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Cetti's Warbler *Cettia cetti*: analysis of an expanding population

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Capsule Productivity in the UK Cetti's Warbler population is constant, but overwinter survival has become increasingly dependent on winter temperatures.

Aims To demonstrate how constant effort (CE) ringing can be used to estimate productivity of breeding populations, using the expanding Cetti's Warbler population as an example.

Methods A logistic generalized linear model is developed from an established method of estimating abundance to generate an annual index of productivity from CE catches. Dispersal of birds from ring-recapture data is modelled using a simple exponential model of dispersal.

Results The number of Cetti's Warblers on CE sites has increased markedly, particularly since 1998, but productivity has remained largely constant. The rate of population increase has slowed in recent years, in part because of an increasing sensitivity of the population to cold winters. Juveniles disperse further than adults, and the distance over which they disperse has increased.

Conclusions CE catching provides a way of easily measuring whole-season productivity. The future of Cetti's Warblers in Britain looks secure, but the population may be approaching its maximum size under current conditions.

Cetti's Warblers *Cettia cetti* are small brown bush warblers that are common in southern and central Europe, with a range that extends east into central Asia. Previously confined in Europe to Mediterranean areas, they have colonized the cooler, oceanic western regions since the 1920s (Bonham & Robertson 1975). Cetti's Warblers were first recorded in Britain in 1961, at Titchfield Haven, Hampshire. Numbers began to increase substantially from the early 1970s, with breeding first confirmed in Kent in 1973 (Harvey 1977). The species was removed from the Rare Birds List in 1976, and since then numbers have been monitored by the Rare Birds Breeding Panel (Brown & Grice 2005). The species initially spread throughout the southern and eastern counties of England, with the centre of distribution later shifting from southeast England to southwest England (Brown & Grice 2005).

The British Trust for Ornithology's (BTO) constant effort (CE) sites scheme uses changes in annual catch sizes of adults and juveniles at standardized mist-netting sites to measure long-term changes in abundance,

productivity and survival in a range of passerine species (Peach *et al.* 1996). This information feeds into the BTO Integrated Population Monitoring Programme, which aims to identify the demographic causes of population change in monitored species (Baillie 2001). In this paper, we describe the increase in Cetti's Warbler numbers on CE sites and look at changes in abundance, productivity and dispersal in order to determine the possible demographic drivers of the population expansion. CE sites are located throughout Britain, thus are well placed to monitor a spreading population. We extend the methods of Peach *et al.* (1998) for calculating abundance to show how to estimate productivity in a similarly robust fashion. As this extension may be useful for other CE (and similar) schemes, we describe the method in some detail.

METHODS

The CE catching protocols are published in detail elsewhere (Peach *et al.* 1996, 1998). In brief, ringers aim to catch birds using mist-nets at their sites once in each of 12 consecutive time periods (each of 10–11 days' duration) from May to August each year. Mist-netting

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is not permitted on a CE site within three days prior to one of these 12 main visits, in order to minimize problems of the birds learning to avoid the nets. Precise visit times and net arrangements are not specified by BTO for sites within the scheme; however, the duration and timing of visits, and the number, type and position of nets used are standardized at individual sites across years. Thus changes in numbers of birds caught can safely be attributed to changes in the population, rather than to sampling intensity or method.

Estimating abundance

Peach *et al.* (1998) adopted a generalized linear model (GLM) approach and modelled the expected numbers of adults caught at each site as the product of site and year effects (i.e. sites differ in their average 'quality', but numbers vary proportionately across sites between years). Sites that do not receive coverage in certain years, either because they are no longer surveyed or because a year is missed due to particular circumstances, effectively constitute missing data, which are readily handled (ter Braak *et al.* 1994). Occasionally, weather or personal circumstances mean an observer is unable to complete all 12 visits in a year. Peach *et al.* (1998) describe a correction factor, which we also invoke here to adjust counts in years where eight to 11 visits to a site were made; if a site was visited less than eight times, data for that year are omitted from the analyses. All model fitting was carried out using SAS (SAS Institute Inc. 2000), assuming a Poisson distribution for the observed catches and a logarithmic link function.

Estimating productivity

To estimate trends in productivity, we developed a model based upon logistic regression. The number of juvenile birds caught at a site in a given year is assumed to be a binomial variable, with the probability (p) of a caught bird being juvenile being estimated from the number of juvenile birds caught divided by the total number of birds (adults plus juveniles) caught, at each site in each year. Then, in the absence of any missing visits, if p_{ij} is the expected proportion of juveniles in the catch at site i in year j , year (Y_j) and site (S_i) effects can again be estimated via a simple linear model:

$$\text{logit}(p_{ij}) = S_i + Y_j$$

The use of a logit link function ensures that the

estimated probability lies within the valid range (zero to one). This model can be fitted to the annual observed juvenile and total site catches via any standard GLM software. In practice, some visits are inevitably missing. Since most juvenile birds will be caught later in the season, in the productivity analyses we include data only for those years in which a site achieves four visits from the first six, and also four from the last six. Provided these criteria are met, adjustments for missing visits are implemented throughout the analyses by obtaining corrected catches for juveniles and adults (e_{juv} and e_{ad}) at each site through multiplying the observed adult (c_{ad}) and juvenile (c_{juv}) totals by the correction factor of Peach *et al.* (1998). These values will not, in general, take the integer values required for a binomial model such as Equation 1 but, noting that the difference between the observed juvenile ratio and that expected corrected for missing visits can be expressed as:

$$\text{logit}\left(\frac{c_{\text{juv}}}{c_{\text{juv}} + c_{\text{ad}}}\right) - \text{logit}\left(\frac{e_{\text{juv}}}{e_{\text{juv}} + e_{\text{ad}}}\right) = \ln\left(\frac{c_{\text{juv}} e_{\text{ad}}}{c_{\text{ad}} e_{\text{juv}}}\right)$$

then the right-hand expression provides an offset for the model, accounting for the missed individuals:

$$\text{logit}(p_{ij}) = \ln\left(\frac{p_{ij}}{(1-p_{ij})}\right) = S_i + Y_j + \ln\left(\frac{c_{\text{juv}} e_{\text{ad}}}{c_{\text{ad}} e_{\text{juv}}}\right)_{ij}$$

This is again readily fitted to the observed proportions of juvenile birds in the annual total (unadjusted) catches at each site. Inverting the log (rather than logistic) transformation of the year effects produces a more natural productivity index, which is proportional to the number of young produced per adult for each species.

If all 12 visits are made, the offset reduces to zero, as $c_{\text{juv}} = e_{\text{juv}}$ and $c_{\text{ad}} = e_{\text{ad}}$. Sites where the total catch consists of adults or juveniles exclusively lead to the correction factor being undefined, and excluding such sites could lead to under- or over-estimation of the productivity index, respectively. In the present study, sites where only juveniles or only adults were caught were retained (assuming the criterion for the minimum number of visits was met), but the zero value could not be corrected for any missing visits as above. In the case of $c_{\text{juv}} = 0$ (for example), an offset was constructed based on the missing visit correction for c_{ad} alone as follows:

$$\ln\left(\frac{p_{ij}}{(1-p_{ij})}\right) = S_i + Y_j + \ln\left(\frac{e_{\text{ad}}}{c_{\text{ad}}}\right)_{ij}$$

A similar expression can be derived for cases where $c_{ad} = 0$. Sites where neither adults nor juveniles are caught do not contribute any information and so are excluded from all analyses.

This estimate of productivity integrates fecundity (number of eggs laid), losses in the nest, and mortality during the immediate post-fledging period. It is important to recognize that this index is not an estimate of 'true' productivity (i.e. the number of fledged young produced per pair per year) because the probabilities of catching adult and juvenile birds may differ for behavioural or ecological reasons (which may vary between species). The use of catches at CE sites to estimate annual indices of productivity relies on the assumption that the difference in the probability of catching juvenile versus adult birds of the same species is constant between years, which seems likely.

Dispersal

We quantified dispersal from movements of ringed birds. Of 6157 Cetti's Warblers that have been ringed in Britain, 105 have been recovered, mostly as recaptures at sites away from the original ringing location. Birds were aged and sexed at ringing according to criteria given by Svensson (1992). Although many of the recoveries were two to three years or more from ringing, we assume that most of the dispersal occurs in one period of movement. This is supported by multiple capture occasions of 11 birds initially ringed as juveniles: the first movement between captures was substantial (median 53 km), while all subsequent captures were at (or near) this second location (all less than 5 km). Such subsequent movements were excluded from the analysis. Dispersal distances were assumed to be exponentially distributed, so the effects of age and sex were investigated using simple models, in which the expected movement (log-transformed) was a linear function of the relevant covariates and model fit was estimated by maximum likelihood; significant relationships were then identified using standard likelihood ratio tests. Trends over time were similarly calculated using a log-linear relationship between movement and year of ringing.

RESULTS

The number of Cetti's Warblers has increased markedly on CE sites, though most of this increase has occurred since 1998 (Fig. 1). This increase has been accompanied by an increase in the number of sites hosting the

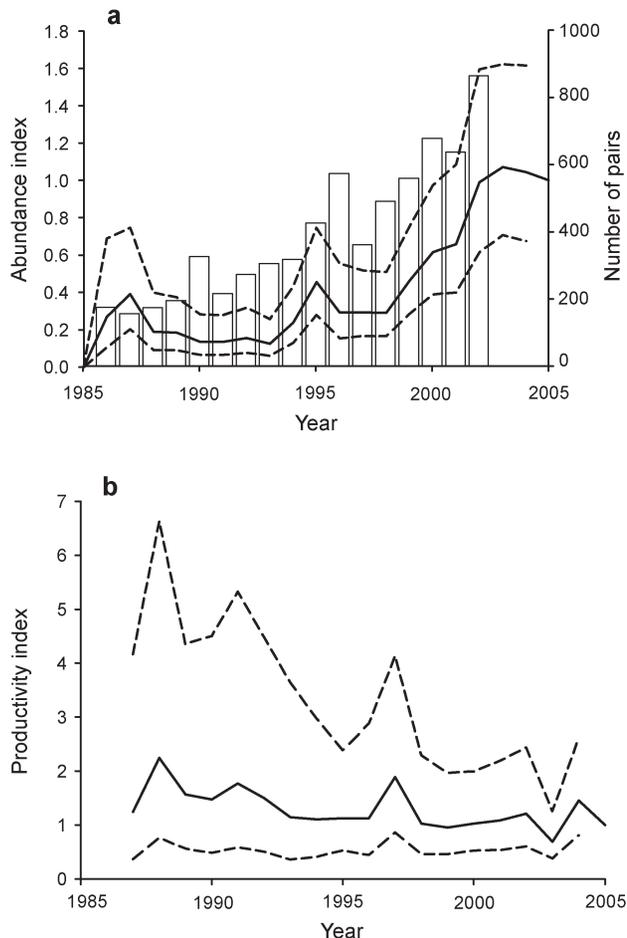


Figure 1. (a) Cetti's Warbler breeding population in Britain. Line (and left axis), index of adult numbers on CE sites (with 95% CI); bars (and right axis), number of pairs recorded by the Rare Breeding Birds Panel. (b) Index of productivity (juveniles per adult) on CE sites (with 95% CI). In both cases, the CE index is arbitrarily set to 1 in 2005.

species. Before 1990 Cetti's Warblers were recorded on up to five sites of about 130 operated each year; since 2000, they have been recorded on an average of 13 sites from a similar total each year. Numbers caught at individual sites, however, are still low, with most sites catching fewer than five birds each season. This increase is mirrored nationally, as figures from the Rare Breeding Birds Panel show (Fig. 1). In contrast, data from CE sites show no evidence of an increase in productivity over the same time period, with the ratio of juvenile to adult birds caught remaining roughly constant. The paucity of records early on, reflected in the confidence limits of Fig. 1, does mean there is limited power to detect trends during that time.

Between 1998 and 2003, the annual rate of population increase, calculated via the ratio of the abundance

indices (n_t) in consecutive years, has been rapid, averaging 30% per annum, though this may now be beginning to slow a little (Fig. 1). The annual rate of population change is related to the degree of winter severity, but only at higher population densities (Fig. 2). In years with relatively low population size (i.e. before 1995, Fig. 1), there was no relationship between annual population change and winter temperature. However, in more recent years when the population has been higher, there is a correlation between annual population change and winter severity ($r_s = -0.698$, $P = 0.03$).

Birds ringed as juveniles ($n = 58$) dispersed much further (median distance moved 39 km, Fig. 3) than birds originally ringed as adults (11 km, $n = 25$; likelihood ratio test $\chi^2_1 = 11.06$, $P < 0.001$). Females also tended to disperse, on average, further than males (for adults, median of 15 km versus 6.5 km; for juveniles, 45 km versus 33 km), a difference that was highly significant ($\chi^2_1 = 7.94$, $P = 0.005$).

There is also a suggestion of juvenile birds starting to travel further from the natal area now that the population is established (Fig. 4). Of 24 such birds recovered or re-trapped after ringing in or since 1995, 13 (59%) represent movements of more than 50 km; only nine of 28 (29%) birds ringed in earlier years had moved this distance. The distance moved between capture occasions for juvenile birds increased by 3.8% per year; a likelihood ratio test comparing the slope to zero (i.e. no temporal trend) shows that this is

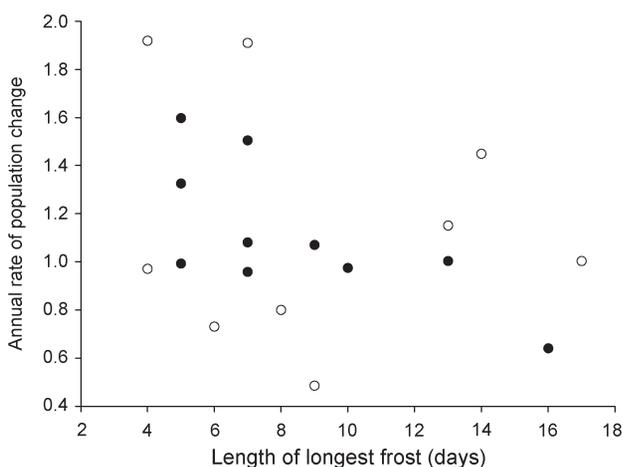


Figure 2. Annual population change (n_{t+1}/n_t) of Cetti's Warbler with severity of winter (length of longest consecutive period with daily minimum temperature $<0^\circ\text{C}$). ○, Years (n_t) with low population size (1986–94); ●, years of high population size (1995–2004).

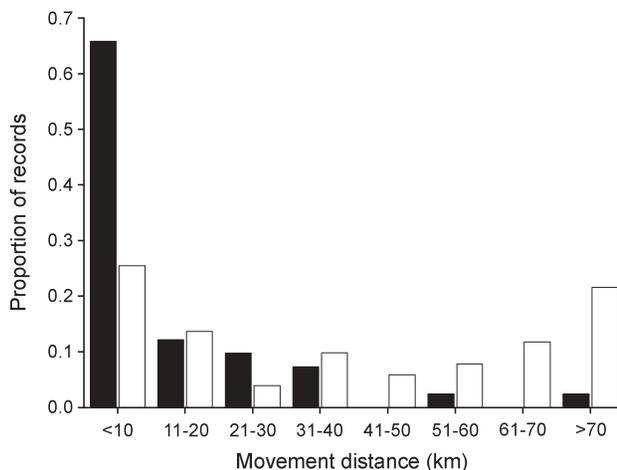


Figure 3. Movements of adult (■) and juvenile (□) Cetti's Warblers, between capture occasions.

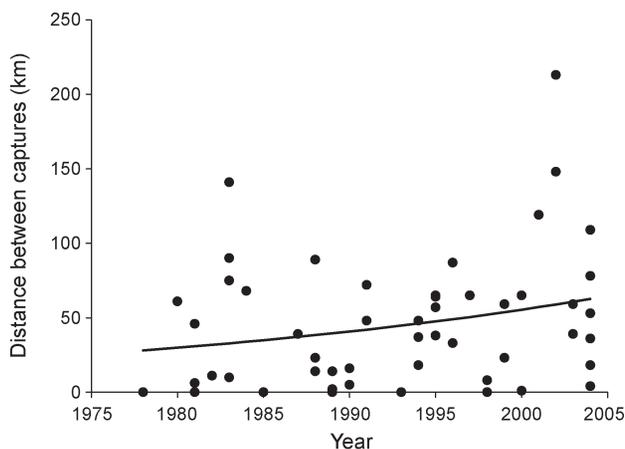


Figure 4. Movements of Cetti's Warblers between ringing (as juveniles in a given year) and subsequent recapture or recovery. Solid line represents the fit of an exponential model for distance moved. One record of a juvenile ringed in 1993 that moved 649 km is not shown (but is included in the analysis; removing it does not alter the results greatly).

significant ($\chi^2_1 = 4.34$, $P = 0.037$). No such trend over time was found for movements of adult birds.

DISCUSSION

Using constant effort sites to measure productivity

CE ringing data provide a useful means, via a simple GLM, of estimating trends in avian abundance over time and we have demonstrated that this can easily be extended to indices of annual productivity through the application of logistic regression. These data provide the only practical source of productivity across an

entire season, rather than on a per attempt basis in the manner of nest record data (Crick *et al.* 2003). Productivity estimates derived from CE data automatically incorporate annual variability in the number of nesting attempts in multi-brooded species (like Cetti's Warbler, which is typically double-brooded), as well as a component of post-fledging mortality, which can be appreciable (Robinson *et al.* 2004). Thus data from such schemes, and the model described here, are of great value in population monitoring (Baillie 2001).

Population expansion in Cetti's Warblers

Clearly, immigration was responsible for the initial colonization of Britain by Cetti's Warblers. There have been two reports of foreign ringed birds in Britain, one each from Belgium and France, but none the other way (Bibby 2002). Because the CE scheme only provides an index of productivity it is hard to compare this to other estimates of young produced, but it does suggest little change over the last 20 years. Being double-brooded means that Cetti's Warblers can have quite high productivity (Bibby 1982), and it seems likely that this has fuelled the population expansion. Prior to the main period of population growth on CE sites, commencing in the late 1990s, the low population size meant that in relatively mild winters there was little competition for food, so little impact of weather on (overwinter) survival (the last severe winter in Britain was in 1991). Since the population has expanded, however, relatively colder winters have led to lower growth rates, i.e. density-dependent population regulation is becoming apparent. Such density dependence will result from greater competition for resources, either food supply directly, or good quality overwintering habitat more generally, as birds expand their range into less suitable areas. It is notable that the stronghold of the population has shifted away from the original colonization area (in Kent, southeast England, close to continental Europe) to the milder southwest of Britain (Wotton *et al.* 1998), where winter temperatures tend to be higher.

In common with most bird species, female Cetti's Warblers disperse further than males, and juveniles in search of a breeding territory disperse further than adult birds (Paradis *et al.* 1998). As the available habitats have filled up from their original colonization area, individuals (primarily juveniles) have had to disperse further. In Britain, suitable habitat (reed swamp with scrub) is relatively patchy, and even scarcer further north and west (i.e. further from the site of original colonization), which may limit the spread of this

species. Continued spread will, presumably, be reliant on the production of sufficient juveniles to disperse, and sufficiently warm winters for them to survive. As the range expands it is likely that average productivity will tend to decrease, as less suitable habitat is occupied, though the increased winter temperatures predicted as a result of global climate processes (Hulme *et al.* 2002), mean the future for Cetti's Warblers in Britain looks relatively good. Density dependence of winter demographic processes is already becoming apparent and may limit future population growth, as the suitable habitat, in both biological and climatic terms, fills.

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