future this issue will be resolved through the incorporation of first-encounter data.

While traditional mark–recapture studies, such as those based on Constant Effort Sites or Retrapping Adults for Survival projects, focus mainly on survival (Peach *et al* 1999, Robinson *et al* 2008) more elaborate study designs allow a wider range of questions to be addressed. For example, if data are gathered from several locations, movement rates among locations can be estimated (Blums *et al* 2003). Other studies have addressed a wide range of issues including breeding propensity (Reed *et al* 2004), age at first breeding (Tavecchia *et al* 2001) and disease dynamics (Conn & Cooch 2009). All these analyses require the application of multistate capture–recapture models (Lebreton *et al* 2009). Methods have been developed that allow the estimation of the target parameters even if the states are partially unknown or recorded with errors (Kendall 2004, Pradel 2005).

Capture–recapture data from properly designed studies provide a rich source of information. Besides demographic parameters, the size of the population (Schwarz & Seber 1999), population density (Royle & Young 2008) and the population growth rate (Pradel 1996) can also be estimated. EURING analytical meetings have played an important role in the development of these methods (Thomson *et al* 2009, Schaub & Kendall 2012, Francis *et al* 2014).

Future opportunities and challenges

Mechanisms for data sharing

Large-scale sharing of data and information forms an essential part of contemporary research in many areas, and is particularly important when addressing large-scale processes such as bird migration and the effects of land use and climate change on population processes. However, it is essential to acknowledge the contributions of those individuals and organisations that collected the data, and to ensure that the outcomes of data sharing provide positive enhancement of the data-gathering process. These considerations are particularly important in the case of the long-term population studies which are so critical to our understanding of population processes and require the dedicated commitment of researchers over decades (Mills *et al* 2015). Where data gathering is funded wholly by public bodies, it may be appropriate for data to be available without restriction to anyone who wishes to use them. However, in many cases the collection of bird-ringing data is funded from a wide range of sources in addition to public funding, including charitable foundations, research councils, private individuals, independent organisations coordinating data gathering and analysis, and the ringers themselves. Most importantly, European ringing data gathering relies on a huge input of unpaid time from volunteers. Given all of these stakeholders, and the complex interrelationships between them, EURING believes that it has a responsibility to balance the desirability of open data with some limited controls that give appropriate priority to the interests of data gatherers. This is done by acknowledging that individual ringing centres are the primary owners of the data sets that they contribute to the EDB. These centres will normally be best placed to balance the requirements of data contributors and potential users, taking account of expectations, funding streams and specific circumstances amongst their own ringers, funders and data users.

This rationale provides the basis for operating the EDB. Its data holdings and availability are widely advertised via the EDB index. On receipt of a formal application all schemes are automatically consulted and have a set time in which to respond. Where necessary any issues around data access, conflicts with existing work and the need for collaboration can be discussed and resolved. In the vast majority of cases the data are released in a timely manner. The EDB does make some charges in order to cover part of its costs. In recent years it has had no other external source of funding, with the balance of costs being made up through modest contributions from EURING's member schemes. This is despite much of the work being undertaken by a volunteer (CRdF) and the costs of building a new database having been funded by the BTO.

EURING is very keen to increase the availability of results from the EDB further, building particularly on success of the EDB index (du Feu *et al* 2016) and the Migration Mapping Tool (Atkinson *et al* 2007). The most obvious opportunity is to produce a significant online component towards a European Migration Atlas, with EURING providing maps and tables documenting the movements and migratory connectivity of many species. As the availability of first-capture data, moult data and measurements within the EDB develops, it may also be possible to provide online continental-scale information on annual cycles and demographic monitoring, complementing online information that is now available within some individual countries (*eg* Baillie *et al* 2014, Robinson *et al* 2015).

Quantifying movement patterns

Ringing and recovery data are not uniformly distributed in space or time. They depend on local or clustered catching activities as well as on heterogeneous finding and reporting probabilities of ringed birds. To date, most analyses of movement patterns based on ring recoveries have focused on the description of observed recovery distributions combined with qualitative interpretation of the observed patterns based on knowledge of human population density, recovery circumstances and other factors (examples above). It has been known for some time that, where numbers ringed and recovered across several areas are known, then quantitative inferences are possible (Kania & Busse 1987), but use and development of such methods has been hindered by the lack of availability of data on numbers ringed in different areas. Recently there has been increased interest in quantitative analyses of movement patterns based on ring recoveries, resulting in the development of a number of complementary statistical approaches (Korner-Nievergelt *et al* 2010, Thorup *et al* 2014). Inferences from such analyses may also be strengthened by incorporating multiple species so as to provide additional information on geographical variation in reporting rates (Cohen *et al* 2014).

There remain some circumstances in which recoveries can never provide a complete picture. In remote areas finding and reporting probabilities can be so low that the use of these areas by a certain bird species is unlikely to be recorded. In one of the first large-scale satellite-tracking studies of birds, Berthold *et al* (2001) found that White Storks using the eastern Mediterranean flyway have an important early-winter resting area in Chad and western Sudan – an area where almost no ring recoveries originated. In these cases, tracking and geo-logging approaches provide vital additions to ring-recovery data. However, tracking studies remain expensive and in most cases will provide high-quality data for only relatively small numbers of individuals. Hence interpretation of these data from a few individuals – often carrying quite significant loads of electronic devices – will often need to be evaluated in combination with the findings revealed by ring recoveries. We envisage that future statistical developments will allow joint analyses of these different data types. Detailed tracking data then help to reduce bias while the ring-recovery data will continue to provide information at large temporal and spatial scales.

Demographic modelling

Demographic analyses based entirely or partially on marked individuals are likely to develop in the following directions. First, more sophisticated models will be applied more frequently, allowing some of the underlying assumptions of standard models to be relaxed. The development of Bayesian analyses in particular offers extreme flexibility in modelling (Kéry & Schaub 2012). For example, for modelling purposes it has usually been assumed that individuals are subject to identical demographic parameters (*eg* probability of surviving over a particular time period). The application of models incorporating individual random effects now makes it possible to study variability among individuals (Cam *et al* 2013) or the impact of morphological traits on demography (Gimenez *et al* 2006). Second, the combination of information originating from different data sources will become more widely used. For example, integrated population models (Besbeas *et al* 2002, Schaub & Abadi 2011, Robinson *et al* 2014) combine population survey data with demographic data (capture–recapture, recoveries, reproductive success). Advantages of joint analyses include more precise parameter estimates, the ability to estimate parameters that cannot be estimated with a separate analysis of the available data and the ability to test the consistency of different data sources. Third, the development of spatially explicit models is advancing rapidly (Royle *et al* 2013) offering the possibility of obtaining new insights into dispersal, together with improved estimates of survival and population density.

The main challenge for the EDB in meeting future needs in this area is that comprehensive first-encounter and local reencounter data should be stored, in addition to conventional live and dead recoveries. Survival analyses are often impossible if data on cohort sizes of ringed birds are not available. Ideally, capture data will be stored with individual covariates such as morphometrics, exact location and, where appropriate, factors such as breeding status. This would facilitate analyses that that incorporate the effects of factors such as morphology, sex or state. Finally, since the design of the studies has consequences for their analyses, there is a need to develop methods for storing relevant meta-data about study design.

Morphometrics, body condition and moult

The collection of data on measurements, weights and moult through structured networks of volunteer ringers is a potentially powerful way to address a range of biological questions (Bairlein 2003, Cresswell 2009). Thus the planned addition of such data to the EDB will open up a huge range of additional studies that were previously very difficult to undertake at a European scale. In a brief review of this kind it is not possible to detail all the potential research areas where such data could make an important contribution. Here, we highlight a few key examples of research based on these kinds of data.

Body size usually varies geographically both within and between species and subspecies, so measurements can provide important supplementary information about the origins of migratory populations (Summers *et al* 1988, Pérez-Tris *et al* 1999). Weights and measurements also provide critical information on the accumulation of body reserves prior to migration, as has recently been illustrated by studies of Barn Swallow at both a country and European scale (Rubolini *et al* 2002, Coiffait *et al* 2011; Figure 7). To understand migration strategies fully and the role of stopover sites, such large-scale studies need to be complemented with more intensive mark–recapture/resighting investigations at a limited number of sites to measure length of stay and rate of fattening, and to understand the stopover decision rules used by migratory species (Schaub *et al* 2008, Bairlein & Schaub 2009).

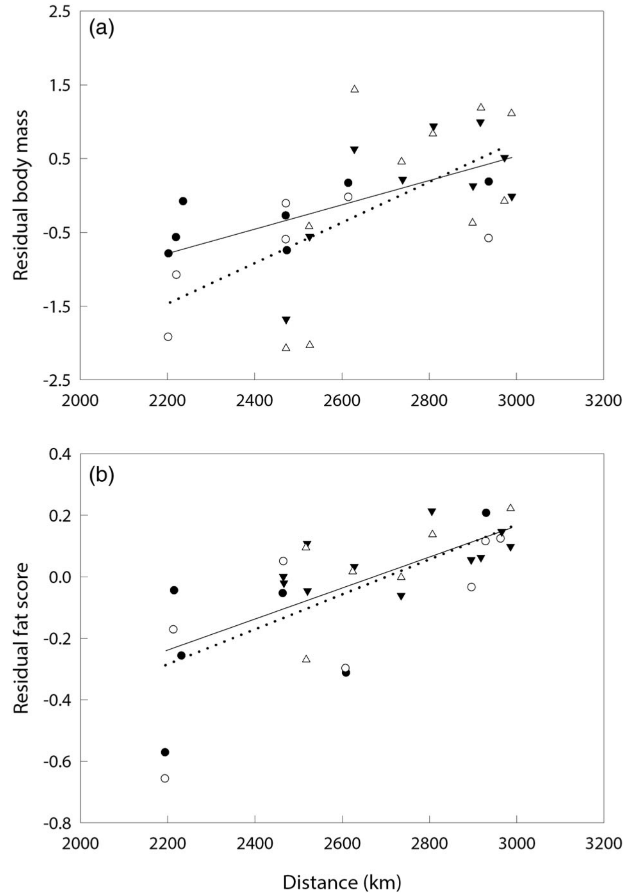

Figure 7. Mean residual body mass (a) and fat score (b) of Barn Swallows *Hirundo rustica* for each sampling location (n = 10 or more individuals) in relation to linear distance between the sampling location and the southern margin of the Sahara Desert. Triangles, adults; circles, juveniles; filled symbols, Italian sites; open symbols, Iberian sites. Redrawn from Rubolini *et al* (2002).

Another topical area of research drawing on large-scale data on weights and measurements involves the accumulation of winter fat reserves and the trade-off between the risks of starvation and predation (Cresswell 2009). In temperate and northern regions most small passerines accumulate substantial winter fat reserves to allow them to survive the longer winter nights and as an insurance against sudden cold spells and other unpredictable food shortages. An analysis of long-term trends in the weights of Great Tits *Parus major* across southern Britain found that winter weights increased when Sparrowhawk *Accipiter nisus* numbers were reduced due to pesticides, and then declined as the Sparrowhawk population recovered (Gosler *et al* 1995). These results were subsequently extended to show an interaction between the effects of predation and winter temperature on fat reserves. In colder winters, higher Sparrowhawk abundance was associated with lower Great Tit body mass while in warmer winners it was associated with higher Great Tit body mass (Cresswell *et al* 2009). This and other studies suggest that body-mass responses to environmental conditions may be subject to change as a result of both phenotypic plasticity and micro-evolutionary adaptations (Salewski *et al* 2010). Thus understanding the large-scale response of such processes to climate change is likely to be an important area for future research that the EDB can help to facilitate.

Moult, and in particular the main annual moult of the primary feathers, is a key component of the annual cycle of birds that can easily be studied by bird ringers (Kjellén 1994, Newton 2009). For most European bird species moult is a discrete phase of the annual cycle undertaken at a separate time from breeding or migration such that its timing and duration may be critical with respect to these other life-history events (Holmgren & Hedenström 1995, Hedenström 2008). Indeed, for many both resident and migratory populations the onset of primary moult may provide a good measure of the end of the nesting season (Newton 2009). In some migratory populations moult may be arrested to enable migration to proceed, with the extent of such arrested moult differing between populations in different parts of Europe in relation to specific life-history constraints (Mead & Watmough 1976, Swann & Baillie 1979). A recent study of 15 species undertaking primary moult within Britain found that, within species, the speed of primary moult varied according to the length of the breeding season, illustrating the importance of understanding the extent to which species are able to vary their moult patterns in relation to environmental change (Morrison *et al* 2015). In general, there is huge potential to increase our understanding of moult patterns through the types of large-scale analyses that could be facilitated by the EDB.

Synthesis

The EURING Data Bank provides a substantial and reasonably comprehensive resource for conducting analyses of what may be described as traditional ring-recovery data – ringing and reencounter records for birds that have subsequently been recovered. Such data have been used to address a wide range of questions involving the description of movements and mortality patterns, including the documentation of migration patterns, temporal and spatial variation in anthropogenic causes of death such as oil pollution and hunting, and the potential role of birds in disease transmission. With careful analysis and interpretation, such data can also be used to measure average survival rates and dispersal patterns, and can therefore contribute to studies of population dynamics designed to elucidate the demographic and environmental causes of population changes.

In order to model patterns of movements and survival formally and in more detail, it is usually necessary to have information on the numbers of first-encounter records, so that variation in ring reporting rates can be accounted for in the models. Furthermore, mark–recapture analyses can often provide more precise estimates of survival than ring recoveries, and for these local recaptures and a clear study design are needed. Thus a desirable future enhancement for the EDB, and also many individual ringing centres, would be to add data on the design of mark–recapture studies. Recent developments in the EDB, building on advances within individual ringing centres, will soon make it possible to incorporate large volumes of first captures and local recaptures within the Data Bank. This in turn will facilitate many more high-quality analyses at a European scale, addressing issues such as the causes of population changes in migratory species, the impacts of climate change, the role of protected areas in a changing environment and the effects of landscape configuration and connectivity on avian distributions and abundances. Further capability will be provided by the addition of data on measurements, weights and moult. While such data might appear to be of mainly academic interest they may in fact be crucial for understanding a range of applied issues, ranging from the effects of climate-related phenological changes on population dynamics to changes in the quality of wintering and staging areas under the influence of environmental change.

While we develop the capacity to address these important, challenging and exciting questions, EURING has identified an immediate priority for the production of a European Migration Atlas. This would provide a synthesis of information on movement patterns at a flyway scale that would be of immense value to policymakers, conservationists, ecological researchers and ornithologists. Its listing as one of the key evidence needs for the African–Eurasian Migrant Landbird Action Plan developed under the Convention on the Conservation of Migratory Species (CMS) clearly demonstrates its policy relevance. We envisage a series of high-level summaries of the movement patterns of individual species, backed by an online resource that would allow users to explore recovery patterns in more detail. We aim to support this with a series of cross-species reviews addressing issues such as the importance of key stopover areas for migratory species, the wise management of hunted populations, changing migratory strategies in the face of climate change and relationships between migratory behaviour and conservation status. In addressing all of these issues it must be stressed that ringing data are of most value when combined with other information sources, including counts, tracking data, genetic studies and many other types on information. Bird ringing has a great deal to offer conservation science, and the EDB provides a mechanism through which such research can be delivered at a range of scales.

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Appendix

Useful websites referred to in the text:

Topic	URL
European multi-language ring reporting website	www.ring.ac
EURING code manuals and tables	www.euring.org/data-and-codes/euring-codes
Reportable recovery definitions, by scheme	www.euring.org/data-and-codes/reportable-recovery-definitions
EURING Data Bank index	www.euring.org/data-and-codes/euring-databank-index
EURING Data Bank application procedure	www.euring.org/data-and-codes/edb-application-procedure
List of bird migration atlases	www.euring.org/research/migration-atlases
Migration Mapping Tool	www.euring.org/research/migration-maps
Current BTO annual BirdTrends report for the United Kingdom	www.bto.org/birdtrends
Current BTO online ringing and nest recording report for Britain and Ireland	www.bto.org/volunteer-surveys/ringing/publications/online-ringing-reports
Phidot, supporting mark–recapture/recovery research	www.phidot.org/
Proceedings of EURING 2013 analytical conference – papers from *Methods in Ecology and Evolution* and *Ecology and Evolution*	www.methodsinecologyandevolution.org/view/0/VI_MDPMP.html
List of Proceedings of EURING analytical conferences	www.euring.org/meetings/analytical-meetings/analytical-meeting-proceedings