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Constant effort: studying avian population processes using standardised ringing

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Bird ringing has played a central role in the study of avian populations, both through providing data and in stimulating the development of analytical methods. Constant-effort (CE) ringing provides an effective way of monitoring bird populations through standardising ringing effort. In Britain & Ireland CE ringing began in the early 1980s, and CE schemes now operate in nearly twenty countries across two continents where they provide annual information on abundance, productivity and survival for a range of common passerine birds. CE schemes fulfill three aims: to monitor demographic rates in bird populations; to establish links between these demographic rates and population changes and environmental conditions; and to inform habitat management to conserve populations. We give examples of how CE ringing has been used to address these objectives and briefly discuss possibilities for future developments that will further enhance the value of CE data.

The use of marked individuals to study animal populations has a long history in ecology and bird ringing has played a central role in this story. Although many early bird ringing studies were largely concerned with studying site fidelity and migration, attention soon shifted to estimating population size. Yet, because birds and other animals can be hard to detect and seldom stay still, estimating population size, in all but the simplest of cases is one of the hardest tasks a wildlife biologist is asked to do (Seber & Schwarz 2002). Population change on the other hand is often easier to calculate, and can provide information that is more useful to the population manager. Rates of population change, however, are only half of the story; one needs to determine causes of change to manage populations effectively (Baillie 1990, DeSante *et al* 2005a). Three vital rates drive population change: birth rate (productivity), survival (or mortality) rate and, when the study population is a subset of a larger one, dispersal (immigration/emigration) rates. Monitoring of these vital rates (demographic monitoring) shifts focus from the population pattern to the underlying process and should provide greater accuracy and sensitivity in detecting the impacts of environmental change (Temple & Wiens 1989, Baillie 2001).

Demographic monitoring of many bird species can be accomplished effectively with bird ringing. Indeed, application of capture–recapture models to bird ringing data is the only reliable method of obtaining estimates of survival and dispersal in wild bird populations. By standardising field methods and capture effort of bird-ringing studies among sites and between years, estimation and indexing of demographic parameters can be greatly facilitated. Such standardisation provides the basis of national and international constant-effort (CE) ringing programmes. Here we provide a brief overview of CE ringing, highlight important insights that have been gained from broad-scale co-operative CE ringing studies, and briefly outline future applications that will enhance the utility of CE data.

CONSTANT-EFFORT RINGING: AN OVERVIEW

In Britain & Ireland CE ringing as a means of monitoring bird populations began in the late 1960s when ringers, mostly unpaid volunteers, began to consider how to increase the value of their ringing; standardising mist-netting effort was one obvious way in which to do so. Much of this interest stemmed from the possibility of using CE ringing to monitor breeding population size, particularly of species and habitats not well covered by the (then relatively new) Common Birds Census. Initially, such sites were largely operated independently, but the value in combining data was soon realised, both by pooling data and in the opportunity to look at processes at larger spatial scales. In the late 1970s a national CE scheme was proposed by the

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BTO and a pilot scheme (1981–86) initiated. This was run by a volunteer (Mike Boddy), and drew on experiences from pre-existing sites to formulate a widely applicable protocol. The CE Sites (CES) scheme was formally adopted as part of the BTO's Integrated Population Monitoring Programme in 1986 (Peach *et al* 1996), though sufficient data are available since 1983. Subsequently, CE ringing schemes started in at least 15 European countries (co-ordinated through EURING) and in North America (DeSante *et al* 1995). At around the same time as CE ringing was being developed in Britain & Ireland, a scheme was initiated in Germany/Austria at three sites (Mettnau, Reit and Illmitz: MRI) using year-round CE ringing and this provided some of the first evidence for declines in migratory bird populations (Berthold *et al* 1986).

CE programmes can operate at large spatial scales because they rely heavily on volunteer input and so can gather detailed demographic data in a cost-effective way. Such programmes work towards three complementary and interlinked goals:

1. Monitoring – to provide long-term estimates or indices of abundance, productivity and survival in a range of common species, usually in concert with other monitoring schemes.
2. Research – to investigate the contribution of different demographic rates in determining population dynamics and their relationship with various ecological and environmental drivers.
3. Management – to understand how habitat may best be managed in conserving local populations.

CE capture–recapture data fulfill these functions by providing information on productivity; recruitment, *ie* number of new adult birds entering the breeding population, and adult survival. Recruitment combines aspects of both productivity and overwinter survival of first-year birds; thus, by examining patterns of recruitment, survival, and productivity measured at the same set of sites, we gain unique insights into the relative importance of drivers acting on each of the different life-cycle stages in determining population change (Julliard 2004, Saracco *et al* 2008). This can be essential for designing conservation and management plans that can reverse population declines and maintain healthy populations, as it identifies the key stages affecting population change and narrows the range of environmental factors to be considered; data from CE sites have been critical in this regard, and will continue to be so.

In the space available it is not possible to mention all the results that have been generated by CE ringing schemes; rather, we give a small selection below, highlighting the broad range of information that may be gathered.

METHODS

Methods of operation and analysis for the various CE schemes are well described elsewhere (DeSante *et al* 1995, Peach *et al* 1996, 1998, Julliard 2004, Balmer *et al* 2004, Robinson *et al* 2007), so we provide only a brief outline here.

Most national CE schemes monitor populations of breeding birds and follow a protocol largely based on that of the BTO's CES scheme. The breeding season (May to August, though this varies with latitude) is divided into a number of equal periods (often 12), typically of *c* 10 days duration, with ringers operating a catching session in each period. In most cases, mist-nets are erected from dawn for about six hours which represent the peak catching period, but there is some variation between sites and schemes. In France a reduced effort scheme is operated, with 3–5 visits between May and mid July; this means a greater number of sites can be operated (40% of ringers participate at over 160 sites) but the extent to which information (especially on productivity) is lost has not yet been evaluated. Inevitably, some visits are missed due to adverse weather conditions or a shortage of manpower, in most schemes some missing visits are tolerated at the analytical stage, though too many cause the site to be excluded for that year. In practice, the frequency of missing visits is small (*eg* in Britain & Ireland *c* 4%) and their impact, at least on the calculation of abundance and productivity indices, appears to be small (Miles *et al* 2007).

Most CE sites are situated in thorn scrub or marsh/reedbed, but woodland, farmland and garden sites are also

Table 1. Habitats in which CE sites are operated in some European schemes. For each scheme, the number of sites that have contributed (not necessarily in all years) is given, and the percentage of sites in each habitat.

	Sites (n)	Reedbed (%)	Wet scrub (%)	Dry scrub (%)	Farmland (%)	Garden (%)	Woodland (%)
Catalonia, Spain	58	0	61	16	0	12	11
Finland	90	45	15	34	0	2	0
Germany	47	19	15	28	12	0	26
The Netherlands	65	25	32	9	3	11	20
Britain & Ireland	421	21	30	36	0	0	13

operated (Table 1). In most European countries sites are generally operated by volunteers. In North America, the Monitoring Avian Productivity and Survivorship scheme (MAPS) run by the Institute for Bird Populations (IBP) follows a similar protocol to the CES scheme, and indeed was very much inspired by it (DeSante *et al* 1995). This continent-wide scheme has operated since 1989 and has a much higher professional input than most European schemes. The current MAPS programme includes 400–500 sites (with 20% operated by IBP personnel) that are operated annually in a wider range of habitats than in European schemes. Both the MAPS and French scheme include a degree of standardisation in net placement within the site according to a formal sampling plan, though how much this improves estimates over the more subjective placements in other schemes has not been assessed.

Annual indices of abundance and productivity from the CE capture data can be calculated using a generalised linear model approach, whereby the number of birds caught or the ratio of juveniles to adults can be modelled in response to categorical site and year variables (Peach *et al* 1998, Robinson *et al* 2007). In each case, missing visits can be corrected by comparison to years in which all visits were completed (Peach *et al* 1998, Cave *et al* 2009). R scripts implementing these methods are available from the correspondence author for this paper (RAR).

For adult birds, which usually return to the same site to breed, the pattern of recaptures of individuals between years can provide estimates of both survival and recruitment rates. Dispersal of juvenile birds is much greater than that of adults and this cannot be separated from mortality: in both cases the individual is not available for capture, so apparent return rates are much lower than the 'true' survival rate. A major benefit of CE ringing is that recapture probabilities can be considered constant between years (because of the standardisation of effort), thus simplifying the modelling process. However, modelling survival and recruitment rates is complicated by relatively low capture totals at many sites and the fact that individuals may have different capture probabilities: birds with territories further from nets are less likely to be captured, for example. Development of analytical techniques to make best use of these data is a current area of research (*eg* Hines *et al* 2003).

RECENT RESULTS

Perhaps the most common use of CE data is in monitoring annual patterns of abundance, productivity and survival. For instance, Peach *et al* (1999) demonstrated that the decline of the Reed Bunting *Emberiza schoeniclus*, a bird of conservation concern in Britain, was consistent with observed changes in (first-year) survival rates (Fig 1). Furthermore, other evidence suggested that the winter food supplies of this and of other seed-eating species had declined, leading to an expectation of reduced overwinter survival. Such results have played a key role in shaping conservation action for farmland species in Britain.

The pattern of population change recorded on CE sites across species agrees remarkably closely with those from other schemes. In Britain, long-term trends for 22 species on CE sites correlated well ($r = 0.63$, $P < 0.001$) with those determined by territory mapping censuses (Peach *et al* 1998). Concordance is seen even at a continental scale, with trends in 33 species across North America on CE sites also correlating well ($r = 0.64$, $P < 0.001$) with those from a large-scale point-count survey (Saracco *et al* 2008). This indicates that the demographic monitoring on CE sites is representative of wider populations. In fact, CE ringing might actually provide the best estimates of population change for some habitat-specialist species, such as Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus* in Europe, which are poorly covered by general census schemes.

Monitoring on CE sites can also provide direct evidence of the demographic mechanisms of population change. For example, DeSante *et al* (2001) compared demographic data from CE sites for Gray Catbird *Dumetella carolinensis*, a common migrant of North American scrub and understorey habitats, among physiographic regions where census counts showed differences in population trends. Productivity of catbirds did not differ significantly between regions where populations significantly increased and those where they declined significantly, whereas survival rates of adult catbirds did. Moreover, differences in adult survival rates were of the magnitude needed to cause the observed

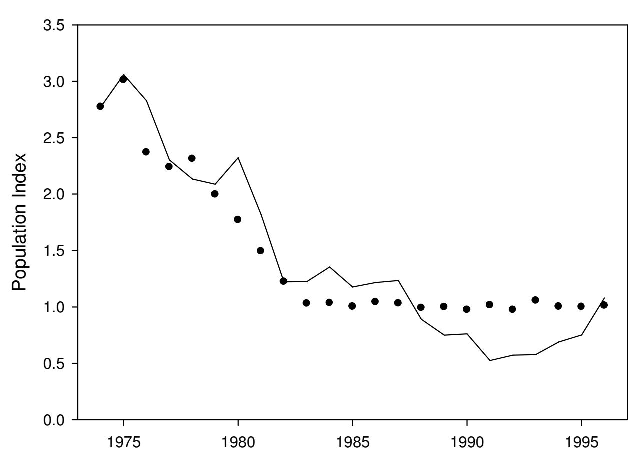

Figure 1. Predicted changes in the abundance of Reed Buntings with year-specific first-year survival but constant adult survival and productivity (line). Points show the observed changes in abundance as measured by the Waterways Bird Survey. From Peach *et al* (1999).

differences in population trends; thus, factors influencing survival, rather than productivity, were probably the reason for the differing population status.

A number of studies have used CE ringing data to show that ecological factors on the non-breeding grounds can determine population status, both of migrant and resident species. Most Afro–Palaearctic migrant passerines cross the Sahara Desert and Mediterranean Sea on their northward migration which, in combination, represent a significant ecological barrier. Sedge Warblers, a common migrant of wet scrub, stop over in oases on the southern edge of the Sahara to lay down large fat deposits, before flying to Europe. Feeding conditions in this arid Sahelian region are strongly dependent on rainfall to stimulate sufficient primary productivity, and during the late 1980s when droughts were common, return rates of Sedge Warblers between years were strongly correlated with rainfall levels in the Sahel (Peach *et al* 1991). Similarly, analyses of CE data have shown that survival of two resident passerines wintering in Britain is related to the severity of winter weather (Peach *et al* 1995), while productivity in North American migrant passerines is related to spring rainfall (Nott *et al* 2002); in each case the impacts of weather are mediated through the availability of food. Understanding the role of climate in population processes is critical in the face of current climate changes, particularly if we wish to predict the impacts on species' ranges and numbers. Climate change is likely to affect migrant species to a greater extent, and so monitoring of these species is particularly important (Robinson *et al* 2009).

A strength of CE schemes is their multi-species approach. Julliard *et al* (2004) studied how productivity was affected by an exceptional heatwave that occurred in France in the spring/summer of 2003. Productivity was relatively high for 27 of 32 (84%) species; variation between species in productivity, however, was strongly correlated to variation in population growth rate. The previous 15 years had been marked by several warm springs, probably as a result of global warming. The exceptional spring of 2003 magnified an ongoing process: species that benefit from warm springs had relatively high productivity and increased in numbers, while species decreasing in the longer term fared poorly. This demonstrates the importance of understanding the impacts of global climate change, as they may disproportionately affect species already of conservation concern.

Although the primary aim of CE monitoring studies is to assess spatial and temporal variation in numbers and demographic variables over relatively large spatial scales, clearly they can also provide information on the impacts of habitat management at local scales. For example, Harrison *et al* (2000) showed that, despite marked vegetational change, between-year changes for most of ten species on their wet scrub CE site over a ten-year period were similar to those seen in the national scheme. This implies that large-scale environmental drivers, such as weather, play a large part in determining demographic processes. Only two species, both wetland specialists (Sedge and Reed Warblers), showed markedly different changes, suggesting that local vegetation changes were more important in determining the population status of these species.

FUTURE DIRECTIONS

CE programmes have yielded much towards their primary goals of monitoring and characterising population processes. Because they are mostly operated by volunteers they represent a cost-effective mechanism for gathering detailed demographic data at large spatial scales. Understanding demographic processes is important for interpreting patterns of population change and, hence, implementing effective conservation strategies. CE schemes are uniquely suited to measuring such demographic parameters: their measure of productivity integrates over all nesting attempts through the season, but at the cost of detailed stage-specific information provided by nest recording schemes (Crick *et al* 2003). Mark–recapture data gathered on CE sites provide estimates of adult survival and recruitment into the breeding population. Recruitment of young birds into the breeding population is a key demographic parameter (combining as it does the effects of productivity and first-winter survival) for many populations; however it is extremely hard to measure, and the utility of CE data needs to be better exploited in this regard. Also on the analytical front, hierarchical modelling methods (*eg* Royle & Dorazio 2007) seem well suited to analysing mark–recapture data from CE schemes and their continued development and implementation is a key priority for future analytical work. Such models better reflect the structure of CE data, so should increase the utility of the data for understanding population processes. For example, one can explicitly estimate spatial variation in demographic parameters, allowing more robust conclusions about how these may relate to population changes, which also differ between locations (Saracco *et al* 2008).

Although most applications of CE data have focused on understanding patterns of population change, it is increasingly being realised that such data have many other uses as well. One such use might be in characterising patterns of breeding phenology. This could be achieved through looking at the relative number of captures through the season or by recording auxiliary variables, such as body condition, the presence of incubation patches in female birds or the onset of post-breeding moult. Data from birds on CE sites are particularly valuable in this regard because of the standardised nature of the ringing, and all CE ringers should be encouraged to record such information as a matter of routine. Moreover, CE sites potentially provide a network for collecting samples for isotope or genetic analyses (*eg* Kelly *et al* 2005, Boulet & Norris 2006). Undoubtedly other uses for the data will emerge in future.

CE ringing also provides a valuable and structured opportunity for training: a trainee will see most plumage conditions for many common species throughout the season. Moreover, it is easy to understand the rationale for ringing from CES local experience: anyone can see the appearance of juveniles in the catches or the age structure of birds retrapped between years. Such experiences encourage ringers to look at their own data, generating questions and results and stimulating the ringing scheme as a whole.

Most national CE programmes are aimed at understanding changes in breeding populations. It is possible, however, to use CE ringing to investigate population processes in the wintering grounds and this is a key direction for future developments. Declines in many Nearctic–Neotropical migratory passerines are thought to be related to processes operating in the non-breeding grounds in Central and South America, and so the Monitoreo de Sobrevivencia Invernal (MoSI) scheme was initiated in Neotropical countries to investigate demographic processes in those areas (DeSante *et al* 2005b). This has shown, for example, that survival in overwintering areas is correlated with habitat quality; quantifying such relationships is crucial if we are to understand the population processes in migratory birds. Such a scheme requires a reasonable degree of site fidelity of birds between years and relatively low mixing of populations, so would not work in temperate Europe where populations exhibit a mix of migratory strategies, but the possibility of instigating such a scheme in Africa in order to improve our understanding of the population dynamics of Afro–Palaearctic migrants is worth investigating.

The success of CE ringing has seen it adopted widely across two continents, offering the potential to quantify demographic parameters at large spatial scales. For example, in recent decades, long-distance migrant species have declined across Europe (Sanderson *et al* 2006) and a project is currently under way, under the auspices of the European Union of Ringing Schemes (EURING) to quantify both spatial and temporal variation in abundance and demographic parameters across western Europe in a range of migrant passerines with contrasting wintering areas and ecology. Such analyses should illuminate the reasons underlying the declines; analyses at such large spatial scales are required to capture the range of variation in population processes induced by variation in wintering location and global climatic change. The existence of comparable schemes in two continents also offers the possibility of essentially independent contrasts in variation in life-history traits which may yet illuminate fundamental patterns contributing to population regulation. CE ringing in Britain & Ireland recently celebrated its 25th birthday – the next 25 years look to offer exceptional promise in improving our understanding of how bird populations work and how they may best be conserved.

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