

## ESTIMATING ADULT SURVIVAL RATES FROM BETWEEN-YEAR RECAPTURES IN THE BRITISH TRUST FOR ORNITHOLOGY CONSTANT EFFORT SITES SCHEME

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*Abstract.* Recent developments in the methodology for estimating survival rates from mark–recapture data are summarized. Transient individuals are common in mist-net samples and, unless catered for in the analysis, can cause survival rates to be seriously underestimated. Mark–recapture data from multiple study sites can now be combined analytically to provide regional estimates of survival. Although permanent emigration away from constant effort sites may result in true survival being underestimated, temporal changes in apparent survival may still be useful in highlighting the demographic mechanisms driving population changes.

*Key Words:* Constant Effort Sites scheme, mark–recapture, survival.

Many passerine species show strong fidelity to breeding sites in successive breeding seasons. This is generally true for long-distance migrants, as well as residents. Consequently, regular captures of marked breeding birds can be an effective means of generating between-year recaptures, and these can be used to estimate apparent survival rates of adult birds. When the sampling effort is standardized across breeding seasons (or at least measured), annual return rates can be estimated with greater precision and less bias.

Birds banded as chicks or as juveniles on constant effort sites have much lower recapture rates in subsequent years than do birds banded as adults (i.e., at least one year old). This is partly because young birds experience higher mortality rates than adult birds, but mainly because many young passerines make their first breeding attempt at sites away from their natal area (Greenwood 1980). For this reason we have not attempted to estimate first-year survival rates using Constant Effort Sites (CES) mark–recapture data (although see Peach et al. 1999). Survival rates of young passerines are probably best estimated using reports of banded birds found dead (Baillie and McCulloch 1993).

In recent years there has been a rapid growth of interest in the application of mark–recapture techniques to the estimation of demographic parameters, in respect to both extensive wildlife monitoring programs and intensive population studies. Comprehensive reviews of the methods and software available for analyzing mark–recapture data have been published (e.g., Pollock et al. 1990, Lebreton et al. 1992, Baillie and North 1999). We have applied these methods to data collected at constant effort sites (Peach et al. 1990, 1995; Peach

1993) and present here a summary of our main findings. For most analyses we recommend the use of program MARK (White and Burnham 1999) combined with program RELEASE (Burnham et al. 1987) for goodness-of-fit tests.

### MODELING SURVIVAL RATES

The estimation of survival rates (strictly, return rates) involves the fitting of open population Jolly-Seber models parameterized in terms of survival and recapture rates (Pollock et al. 1990, Lebreton et al. 1992). An important starting point for many analyses is the Cormack-Jolly-Seber (CJS) model in which both survival and recapture rates are time-dependent (Cormack 1964, Jolly 1965, Seber 1965). Following the notation of Lebreton et al. (1992), models are referred to in terms of survival rate ( $\phi$ ) and recapture probability ( $p$ ) with the subscript  $t$  denoting time-dependence. The CJS model is therefore referred to as  $(\phi_t, p_t)$ .

The CJS model assumes that survival does not vary according to the age of animal, and this is probably reasonable for adults of most short-lived small passerines (e.g., Buckland and Baillie 1987, although see Loery et al. 1987). The choice of a starting model will depend partly on biological knowledge or intuition, and it may be important to consider age-dependent survival models in relatively long-lived species. The goodness-of-fit tests provided by the software RELEASE, now available in the package MARK (White and Burnham 1999), provide explicit tests of the general suitability of the CJS model.

Having decided upon a biologically reasonable starting model that fits the data, the analyst can then

test a series of simpler models, each having fewer parameters than the starting model. For example, an obvious simplification of the CJS model is to constrain recapture probability to be constant over time ( $\phi_r, p$ ). If the sampling effort has remained relatively constant during each of the sampling periods, as is the case at constant effort sites, then the simpler ( $\phi_r, p$ ) model should provide a more parsimonious description of the data than the ( $\phi_r, p_t$ ) model. Estimating fewer parameters from the same data increases the precision of the estimates, although at the risk of introducing bias. Likelihood ratio tests can be used to test specific hypotheses about model structure, and Akaike's Information Criterion (Akaike 1973) can be used to compare large numbers of candidate models without conducting large numbers of statistical tests (Lebreton et al. 1992, Burnham and Anderson 1998). The aim of the modelling procedure is to identify the simplest model that provides an adequate description of the data.

Program MARK has the useful facility of allowing the user to test for linear relationships between time-dependent model parameters and environmental variables (Lebreton et al. 1992, White and Burnham 1999). This can serve both as an aid to model simplification and as a means of testing biological hypotheses about factors affecting survival rates. This facility has, for example, allowed analysts to establish strong relationships between annual survival rates of two long-distance migratory bird species and annual rainfall in the African winter quarters (Kanyamibwa et al. 1990, Peach et al. 1991). It is better to test for relationships between time-dependent survival rates and external variables using the link functions available in MARK, rather than using ordinary least squares approaches, because the latter make no allowance for autocorrelation of successive survival estimates (Lebreton et al. 1992).

If capture effort has varied between sampling periods (e.g., years), then time-dependence in recapture probability can in principal be explained by some measure of capture effort, which can then be incorporated into the model (Clobert et al. 1987). However, in our experience simple measures of capture effort do not always correlate with or explain temporal variation in recapture rates, and we strongly advocate standardization of capture effort whenever this is possible.

#### THE PROBLEM OF TRANSIENTS IN COHORT SAMPLES

Estimates of survival between the year of capture and the first year of recapture may be biased downwards if cohort samples contain transient individuals

that are unlikely to be retrapped in subsequent years (Buckland 1982). One possible approach to this problem is to restrict analyses to individuals recaptured in years after their first year of capture (equivalent to excluding all first encounters). However, in short-lived species this often involves the loss of a high proportion of the available survival information with a consequent loss of precision (Peach et al. 1990).

Pradel et al. (1997) developed a new approach to the problem of transients that involves estimating the proportion of resident birds in banded samples, in addition to apparent survival and recapture rates. This method has the advantage of removing bias on survival estimates and of providing an estimate of the proportion of transient individuals in cohort samples. A disadvantage of Pradel's method is that for all cohorts the estimate of survival during the year after initial capture remains biased, and this may be a particular problem for short-lived species where a high proportion of all recaptures occur during the first recapture period.

An alternative approach is to use within-year recaptures to identify residents in newly banded cohorts (Buckland and Baillie 1987, Peach et al. 1990). Most constant-effort banding schemes involve repeated sampling of study areas throughout each breeding season, and transient birds should have a lower probability of being retrapped within the same season than resident individuals (note the probability of retrapping transients in subsequent years is, by definition, zero; Pradel et al. 1997). Thus, birds retrapped more than some specified minimum number of days after first being trapped are considered "residents" whereas individuals not retrapped over the same period are considered to be a mixture of "residents" and "transients." We have tended to use 6–10 days as the minimum period that must separate same-year captures of an individual during the first year in which it was encountered for it to be considered resident (Peach 1993). This information is included in the analysis by expanding the encounter histories for each bird to have a single additional encounter period immediately after the first encounter. Modelling then proceeds with a dummy "age" structure that partitions survival and recapture rates between first encounter and subsequent same-year recapture (within-year survival and recapture rates), from same-year recapture and the following breeding season (between-year survival and recapture rates). In this way, individuals not retrapped more than 6–10 days apart in the first year of capture but retrapped in subsequent years, are correctly classified as residents and do contribute to subsequent

estimates of annual survival. Within-year survival and recapture rates can be modelled as constant across years or year-specific. These "within-year" transients models are straightforward to fit using program MARK.

The effect of the "within-year recapture" transients models is to substantially reduce, but not remove, the negative bias on apparent survival estimates caused by the presence of transient individuals in cohort samples (Peach et al. 1990, Peach 1993). However, our approach maximizes the precision of survival estimates by fully using recapture information from the breeding season following initial capture, which often constitute a high proportion of all between-year recaptures for short-lived species. Using within-years recaptures to minimize problems caused by transients will be most appropriate where precision may be limiting statistical inference and small amounts of bias can be tolerated, as is often the case in studies attempting to detect temporal changes in survival rates. The approach is less suited to studies whose primary focus is absolute levels of survival, such as comparative life histories.

#### COMBINING SURVIVAL INFORMATION ACROSS STUDY SITES

An analytical development of particular importance to the CES Scheme was the capability of programs like SURGE and MARK to handle multiple groups of marked animals within a single analysis (Pradel et al. 1990, White and Burnham 1999). This facility allows the analyst to test for differences in survival or recapture probabilities between groups, which in the CES-context might include study site or sex. The general approach is to fit starting models in which parameters differ between groups, and then to constrain parameters to be identical or even additive across groups (Pradel et al. 1990, Lebreton et al. 1992). In the CES context, this allows the analyst to check whether apparent survival rates differ between sites and, if they do not, to pool survival information across sites to provide more precise regional survival estimates.

The modelling framework for multiple-site analyses is analogous to that used in analysis of variance. An approach that we have adopted in the analysis of CES data is to have a starting model in which survival and recapture probabilities are both year- and site-specific, with an interaction between year and site (Peach 1993). We then attempt to simplify recapture probability, initially by dropping the year-site interaction term, and then by removing the time-dependence. These simplifications are usually

parsimonious because of the constant sampling effort maintained at CE sites. Recapture probabilities often differ significantly between sites, which probably reflects the differing numbers and densities of nets at different sites. We then attempt to simplify the survival side of the model, first by seeking to remove the interaction term, and then by removing the site term. We have used this modelling approach to combine mark-recapture data from up to 10 CE sites to provide regional estimates of annual adult survival rates for the Willow Warbler (Peach et al. 1995; scientific names in Table 1).

We compared estimates of adult survival for five passerine species derived from multiple-site CES mark-recapture data (Table 1) with independent estimates from national BTO band recovery data relating to birds found dead (taken from Peach 1993 and Baillie and McCulloch 1993). Survival estimates from recaptures were generally lower than those based on recovery data (Table 1). Although these differences could be a consequence of the differing time periods covered by the two sets of analyses, they are probably partly caused by the permanent emigration of some birds away from constant effort sites (Peach et al. 1990, Cilimburg et al. 2002). Even if apparent survival rates estimated from mark-recapture data do underestimate true survival, they may still constitute a useful index of temporal changes in true survival rates. Moreover, the precision of the survival rates of small passerines estimated from the CES data is generally comparable to or better than that attainable from the national United Kingdom band recovery data, because these species have low band reporting rates (Table 1).

#### DISCUSSION

Despite the potential problems of negative bias affecting apparent survival estimates, recent developments in both theory and software for analysing mark-recapture data make this aspect of the CES data an exciting prospect for the future. The main application of the CES mark-recapture data will be in the detection of long-term temporal trends in the apparent survival rates of adult passerines, and the testing of relationships between survival and environmental variables such as rainfall in the winter quarters of migrants (e.g., Peach et al. 1991). Knowledge of apparent survival rates is likely to be an important factor affecting the population dynamics of small passerines (Baillie and Peach 1992), and may be critical to our understanding of the mechanisms leading to wide-scale population changes

TABLE 1. ESTIMATES OF AVERAGE ANNUAL ADULT SURVIVAL RATES (AND ASSOCIATED STANDARD ERRORS) DERIVED FROM POOLED MARK-RECAPTURE DATA FROM MULTIPLE CONSTANT-EFFORT BANDING SITES AND FROM RECOVERIES OF DEAD BIRDS Banded IN BRITAIN AND IRELAND

| Species  | Mark-recapture analyses (1983-1991) |                                 |               |       | Recovery analyses (1985-1990) |               |       |
|--|-------------------------------------|---------------------------------|---------------|-------|-------------------------------|---------------|-------|
|  | Number of combined                  | Number of individuals retrapped | Survival rate |       | Number of recoveries          | Survival rate |       |
|  |                                     |                                 | $\phi$        | SE    |                               | S             | SE    |
| Willow Warbler ( <i>Phylloscopus trochilus</i> ) | 7                                   | 183                             | 0.371         | 0.025 | 385 <sup>a</sup>              | 0.554         | 0.056 |
| Blackbird ( <i>Turdus merula</i> )               | 4                                   | 113                             | 0.566         | 0.036 | 1307                          | 0.668         | 0.020 |
|  | 4                                   | 165                             | 0.581         | 0.029 |                               |               |       |
| Blackcap ( <i>Sylvia atricapilla</i> )           | 3                                   | 51                              | 0.443         | 0.057 | 197                           | 0.534         | 0.128 |
| Reed Warbler ( <i>Acrocephalus scirpaceus</i> )  | 3                                   | 168                             | 0.496         | 0.026 | 957 <sup>b</sup>              | 0.558         | 0.023 |
| Wren ( <i>Troglodytes troglodytes</i> )          | 2                                   | 29                              | 0.318         | 0.068 | —                             | —             | —     |
| Dunnock ( <i>Prunella modularis</i> )            | 1                                   | 62                              | 0.422         | 0.040 | 265                           | 0.447         | 0.050 |

Notes: All survival estimates were derived from time-independent models that fit the data. CE survival estimates are from Peach (1993) and estimates from recoveries are from Baillie and McCulloch (1993).

<sup>a</sup> Estimated from recaptures >5 km from the place of banding.

<sup>b</sup> Estimates based on recoveries of dead birds were supplemented by recaptures >5 km from the place of banding.

(Peach et al. 1999). Other potential applications are the comparisons of apparent annual survival rates between sites (perhaps treatment and control sites), between males and females (e.g., Pratt and Peach 1991), and between different habitats, regions (e.g., Peach et al. 1995), or latitudes.

#### ACKNOWLEDGMENTS

We thank the many individuals and organizations that have contributed to this work, as detailed in Peach et al. *this volume*.