Approaches for the Direct Estimation of Rate of Increase in Population Size (λ) Using Capture-Recapture Data[1]

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Abstract

Recent developments in the modeling of capture-recapture data permit the direct estimation and modeling of population growth rate Pradel (1996). Resulting estimates reflect changes in numbers of birds on study areas, and such changes result from movement as well as survival and reproductive recruitment. One measure of the "importance" of a demographic vital rate to population growth is based on temporal covariation (i.e., do changes in population growth follow changes in vital rates). If data are available to estimate vital rates or their components, then such data can be combined with capture-recapture data in order to estimate parameters of the relationship between population growth and the vital rate. These methods are illustrated using capture-recapture and nest observation data for Black-throated Blue Warblers, *Dendroica caerulescens*, from a long-term study at Hubbard Brook Experimental Forest, New Hampshire, USA. Population growth rate was found to be positively associated with the proportion of birds that double-brood. We encourage use of these methods and believe they will prove to be very useful in research on, and management of, migratory bird populations.

Introduction

Bird management and conservation programs should be based on knowledge of avian abundance, rate of change in abundance, and factors influencing abundance. In particular, we are interested in the difference between actual abundance and population objectives, and in the influence of management actions on population size and change, as these factors will be the primary determinants of appropriate management actions (e.g., Walters 1986, Williams et al. 2002). Historically, most studies of avian abundance have been based on various kinds of count surveys (e.g., see Ralph and Scott 1981, Ralph et al. 1995). However, the vast majority of such count surveys have not incorporated the need for information about detection probability (this can be equated with the proportion of the population that is counted) into survey design, so resulting estimates of population growth reflect both population change and changes in detection probability (e.g., Thompson et al. 1998, Bibby et al. 2000, Pollock et al. 2002, Thompson 2002).

Direct Estimation of λ_i: Approach

It is possible to estimate bird abundance based on studies of marked individuals (e.g., Nichols et al. 1981), but capture-recapture studies of birds have instead typically focused on estimation of survival (e.g., Brownie et al. 1985, Lebreton et al. 1992, Sillett and Holmes 2002) and movement (e.g., Nichols 1996, Bennetts et al. 2001). Because abundance can be estimated using capture-recapture modeling (Seber 1982, Pollock et al. 1990), it is clear that rate of increase in population size ($\lambda_i = \frac{N_{i+1}}{N_i}$, where N_i is abundance at time i) can be estimated from such data as well. Recently, Pradel (1996) developed a model that can be parameterized directly by λ_i, and this model has potential to be very useful in studies of marked birds. Data required for the estimation of λ_i under this model (Pradel 1996) are simply standard capture-recapture or capture-resighting data used for open population studies. A common design for birds involves sampling during a particular season (e.g., the breeding season) each year. Data resulting from such studies are capture histories, vectors of 1's and 0's denoting the sampling occasions (years) at which each individual was, and was not, captured (Seber 1982, Williams et al. 2002). Capture-resighting studies also require counts of unmarked birds at each sampling occasion (Nichols and Hines 2002, Dreitz et al. 2002). Both the intuition and the methodological detail underlying direct estimation of λ_i were presented by Pradel (1996), Nichols and Hines (2002) and Williams et al. (2002).

Note that the parenthetical definition of λ_i provided above involves a ratio of abundances at two points in

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time. Indeed the λ_i estimated using capture-recapture data reflect the changes in numbers of animals on the study area. Changes in numbers can occur because of recruitment of young animals, mortality, and movement into and out of the area of interest. This λ_i differs from an asymptotic λ computed from survival and reproductive rate estimates using a projection matrix (Caswell 2001). The asymptotic λ is of interest as well, and reflects the growth rate expected of a population exposed to the same set of survival and reproductive rates year after year. However, it is important to recognize the distinction between these two metrics reflecting population growth. In particular, the asymptotic projection matrix λ is not necessarily expected to correspond closely to the observed rate of change in numbers of animals on an area. The λ_i estimated using capture-recapture data should reflect short-term changes in abundance and should be especially useful for modeling efforts directed at assessing temporal covariation between λ_i and environmental and other covariates. See the discussion in Nichols and Hines (2002) for further details.

Direct Estimation of λ_i: Example

We used capture-recapture data for Black-throated Blue Warblers, *Dendroica caerulescens*, from a long-term study at Hubbard Brook Experimental Forest, New Hampshire, USA (Holmes et al. 1996; Sillett et al. 2000; Sillett and Holmes 2002, in press), to estimate λ. Capture-recapture data for adult males and females were obtained every breeding season from 1986-2001. We used the general model of Pradel (1996) to compute annual estimates of λ_i (*fig.1*). Point estimates ranged from 0.71 to 1.39 with estimated coefficients of variation falling in the range of about 16 percent to 23 percent. In addition, we fit a different model in which λ was constant over time (i.e., we imposed the constraint that $\lambda_i = \lambda$) and estimated a single overall λ for the entire period as $\hat{\lambda} = 1.02$, $S\hat{E}(\hat{\lambda}) = 0.02$. Thus, over the entire period, the estimated rate of population growth was slightly larger than 1, but the approximate 95 percent confidence interval covered 1.

"Importance" of Vital Rates to λ_i: Approaches

In addition to the ability to estimate λ_i, scientists and managers are interested in the relative "influence" of different vital rates (i.e., rate of survival, reproduction, movement) and demographic components (birds in different age classes or from different locations) on λ_i. The motivation for this interest typically involves the potential to bring about changes in λ_i by implementing management actions or conservation measures directed at specific vital rates or demographic components. This kind of thinking was important in the establishment of the MAPS avian monitoring program directed at avian survival and production (DeSante et al. 1995). Several approaches exist for assessing the "influence" or "importance" of a vital rate or demographic component on population growth, and two of these use capture-recapture data. One capture-recapture approach is similar to the projection matrix concept of elasticity (Caswell 2001) and addresses the question: "If a certain vital rate or demographic component exhibited a proportional change over a period of interest (e.g., if adult survival between periods i and i +1 had been reduced by 25 percent), what would the corresponding change in the population growth rate have been (e.g., what would the proportional decrease in λ_i have been)?" This kind of question can be addressed directly with capture-recapture data using reverse-time modeling and estimation methods that are very similar to those used to estimate λ_i (Nichols et al. 2000, Nichols and Hines 2002, Williams et al. 2002).

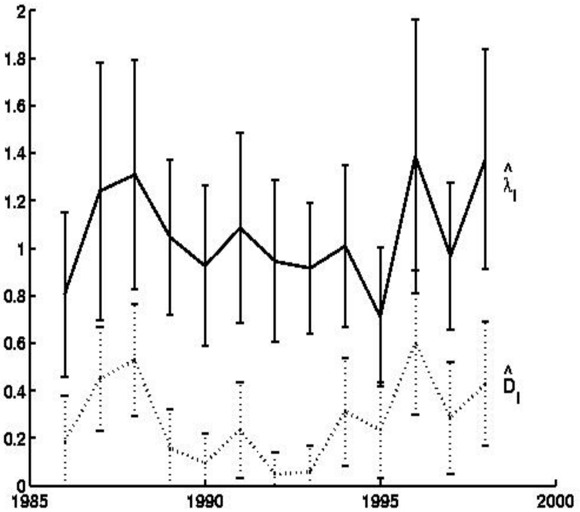

Figure 1—Point estimates of finite rate of population increase, λ_i, and proportion of birds double-brooded, $\hat{D}_i$, for Black-throated Blue Warblers from Hubbard Brook, New Hampshire. Estimates of population growth rate were obtained using capture-recapture models (Pradel 1996) and data, and estimates of double-brooding were obtained as binomial parameters based on observations of nesting birds.

The second approach to assessing "importance" of a vital rate or demographic component to λ_i involves temporal (or spatial) covariation. The sort of question addressed is: "Temporal variation in which vital rate(s) or demographic component(s) is most closely associated with temporal variation in λ_i?" This approach thus focuses on actual temporal covariation over a period of study rather than potential variation in λ_i resulting from hypothetical variation of a vital rate or demographic component. This approach can be implemented with capture-recapture data by direct modeling of λ_i as a function of a vital rate or a component of a vital rate. Such modeling results in estimation of a slope parameter relating variation in the vital rate to variation in λ_i.

"Importance" of Vital Rates to *λ_i*: Example

In order to illustrate this approach of modeling λ_i, we again used capture-recapture data for Black-throated Blue Warblers from Hubbard Brook, New Hampshire. We used additional data from this study on the proportion of nesting females that was double-brooded each year (Holmes et al. 1992, Sillett and Holmes in press), as this proportion is an important component of reproductive rate. Data to estimate this proportion were simply the number of nesting females located early in the nesting season each year, and the number of those that produced a second brood. Estimates of this proportion (D_i) varied substantially from year to year and appear to covary with estimates of λ_i (*fig.1*).

There are two approaches for modeling λ_i as a function of this proportion of double broods. The first is to estimate this proportion as a binomial model parameter (D_i) and then to treat this estimate as a covariate of known value in a capture-recapture model of λ_i. The second approach is to develop a joint likelihood in which the double-brooding parameter is directly estimated from the relevant data, and both λ_i and the relevant slope parameter are estimated directly using the joint likelihood. The advantage of this approach is that it properly incorporates the sampling variance associated with the estimation of D_i, rather than treating these parameters as known values. We believe that this joint likelihood approach provides a better basis for inference.

We used the second approach to directly estimate the parameters of the following model:

$$\log(\lambda_i) = \beta_0 + \beta_1 D_i \, ,$$

where D_i is again the proportion of females that were double-brooded in year *i*, and the β_j are model parameters. The data for double-brooding were included in the analysis, as were the capture-recapture data, 1986-2001. The modeling was done using program SURVIV (White 1983) with cell probabilities generated using both the double-brooding and capture-recapture portions of the likelihood. The resulting estimates for the parameters defining the above relationship between double-brooding and population growth rate were:

$$\hat{\beta}_0 = -0.18, \; \hat{SE}(\hat{\beta}_0) = 0.07,$$
$$\hat{\beta}_1 = 0.79, \; \hat{SE}(\hat{\beta}_1) = 0.23$$

The positive value of $\hat{\beta}_1$ indicates evidence of a positive relationship between the proportion of birds double-brooding in year *i* and population growth between spring of year *i* and spring of year *i*+1.

Likelihood ratio tests and Akaike's Information Criterion (see, e.g., Lebreton et al. 1992, Burnham and Anderson 1998) indicated that the above model provided a good description of the data. We conclude that this analysis provides strong evidence of temporal covariation between double-brooding and population growth, with years of substantial double-brooding associated with years of high population growth rate. Double-brooding thus appears to be an important component of reproductive rate that is associated with changes in population growth.

Discussion

We believe that these new approaches to the direct estimation of λ_i, and metrics reflecting the importance of vital rates and demographic components to λ_i, have great potential for population studies of marked birds. Although observation-based methods will continue to be important for estimating avian abundance and density, we recommend that ecologists involved in studies of marked birds take advantage these new capture-recapture methods for estimating λ_i.

Finally, we believe that there is great potential for developing models that use both capture-recapture and count data to estimate population growth rate and to investigate sources of variation in population growth. Such joint models would contain one component for each data source. The capture-recapture data would be modeled with capture, survival and population growth parameters as described in Pradel (1996), and the count data would be modeled with an initial abundance parameter and population growth parameters (Nichols and Hines 2002). Thus, the λ_i parameters would appear in both portions of the model, with the consequence that both sources of data contribute to their estimation. We would hope that this sort of modeling should permit more precise estimation of population growth rate and, more importantly, provide additional opportunities for modeling population change as functions of relevant covariates.

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