Understanding changes in bird populations – the role of bird marking

STEPHEN R. BAILLIE[1]* and MICHAEL SCHAUB[2]
[1]*British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK* [2]*Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland and Conservation Biology, Institute of Ecology and Evolution, Universität Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland*

Studies of marked birds play a central role in research on avian population dynamics and life histories because they are the main means of estimating survival, recruitment and dispersal. Integrated Population Monitoring aims to combine such information from ringing with data on abundance, productivity and the environment in order to develop population models that address applied questions. Diagnosing the demographic and environmental causes of population declines provides a basis for developing management prescriptions for population recovery. We discuss examples of how such studies are contributing to the conservation of European farmland birds and to understanding declines in Afro–Palaearctic migrants. Adaptive harvest management of North American duck populations demonstrates that similar principles apply to the management of quarry species. Over the next two decades we expect significant advances in our understanding of seasonal variation in demographic rates, of density dependence and of the ways in which continental-scale population dynamics are built up from processes operating at much smaller spatial scales. This will be achieved through analyses of large-scale data sets, the combination of conventional and new technologies and the widespread application of fully integrated modelling methods. Large-scale data gathering through national ringing centres will play a key part in this process.

Many bird populations are changing rapidly as a result of widespread environmental change, and these rates of change are expected to accelerate over coming decades, particularly as a consequence of global climate change (Robinson *et al* 2009a, Gregory *et al* 2009). Over the past two decades there has been an increasing conservation focus on declines of relatively widespread and abundant species, in addition to declines in species that are already rare. Indeed, whilst conservationists in Britain and Ireland have had considerable success in reversing declines in very rare species, declines in a range of widespread farmland birds, woodland birds and Afro-Palaearctic migrants are proving much more challenging to address (Eaton *et al* 2009). To develop effective conservation strategies to reverse such changes, it is necessary to understand the demographic and environmental causes of change, together with the demographic consequences of proposed management actions (Baillie 2001). Where conservation programmes involve introductions of captive-reared or translocated birds, understanding the demographic consequences of these actions is also important.

While the focus of conservation effort tends to be on declining species, similar considerations apply to the management of populations that are hunted and to the control of introduced populations, and other species

regarded as pests. These issues of population management require an understanding of the demographic processes and underlying environmental factors that determine abundance. In this paper we review the development and application of techniques for investigating the demographic and environmental processes that bring about changes in bird populations. We give particular emphasis to studies carried out at large spatial scales and to the components of these studies that are based on bird marking. Most such studies are only practical in areas where there are well-established networks of volunteer ringers and birdwatchers. For this reason most such work undertaken to date has been in Europe or North America. There is a very extensive literature on avian population dynamics, life histories and behavioural ecology based on intensive long-term studies of the populations of relatively small study areas (Newton 1998). Such work provides much of the theoretical underpinning for applied studies undertaken at larger spatial scales, but is largely outside the scope of the present review.

PRINCIPLES AND METHODOLOGY

Population dynamics
At its simplest level, population dynamics involves accounting for population changes in terms of births,

* Correspondence author
  Email: stephen.baillie@bto.org

deaths, immigration and emigration (Appendix). Where we are dealing with populations at large spatial scales (*eg* national population indices) it is often reasonable to assume that immigration and emigration will be negligible. Key population dynamics variables can be measured either from intensive local population studies or from extensive programmes involving some combination of censuses, nest recording and ringing.

To understand the causes of population change, it is necessary to measure how individual demographic rates vary in relation to environmental variables and to the abundance of predators, pathogens, and competitors of the same or different species. Competition between individuals of the same species, and sometimes also the impacts of predators and pathogens, give rise to density dependence, which tends to regulate the population around the number of individuals that the environment can support (Newton 1998). Nearly all populations are affected by both density-independent factors (*eg* severe weather mortality, road deaths) and density-dependent ones (*eg* competition for food or nest sites). In general it is the relative strength of these factors that determines whether or not the population fluctuates greatly from year to year. However, density-dependent regulation causes the population to fluctuate around a level set by key environmental resources. When these resources change, as might result from a long-term reduction in food supplies or habitat quality, the average population level will be expected to track changing resource levels rather than to remain constant.

The rigour with which the causes of population declines can be diagnosed depends on what information and resources are available (Caughley 1994, Green 1995). In principle it may be possible to relate spatial or temporal variation in abundance directly to environmental resources, without any measurement of underlying vital rates. However, while this approach may work quite well in straightforward cases, it is unlikely to provide robust predictions where more complex population processes are involved. Environmental variables act directly on vital rates and measuring such relationships directly should improve the chances of identifying key variables and quantifying their effects on abundance (Temple & Wiens 1989, Baillie 1990).

Much of our knowledge of the processes that determine avian abundance is derived from correlative analyses of data from a limited number of long-term population studies, most of which have been carried out at small geographical scales (Perrins *et al* 1991). Such studies are increasingly being complemented by analyses of extensive data gathered at much larger spatial scales, building on the pioneering work of former BTO Directors David Snow (1966), and Raymond O'Connor (1980), which eventually

gave rise to the BTO's Integrated Population Monitoring Programme (Baillie 1990, 2001; Fig 1). The results from such studies should ideally be combined to produce population models that allow the effects of environmental change and management options to be explored, taking account of interactions between key relationships (Potts & Aebischer 1995, Aebischer & Ewald 2004). Where possible, predictions from such field studies and modelling should be tested through experiments. There is now a considerable body of experimental evidence for a range of factors that affect avian abundance and population dynamics (Newton 1998). However, there remain many situations where it is not practical or not ethical to carry out experiments at appropriate spatial scales, making it necessary to rely on evidence from field studies and modelling alone.

Estimating demographic parameters

Survival, recruitment and dispersal rates are normally estimated from studies of marked birds. Two main approaches are used, one based on recoveries of birds that have been killed or found dead and subsequently reported (dead recoveries) and the other on live recaptures or resightings (mark–recapture). There is now a very extensive body of work on these methods (Williams *et al* 2002, Thomson *et al* 2009; proceedings of previous EURING analytical conferences listed at www.euring. org). The main parameters in these models are survival rates, reporting rates and recapture rates. These are generally modelled as some function of time, age, location, environmental covariates and population density. Classes of models involving individual covariates (*eg* body size) are also available. More-complex models may exhibit a wide range of features, including combining both classes of data, movements between subpopulations and transitions between states (*eg* breeders and non-breeders).

Ring recoveries from dead birds normally are modelled as functions of annual survival rates and ring reporting rates. Most of the information about survival is contained in the recovery data, so higher ring reporting rates lead to more precise estimates of survival for a given amount of ringing effort. Historically, there has been a lack of sufficiently detailed information on numbers ringed, leading to the need to conduct analyses under the unrealistic constraint of constant reporting rates within cohorts. This problem is now being addressed through widespread computerisation of ringing data, but it is still an issue for a number of important historical data sets. There is much evidence of recent declines in reporting rates (*eg* Robinson *et al* 2004, Freeman *et al* 2007, Robinson *et al* 2009b), which emphasises both the importance of modelling such changes explicitly and the need to improve reporting rates so as to increase the precision of survival estimates. In North America, reward band studies have been used to estimate
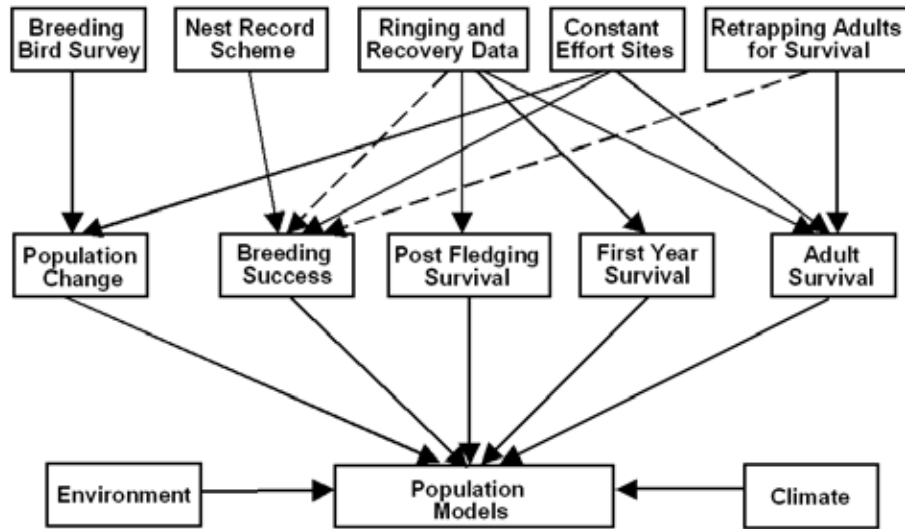
Figure 1. Structure of the BTO's Integrated Population Monitoring Programme (Baillie 1990, 2001). Solid lines indicate the provision of good information for at least some species while broken lines indicate the provision of less-complete information. There is considerable variation in the numbers of species covered by different schemes, and consequently in the numbers of species for which particular vital rates can be estimated.

the proportions of ringed birds encountered by hunters that are reported to the banding lab. These indicate that without rewards only 32% of the rings encountered by hunters were reported (Nichols *et al* 1991). However, the use of a toll-free phone number on bands since 1996 has more than doubled this reporting rate (Tautin *et al* 1999). In the UK, use of a web address on rings has similarly led to a 26% increase in reporting rates and this approach is now being developed throughout Europe.

For the types of studies discussed here, mark–recapture data are normally modelled as functions of survival and recapture rates. A feature of these capture–recapture models is that they cannot distinguish between mortality and permanent emigration from the study area. Thus they provide an estimate of apparent survival which is the joint probability of surviving and not emigrating. Apparent survival is therefore always an underestimation of true survival, but the bias decreases with increasing spatial scale of the study area (Marshall *et al* 2004, Schaub *et al* 2006). These methods are central to the analysis of data from Constant Effort ringing schemes and the Retrapping Adults for Survival (RAS) project (Robinson *et al* 2008, 2009c). A key point arising from such mark–recapture studies is that planned projects with systematic sampling protocols are needed in order to generate high-quality mark–recapture data. For example, the Constant Effort Sites (CES) protocol usually supports models where recapture rates are constant within sites.

Overall recruitment can be estimated from mark–recapture data based on an analysis of reverse capture histories (Pradel 1996). Where a high proportion of

breeding adults can be identified as first-year or adult birds (*ie* EURING age codes 5 or 6), recruitment can also be estimated as the proportion of first-year birds in the breeding population (Snow 1966). Given its relatively straightforward nature, this technique has seen surprisingly little use.

Recruitment can be viewed as the product of productivity and first-year survival, while productivity itself is the product of breeding success per attempt, number of attempts and post-fledging survival. Within integrated population models, overall productivity is often estimated by difference, based on a combined analysis of data on abundance and survival (Robinson *et al* 2004, King *et al* 2008, Baillie *et al* 2009a). An index of productivity can be obtained for standardised proportions of juveniles in the population obtained from constant-effort sites (Robinson *et al* 2009c) or cannon-netting of waders (Clark *et al* 2006). Age ratios from direct observations in the field can be used to measure the productivity of species such as geese. However, population modelling has shown that, while age ratios of Pink-footed Geese *Anser brachyrhynchus* recorded in Britain in autumn are consistent with other measures of the dynamics of this population, those for Greylag Geese *A. anser* substantially underestimate productivity (Frederiksen *et al* 2004). This highlights the importance of validating such data against independent information wherever possible.

Number of fledglings per attempt can be estimated from nest records data and can itself be broken down into its demographic components, usually clutch size, egg survival and nestling or chick survival (Crick *et al* 2003). Estimating

numbers of attempts per season is more difficult, and usually requires intensive studies based on colour-marked birds. However, this is only a serious problem for multi-brooded species. Indications of the overall length of the breeding season can be obtained from data on brood patches, female weights and moult timing of adults caught for ringing at constant-effort sites or in similar studies.

Survival during the immediate post-fledging survival period tends to be low and is difficult to estimate. Studies based on colour-marked or radio-tagged birds are very labour intensive and may have difficulty separating mortality and emigration, particularly once some juveniles start to disperse a few weeks after fledging (Schmidt *et al* 2008). Recovery-based studies require large numbers of nestlings, juveniles and adults to be ringed, combined with an adequate reporting rate (Thomson *et al* 1999, Freeman *et al* 2007).

Development of integrated population models

The initial development of integrated population models for large-scale data involved simple approaches where each vital rate was estimated from a separate analysis, and the demographic parameters were then combined to give a predicted population trajectory. This can then be compared with the population trajectory measured from census data in order to validate the model. In such models some vital rates can be set to their average long-term values, making it possible to determine the extent to which observed variation in individual vital rates is sufficient to explain population declines (Thomson *et al* 1997, Peach *et al* 1999). An alternative approach to such analyses is to calculate correlations between population growth rate and each individual demographic parameter. Where data are insufficient to provide annual estimates of each demographic parameter it is possible to calculate estimates for blocks of years identified through an analysis of turning points in the population trajectory (Siriwardena *et al* 1998, Robinson *et al* 2004).

More recently, a fully integrated approach to the analysis of such data on population dynamics has been developed. This normally involves the development of a state-space model which incorporates an observation process to account for observation error in the census data and a system process where population changes are a consequence of the underlying demographic rates (Appendix). Using this approach, information about all underlying demographic rates that is included in the population census data can be exploited because it is combined with information about single demographic rates stemming from independent data (*eg* ring recoveries). Model parameters can then be estimated by maximising the resulting joint likelihoods using the Kalman Filter

(Besbeas *et al* 2002) or by drawing samples from the joint posterior distribution of these likelihoods (and non-informative prior distributions) using Bayesian methods (Brooks *et al* 2004, Schaub *et al* 2007). A major advantage of these techniques is that they make the most efficient use of all of the available data under the assumption that all data are samples from the same population. It results in increased precision of parameter estimates which in turn enhances the power to detect relationships between demographic and environmental variables. It also allows variability in the population changes to be quantified (as the observation 'error' is partitioned out), which may be important in understanding the adaptability of populations to environmental change (Lande *et al* 2003). Using Bayesian techniques it is straightforward to derive estimates and credible intervals for correlations between population growth rates and individual vital rates, allowing the contribution of each vital rate to the overall population trend to be evaluated (Brooks *et al* 2004, Baillie *et al* 2009a). Integrated modelling methods also allow the support for a wide range of different models to be evaluated, using AIC, BIC or reversible jump MCMC (King *et al* 2008, Baillie *et al* 2009a).

One difficulty in identifying the contributions of different demographic rates to population change is that, where a demographic rate is density dependent, changes may be masked by the compensatory effects of the density dependence (Green 1999a). Thus while a density-independent demographic rate responsible for a population decline is likely to show a pronounced long-term change, a density-dependent rate may only show a very brief reduction that would be difficult to detect from monitoring data. Thus there is a need for more attention to be given to models that incorporate density dependence.

To date most such integrated models of population dynamics have focused on the estimation of population growth rates, demographic parameters and the relationships between them. Such models are useful for identifying the demographic causes of previous population changes but they are not well suited to predicting future population levels. Future work should give greater attention to the effects of environmental factors, particularly climate and habitat, and of density dependence, so as to produce models with greater predictive capability. In developing such models it will be desirable to give greater attention to spatial variation in population dynamics.

Large-scale integrated analyses of population dynamics have tended to focus either on a limited number of specific study sites thought to be representative of a wider population (Peach *et al* 1995, Grøtan *et al* 2009) or on extensive data gathered across a very large area such as the whole of Britain (Siriwardena *et al* 1999, Freeman &

Crick 2003, Robinson *et al* 2004). Small-scale studies can be challenging, because immigration into and emigration from the study area have to be modelled in addition to survival and fecundity (Abadi *et al* unpublished[3]). Where there are sufficient data, comparisons of population dynamics between regions can reveal large-scale variation in demographic processes (Freeman *et al* 2007). However, a potentially much more powerful approach is to develop spatio-temporal models of variation in demographic rates (Paradis *et al* 2000, Royle & Dorazio 2008).

CASE STUDIES

Declines in farmland bird populations

In the UK and throughout much of Europe, declines in farmland bird populations have become a major conservation issue. Some species, particularly Corncrake *Crex crex*, Stone-curlew *Burhinus oedicnemus* and Cirl Bunting *Emberiza cirlus* have small UK populations for which it has been possible to develop effective recovery programmes through carefully targeted agri-environment schemes. Understanding how demography is influenced by agricultural practices has been important in formulating effective management plans for these species (Evans *et al* 1997, Green & Hirons 1991, Green 1999b, 2008).

Many declines of widespread species started as early as the mid 1970s, but it took a long time for their significance to be recognised. Reversing these changes is much more challenging because it requires modification of agricultural management practices over large parts of the countryside. The first stage in this process has been the successful identification of many of the demographic 12

The UK Government has adopted a target to reverse the declines of farmland bird species by 2020, based on trends in 20 farmland bird species that make up the farmland bird indicator (Gregory *et al* 2004). The main delivery mechanism is the Entry Level Stewardship agri-environment scheme (ELS) which provides a broad range of prescriptions suited to the majority of farmland. A novel demographic modelling approach has been used to assess the level of take-up of particular options that is likely to be required to reverse the declines of individual farmland bird species (Siriwardena & Vickery 2003, Vickery *et al* 2008).

Relationships between the proportion of the population within ELS management and demographic rates were modelled and compared with estimates of the changes in key demographic rates required to increase population size. These models were then combined with estimates of the

[3]**Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M.** Estimation of immigration rate using integrated population models (unpublished manuscript).

effects of specific ELS options on key demographic rates to assess the levels of uptake of particular combinations of options that will be needed to achieve population recovery. ELS was predicted to have the desired effect on most of its target species but there were five species for which current management prescriptions require further development. Despite a number of limitations of the models and data (Siriwardena & Vickery 2003, Vickery *et al* 2008), this work clearly illustrates the applied value of understanding links between management prescriptions, demographic processes and population changes.

Population dynamics of Afro-Palaearctic migrants

It is self evident that the abundance of migratory populations is likely to be affected by processes operating during passage periods and in the wintering areas, as well as on the breeding grounds (Newton 2007). The first key use of ringing data within such studies is to aid identification of the passage and wintering areas of different populations. Such information allows population changes measured on the breeding grounds to be related to environmental conditions in the passage and wintering areas (Baillie & Peach 1992), as well as providing a starting point for population-specific studies of passage and winter ecology. While there are often reasonably good data on the passage areas used by different European populations (Wernham *et al* 2002, Cepák *et al* 2008), information on the African wintering grounds is often very sparse. For larger species such information can now be obtained from satellite tracking and there is increased impetus to develop a range of tracking devices for smaller birds (Fiedler 2009) as well as use of intrinsic markers such as stable isotopes and trace elements (Coiffait *et al* 2009).

A second key use of ringing data is to estimate annual survival rates for breeding populations that can then be correlated with environmental conditions on the wintering grounds. There is a growing body of evidence that the population dynamics of many species wintering in the Sahel region is influenced strongly by winter conditions in that area (Cavé 1983, Peach *et al* 1991, Baillie & Peach 1992, Eraud *et al* 2009). For White Storks *Ciconia ciconia* breeding in eastern Germany and Poland, variation in primary production at one key area in the eastern Sahel visited from October to November explains 88% of annual variation in survival (Schaub *et al* 2005). Thus for some migratory species it appears that population fluctuations can be driven by conditions during short but critical periods of the annual cycle. While many of the strongest relationships reported to date relate to populations wintering in the Sahel region, survival of species wintering in other areas is also related to weather conditions on the wintering grounds. Data from the RAS scheme show

that three species of hirundines wintering in different parts of Africa all show relationships with winter weather conditions (Robinson *et al* 2008).

However, factors operating on the breeding grounds may also be important, and these relationships may also differ between populations. For example the survival of Hungarian Sand Martins *Riparia riparia* is positively related to Sahel rainfall in their wintering areas (Szép 1995). British Sand Martins also show such relationships but they show a stronger negative relationship between breeding-season rainfall and survival (Cowley & Siriwardena 2005). Increased summer rainfall is thought to reduce the availability of insects on which these birds feed. Ringing will continue to play a key role in future research on Afro-Palaearctic migrants, which needs to focus on ecological processes operating on wintering and passage areas and on building integrated models of the population dynamics of key species.

Adaptive harvest management

Effective management for sustainable harvesting of populations that are hunted needs to be based on a good understanding of the population dynamics of the species concerned (Aebischer *et al* 1999, Baillie 2001). Autumn and winter hunting inevitably causes an immediate increase in mortality but this may be partially or entirely compensated by changes in density-dependent mortality later in the same season or by density-dependent compensation at other stages of the annual cycle. To obtain a maximum sustainable yield it is generally necessary to maintain a stable population at a level well below that which it would achieve in the absence of harvesting. Thus the management required to maximise harvests may often be different to that required to maximise population size.

Management must usually be based on incomplete knowledge of the population being harvested, and of the most appropriate models for describing its dynamics. Large-scale experiments based on manipulation of hunting regulations would be the most rigorous way to increase knowledge of the dynamics of hunted populations, but this is rarely practical either politically or logistically. Since 1995 a novel approach to the management of hunted populations in the presence of uncertainty has been operated in North America, initially for mid-continent Mallard *Anas platyrhynchos* populations (Nichols *et al* 2007). Management decisions are based on a set of (in this case four) competing models of the effects of hunting on harvest and population size. These models have weights which sum to 1 and which represent the relative degree of belief in each model. Each year monitoring data on variables such as population size, harvest, survival and reproduction are collected and used to update current belief in the alternative models via the model weights. The updated models are

then used to make predictions that form a basis for setting the next season's hunting regulations. Thus regulations are based on the most up-to-date understanding of the system, and the effects of varying the hunting regulations feed into increased knowledge of the system. The system is considered to have been successful, particularly in getting managers and ecologists working more closely together and in focusing debates about management options onto the underlying biological processes (Nichols *et al* 2007).

A large-scale banding programme is a key element of the monitoring that underpins adaptive harvest management of Mallard in North America, as this provides key estimates of harvest and survival rates. Other monitoring, including breeding counts and hunting-bag surveys, is also required to provide a reasonably complete picture of the dynamics of the system. Overall, the approach is thought to have worked well and is likely to be extended to a range of other waterfowl species (Nichols *et al* 2007). Much waterfowl hunting also takes place in Europe, but pan-European monitoring of the vital rates of waterfowl is needed to support more effective harvest management (Elmberg *et al* 2006).

The approach used in adaptive harvest management is applicable to a much wider range of conservation and management problems (Williams *et al* 2009). For example, in the case of farmland bird recovery programmes discussed above it could be used to develop more effective agri-environment schemes in the context of improving understanding of the effects of large-scale habitat management on the population dynamics of farmland birds.

FUTURE DIRECTIONS

A first priority is to continue to build on the successful development of Integrated Population Monitoring and modelling over the last 20 years, maintaining long-term and large-scale studies, enhancing databases and applying the latest analytical techniques. Over the next five to ten years such studies are likely to have particular emphasis on identifying the demographic mechanisms for declines amongst Afro-Palaearctic migrants. Studies to evaluate and predict the effects of global climate change will also be a priority. Demographic monitoring can never be comprehensive and it is important to ensure continuing long-term data collection for key species and that, as far as is practical, these species include a reasonably representative set of ecologies and life histories.

More emphasis should be given to the development of well-designed population studies undertaken at a representative set of sites, building on the success of CES schemes and the BTO's RAS projects and using new technologies for tracking marked individuals to increase the

range and quality of data (Baillie *et al* 2009b, Fiedler 2009). There should be a continuing effort to improve the quality of the habitat and environmental data that can be used for these studies, both by collecting better measurements in the field and through links to complementary data sets.

Long-term studies have had considerable success in identifying the main life-cycle stages responsible for population declines. However, much less work has focused on identifying the time of year at which the critical population processes take place. This is particularly important for migrants, where conservation action should be guided by knowledge of the way in which critical population processes are distributed between the breeding, passage and wintering grounds (Runge & Marra 2005). Pioneering work on neotropical migrants has shown that, where long-distance migrants are reasonably site faithful during the winter, much useful information can be obtained by conducting mark–recapture studies on the breeding and wintering grounds (Sillett & Holmes 2002). Where birds are resident, or populations can be followed through most of the year, estimation of seasonal survival rates should be more straightforward (Frederiksen *et al* 2004) and RAS projects can be structured to provide this type of information (Robinson *et al* 2009d). Nevertheless, such studies remain rare and should be a priority for future work.

Future integrated population models should adopt a more process-oriented approach, with greater emphasis on key environmental variables, seasonal variation in vital rates and density dependence. This should result in more-predictive models that can be used to explore the implications of alternative climate and land-use scenarios. For many species, developing such models may be impossible using classical approaches alone, because long-term time-series of environmental variables may not be available and density dependence is sometimes difficult to estimate from long-term demographic data. An alternative approach to demographic modelling has been to develop individual-based models (Norris 2004, Goss-Custard & Stillman 2008). In this approach, behavioural relationships based on foraging observations and other relevant behavioural data are used to derive key population-level relationships such as density-dependent functions, which are then fed into population models. Both individual-based models and those based on long-term demographic data have particular strengths and weaknesses and are best regarded as complementary approaches. More work is needed to combine these methods so as to make the best use of data from both sources. The emergence of Bayesian techniques for integrated population modelling provides a natural framework for integrating such techniques at an analytical level.

Most integrated population analyses to date have been based on particular study populations or on the populations of individual regions or countries considered as a single unit. A natural extension of this approach is to examine spatial variation in both abundance and the demographic processes that bring it about (Paradis *et al* 2000, Royle & Dorazio 2008). Such analyses immediately offer increased power to explore a range of questions about population dynamics. However, they also introduce additional methodological issues, because it is necessary to account for spatial variation in nuisance parameters such as detectability and ring reporting rates. Nevertheless we expect greatly increased emphasis on such spatio-temporal modelling approaches over the next ten years.

There is much interest in determining how landscapes can be better designed to support biodiversity, with a recent emphasis on approaches that could mitigate some of the predicted effects of global climate change (Opdam & Wascher 2004). Many populations are profoundly influenced by habitat structure at the landscape scale (Hinsley *et al* 1996, Freckleton *et al* 2005, Dolman *et al* 2007) and are best viewed as metapopulations whose overall dynamics are determined by processes operating within patches and by dispersal between patches. To date, most of the work in this area has involved modelling relationships between distributions, abundances and landscape features. Studies of marked birds can potentially enhance these approaches by providing direct measurements of the vital rates of birds living within different classes of habitat patches and information on movements between patches (Matthysen *et al* 1995, Baillie *et al* 2000). New tracking technologies will increase the extent to which the use of space by individuals and its consequences for survival and reproduction can be followed in detail. This in turn will allow the development of more-refined models of meta-population dynamics, building on the approaches described above. Carefully structured projects coordinated through Ringing Schemes could make a significant contribution to our understanding of the dynamics of avian metapopulations at the landscape scale, and hence to biodiversity conservation within the wider countryside.

ACKNOWLEDGEMENTS

The National Parks and Wildlife Service (Republic of Ireland) and the ringers themselves. We thank all of these individuals and organisations for their ongoing support for the development of bird ringing as a key component of Integrated Population Monitoring. Rob Robinson and Chris Redfern provided helpful comments on the draft manuscript.

REFERENCES

Aebischer, N.J. & Ewald, J.A. (2004) Managing the UK Grey Partridge *Perdix perdix* recovery: population change, reproduction, habitat and shooting. *Ibis* **146** (suppl. 2), 181–191.

Aebischer, N.J., Potts, G.R. & Rehfisch, M.M. (1999) Using ringing data to study the effects of hunting on bird populations. *Ringing & Migration* **19** (suppl.), S67–81.

Baillie, S.R. (1990) Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis* **132**, 151–166.

Baillie, S.R. (2001) The contribution of ringing to the conservation and management of bird populations: a review. *Ardea* **89** (special issue), 167–184.

Baillie, S.R. & Peach, W.J. (1992) Population limitation in Palaearcti–African migrant passerines. *Ibis* **134** (suppl. 1), 120–132.

Baillie, S.R., Sutherland, W.J., Freeman, S.N., Gregory, R.D. & Paradis, E. (2000) Consequences of large-scale processes for the conservation of bird populations. *Journal of Applied Ecology* **37** (suppl. 1), 88–102.

Baillie, S.R., Brooks, S.P., King, R. & Thomas, L. (2009a) Using a state-space model of the British Song Thrush *Turdus philomelos* population to diagnose the causes of a population decline. In *Modeling Demographic Processes in Marked Populations* (eds Thomson, D.L., Cooch, E.G. & Conroy, M.J.), pp. 541–561. Springer, New York.

Baillie, S.R., Robinson, R.A., Clark, J.A. & Redfern, C.P.F. (2009) From individuals to flyways: the future of marking birds for conservation. *Ringing & Migration* **24**, 155–161.

Besbeas, P., Freeman, S.N., Morgan, B.J.T. & Catchpole, E.A. (2002) Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. *Biometrics* **58**, 540–547.

Brooks, S.P., King, R. & Morgan, B.J.T. (2004) A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* **27**, 515–529.

Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation.* Sinauer Associates, Sunderland, Massachusetts.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology* **63**, 215–244.

Cavé, A.J. (1983) Purple Heron survival and drought in tropical West Africa. *Ardea* **71**, 217–224.

Cepák, J., Klvaňa, P., Škopek, L., Schröpfer, L., Jelínek, M., Hořák, D., Formánek, J. & Zárybnický, J. (2008) *Czech and Slovak bird migration atlas.* Aventinum, Prague.

Clark, J.A., Robinson, R.A., Clark, N.A. & Atkinson, P.W. (2006) Measuring wader recruitment. In *Waterbirds around the world* (eds Boere, G.C., Galbraith, C.A. & Stroud, D.A.), pp 488–489. The Stationery Office, Edinburgh.

Coiffait, L., Redfern, C.P.F., Bevan, R.M., Newton, J. & Wolff, K. (2009) The use of intrinsic markers to study bird migration. *Ringing & Migration* **24**, 169–174.

Cowley, E. & Siriwardena, G.M. (2005) Long-term variation in survival rates of Sand Martins *Riparia riparia*: dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study* **52**, 237–251.

Crick, H.Q.P., Baillie, S.R. & Leech, D.I. (2003) The UK Nest Record Scheme: its value for science and conservation. *Bird Study* **50**, 254–270.

Dolman, P.M., Hinsley, S.A., Bellamy, P.E. & Watts, K. (2007) Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis* **149**, 146–160.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Gibbons, D.W., Evans, A. & Gregory, R.D. (2009) Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds* **102**, 296–341.

Elmberg, J., Nummi, P., Pöysä, H., Sjöberg, K., Gunnarsson, G., Clausen, P., Guillemain, M., Rodrigues, D. & Väänänen, V.-M. (2006) The scientific basis for new and sustainable management of migratory European ducks. *Wildlife Biology* **12**, 121–127.

Eraud, C., Boutin, J.-M., Rivière, M., Brun, J., Barbraud, C. & Lormée, H. (2009) Survival of Turtle Doves *Streptopelia turtur* in relation to western Africa environmental conditions. *Ibis* **151**, 186–190.

Evans, A.D., Smith, K.W., Buckingham, D.L. & Evans, J. (1997) Seasonal variation in breeding performance and nestling diet of Cirl Buntings *Emberiza cirlus* in England. *Bird Study* **44**, 66–79.

Fiedler, W. (2009) New technologies for monitoring bird migration and behaviour. *Ringing & Migration* **24**, 175–179.

Freckleton, R.P., Gill, J.A., Noble, D.G. & Watkinson, A.R. (2005) Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. *Journal of Animal Ecology* **74**, 353–364.

Frederiksen, M., Hearn, R.D., Mitchell, C., Sigfússon, A., Swann, R.L. & Fox, A.D. (2004) The dynamics of hunted Icelandic goose populations: a reassessment of the evidence. *Journal of Applied Ecology* **41**, 315–334.

Freeman, S.N. & Crick, H.Q.P. (2003) The decline of the Spotted Flycatcher *Muscicapa striata* in the UK: an integrated population model. *Ibis* **145**, 400–412.

Freeman, S.N., Robinson, R.A., Clark, J.A., Griffin, B.M. & Adams, S.Y. (2007) Changing demography and population decline in the Common Starling *Sturnus vulgaris*: a multisite approach to Integrated Population Monitoring. *Ibis* **149**, 587–596.

Goss-Custard, J.D. & Stillman, R.A. (2008) Individual-based models and the management of shorebird populations. *Natural Resource Modelling* **21**, 3–71.

Gregory, R.D., Noble, D.G. & Custance, J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* **146** (suppl. 2), 1–13.

Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009) An indicator of the impact of climate change on European bird populations. *PLoS ONE* **4**, e4678.

Green, R.E. (1995) Diagnosing the causes of bird population declines. *Ibis* **137** (suppl.), S47–S55.

Green, R.E. (1999a) Applications of large-scale studies of demographic rates to bird conservation. *Bird Study* **46** (suppl.), S279–288.

Green, R.E. (1999b) Survival and dispersal of male Corncrakes *Crex crex* in a threatened population. *Bird Study* **46** (suppl.), S218–229.

Green, R.E. (2008) Demographic mechanism of a historical bird population collapse reconstructed using museum specimens. *Proceedings of the Royal Society B* **275**, 2381–2387.

Green, R.E. & Hirons, G.J.M. (1991) The relevance of population studies to the conservation of threatened birds. In *Bird Population Studies: Relevance to Conservation and Management* (eds Perrins, C.M., Lebreton, J.-D. & Hirons, G.J.M.), pp 594–633. Oxford University Press, Oxford.

Grøtan, V., Sæther, B.-E., Engen, S., van Balen, J.H., Perdeck, A.C. & Visser, M.E. (2009) Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations. *Journal of Animal Ecology* **78**, 447–459.

Grüebler, M., Schuler, H., Müller, M., Spaar, R., Horch, P. & Naef-Daenzer, B. (2008) Female-biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biological Conservation* **141**, 3040–3049.

Hinsley, S.A., Pakeman, R.J., Bellamy, P.E. & Newton, I. (1996) Influence of habitat fragmentation on bird species distributions and regional population sizes. *Proceedings of the Royal Society of London Series B* **263**, 307–313.

King, R., Brooks, S.P., Mazzetta, C., Freeman, S.N. & Morgan, B.J.T. (2008) Identifying and diagnosing population declines: a Bayesian assessment of Lapwings in the UK. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **57**, 609–632.

Lande, R., Engen, S. & Saether, B.-E. (2003) *Stochastic population dynamics in ecology and conservation.* Oxford University Press, Oxford.

Marshall, M.R., Diefenbach, D.R., Wood, L.A. & Cooper, R.J. (2004) Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: designs that may help. *Animal Biodiversity and Conservation* **27**, 59–72.

Matthysen, E., Adriaensen, F. & Dhondt, A.A. (1995) Dispersal distances of nuthatches, *Sitta europaea,* in a highly fragmented forest habitat. *Oikos* **72**, 375–381.

Newton, I. (1998) *Population limitation in birds.* Academic Press, London.

Newton, I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**, 579–600.

Newton, I. (2007) *The migration ecology of birds.* Academic Press, London.

Nichols, J.D., Blohm, R.J., Reynolds, R.E., Trost, R.E., Hines, J.E. & Bladen, J.P. (1991) Band reporting rates for Mallards with reward bands of different dollar values. *Journal of Wildlife Management* **55**, 119–126.

Nichols, J.D., Runge, M.C., Johnson, F.A. & Williams, B.K. (2007) Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. *Journal of Ornithology* **148** (suppl. 2), S343–S349.

Norris, K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining population paradigm. *Journal of Applied Ecology* **41**, 413–426.

O'Connor, R.J. (1980) Pattern and process in Great Tit *Parus major* populations in Britain. *Ardea* **68**, 165–183.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117**, 285–297.

Paradis, E., Baillie, S.R., Sutherland, W.J., Dudley, C., Crick, H.Q.P. & Gregory, R.D. (2000) Large-scale spatial variation in the breeding performance of song thrushes *Turdus philomelos* and blackbirds *T. merula* in Britain. *Journal of Applied Ecology* **37** (suppl. 1), 73–87.

Peach, W., Baillie, S. & Underhill, L. (1991) Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis* **133**, 300–305.

Peach, W.J., Crick, H.Q.P. & Marchant, J.H. (1995) The demography of the decline in the British willow warbler population. *Journal of Applied Statistics* **22**, 905–922.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. (1999) Long-term changes in over-winter survival rates explain the decline of Reed Buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology* **36**, 798–811.

Perrins, C.M., Lebreton, J.-D. & Hirons, G.J.M. (1991) *Bird population studies: relevance to conservation and management.* Oxford University Press, Oxford.

Potts, G.R. & Aebischer, N.J. (1995) Population dynamics of the Grey Partridge *Perdix perdix* 1793–1993: monitoring, modelling and management. *Ibis* **137** (suppl. 1), 29–37.

Pradel, R. (1996) Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.

Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology* **73**, 670–682.

Robinson, R.A., Balmer, D.E. & Marchant, J.H. (2008) Survival rates of hirundines in relation to British and African rainfall. *Ringing & Migration* **24**, 1–6.

Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfisch, M.M., Sims, D.W., Santos, M.B., Sparks, T.H., Stroud, D.A. & Visser, M.E. (2009a) Travelling through a warming world: climate change and migratory species. *Endangered Species Research* **7**, 87–99.

Robinson, R.A., Grantham, M.J. & Clark, J.A. (2009b) Declining rates of ring reporting in common British birds. *Ringing & Migration* **24** (in press).

Robinson, R.A., Julliard, R. & Saracco, J.F. (2009c) Constant effort: studying avian population processes using standardised ringing. *Ringing & Migration* **24**, 199–204.

Robinson, R.A., Kew, J.J. & Kew, A.J. (2009d) Survival of suburban blackbirds *Turdus merula* varies seasonally but not by sex. *Journal of Avian Biology* (in press).

Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities.* Academic Press, London.

Runge, M.C. & Marra, P.P. (2005) Modeling seasonal interactions in the population dynamics of migratory birds. In *Birds of Two Worlds: the ecology and evolution of migration* (eds Greenberg, R. & Marra, P.P.), pp 375–389. Johns Hopkins University Press, Baltimore.

Schaub, M., Kania, W. & Köppen, U. (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology* **74**, 656–666.

Schaub, M., Ullrich, B., Knötzsch, G., Albrecht, P. & Meisser, C. (2006) Local population dynamics and the impact of scale and isolation: a study on different little owl populations. *Oikos* **115**, 389–400.

Schaub, M., Gimenez, O., Sierro, A. & Arlettaz, R. (2007) Use of integrated modelling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology* **21**, 945–955.

Schmidt, K.A., Rush, S.A. & Ostfeld, R.S. (2008) Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology* **77**, 830–837.

Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**, 296–308.

Siriwardena, G.M. & Vickery, J.A. (2003) Population modelling. In *Predicting the Response of Farmland Birds to Agricultural Change.* (eds Aebischer, N.J., Bradbury, R., Eaton, M., Henderson, I.G., Siriwardena, G.M. & Vickery, J.A.), pp 13–48. BTO Research Report 289. British Trust for Ornithology, Thetford.

Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1998) Variation in the survival rates of British farmland passerines with respect to their population trends. *Bird Study* **45**, 276–292.

Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis* **141**, 621–636.

Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. & Wilson, J.D. (2000a) The importance of variation in the breeding performance of seed-eating birds for their population trends on farmland. *Journal of Applied Ecology* **37**, 1–22.

Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., Wilson, J.D. & Gates, S. (2000b) The demography of lowland farmland birds. In *Ecology and Conservation of Lowland Farmland Birds* (eds Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A.), pp 117–133. British Ornithologists' Union, Tring.

Snow, D.W. (1966) Population dynamics of the Blackbird. *Nature (London)* **211**, 1231–1233.

Szép, T. (1995) Survival rates of Hungarian Sand Martins and their relationship with Sahel rainfall. *Journal of Applied Statistics* **22**, 891–904.

Tautin, J., Metras, L. & Smith, G. (1999) Large-scale studies of marked birds in North America. *Bird Study* **46** (suppl.), S271–278.

Temple, S. & Wiens, J. (1989) Bird populations and environmental change: can birds be bioindicators. *American Birds* **43**, 260–270.

Thomson, D.L., Baillie, S.R. & Peach, W.J. (1997) The demography and age-specific annual survival of British Song Thrushes *Turdus philomelos* during periods of population stability and decline. *Journal of Animal Ecology* **66**, 414–424.

Thomson, D.L., Baillie, S.R. & Peach, W.J. (1999) A method for studying post-fledging survival rates using ringing recoveries. *Bird Study* **46** (suppl.), 104–111.

Thomson, D.L., Cooch, E.G. & Conroy, M.J. (2009) *Modeling demographic processes in marked populations.* Environmental and Ecological Statistics Series, Volume 3. Springer, New York

Vickery, J., Chamberlain, D., Evans, A., Ewing, S., Boatman, N., Pietravalle, S., Norris, K. & Butler, S. (2008) *Predicting the impact of future agricultural change and uptake of Entry Level Stewardship on farmland birds.* BTO Research Report 485. British Trust for Ornithology, Thetford.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds) (2002) *The Migration Atlas: movements of the birds of Britain and Ireland.* T. & A.D. Poyser, London.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations.* Academic Press, San Diego.

Williams, B.K., Szaro, R.C. & Shapiro, C.D. (2009) *Adaptive Management: the U.S. Department of the Interior Technical Guide.* Adaptive Management Working Group, US Department of the Interior, Washington, DC.

APPENDIX – ACCOUNTING FOR POPULATION CHANGE

For a typical passerine bird that starts breeding at age one we have:

$$N_{t+1} = 0.5 N_t F_t B_t S_{p,t} S_{f,t} + N_t S_{a,t}$$

where:

N_t is the number of adult females alive in year t

F_t is the number of fledglings per nesting attempt in year t

B_t is the number of nesting attempts per female in year t

$S_{p,t}$ is post-fledging survival (to late summer) in year t

$S_{f,t}$ is first-year survival from years t to t+1

$S_{a,t}$ is adult survival from years t to t+1

For simplicity this equation is written in terms of females and assumes a 1:1 sex ratio amongst fledglings. Note that the first set of terms on the right-hand side can potentially be replaced by a single recruitment rate, but with inevitable loss of detail concerning the underlying demographic processes. Such models can readily be extended to more complex matrix models incorporating delayed start of first reproduction and age-, sex- or group-specific variation in fecundity and survival (Caswell 2001).