

Discussion comments on: ‘Approaches for the direct estimation of λ and demographic contributions to λ using capture-recapture data’

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We thought this was a very nice, comprehensive summary of various approaches to estimating parameters relevant to characterization of population growth (λ). Here, we will focus on several issues which Nichols & Hines (2002) raise. In fact, part of the measure of the significance of this paper is its breadth—it nicely reviews several key approaches to estimation of population growth using data from marked individuals: (i) the Jolly-Seber model and the robust design; (ii) the super-population approach (Schwarz & Arnason, 1996); and (iii) the temporal symmetry approach recently described by Pradel (1996). Nichols & Hines (2002) also force the reader to evaluate the relevant metric for analysis; specifically, population abundance, or population growth rate λ . Concerning population growth, the authors usefully distinguish between *projected* and *realized* growth rate. We briefly discuss this distinction later. Finally, and perhaps of greatest interest to ecologists, the paper describes several recent advances to partitioning variation in growth into contributions due to survivors and new individuals. This clearly reflects increasing interest in fully exploring the information contained in encounter histories of marked individuals. Recently renewed emphasis on analysis of recruitment, movement, emigration and so forth are very much motivated by development (or, in some cases, clarification) of methods aimed at partitioning sources of variation in the dynamics of a population. Much of this development has been prompted by previous EURING meetings but

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is very technical in nature. Adapting mark-recapture models to accommodate a variety of data types is important but the issues of overriding interest to biologists involve population processes not sampling processes. This paper usefully serves this need, while simultaneously pointing towards areas for future work.

Much of this paper is motivated, at least conceptually, by recent work by Pradel (1996) and Schwarz & Arnason (1996) who focused on alternative parameterizations of the Jolly-Seber model. As pointed out by Nichols & Hines (2002), these alternative parameterizations allow biologists to focus on biological problems. Despite the opening sentence of their paper: 'Population size ... is the state variable of interest in most management and conservation programs ... for animal populations', Nichols & Hines usefully emphasize λ , the rate of change in population size, as a measure of fundamental importance. It is precisely the developments of Pradel and Schwarz & Arnason that allow us to move away from abundance estimation to estimation of λ and associated parameters. However, we note that neither we, nor Nichols & Hines, are advocating eliminating consideration of abundance estimation, since variation in population growth as a function of changes in abundance is of fundamental importance to population and evolutionary ecologists. It is merely, that λ is a good omnibus measure, which integrates the combined effects of variation in a variety of demographic processes.

Nichols & Hines also consider several extended applications of the consideration of population growth rate to other questions of interest to biologists. For example, they present an interesting case involving data from a roseate tern study where mark-recapture modelling is used to assess the reliability of an index of population growth. Indices are a somewhat controversial topic. Often, the use of indices rests on the (generally) unreasonable assumption that p in the relationship $E(n_i) = pN_i$ is truly time-invariant. Yet indices probably represent the commonest form of population monitoring data. What makes the roseate tern example unusual is that the assumption of time-invariant p is explicitly tested. Because there will inevitably be at least some small temporal variation in p , an alternative approach that would be of interest would be to use mark-recapture modelling to decompose $\text{Var}(\hat{\lambda}_i)$ into $\text{Var}(\lambda_i)$ and also a sampling component due to temporal variation in p . It is the size of the relative contribution of temporal variation in p to $\text{Var}(\hat{\lambda}_i)$ that ultimately determines whether changes in $\hat{\lambda}_i$ are reflecting biological changes or artefacts arising during sampling.

Given these significant contributions, Nichols & Hines also raise several important issues, which we briefly elaborate.

1 Equivalence of the temporal symmetry and super-population approach

Nichols & Hines present the temporal symmetry approach (Pradel, 1996) and the 'super-population approach' (Schwarz *et al.*, 1993; Schwarz & Arnason, 1996) separately. However, because of the invariance of the principle of maximum likelihood, both approaches should be expected to give the same likelihood, with any differences reflecting how losses on capture are handled. Thus, the two approaches are in fact equivalent.

This can be demonstrated easily as follows. From equation (9) in Nichols & Hines (2002), the expected number of animals exhibiting capture history 011010 under Pradel's (1996) temporal symmetry model can be written as:

$$E(x_{011010} | N_1^-) = N_1^- \lambda_1 \xi_2 p_2 \phi_2 \dots \phi_4 p_5 \chi_5$$

However, it can be shown that

$$\begin{aligned}
 N_1^- \lambda_1 \xi_2 p_2 \phi_2 \dots \phi_4 p_5 \chi_5 &= N_1^- (\phi_1 + f_1) \left(1 - \frac{\phi_1}{\phi_1 + f_1} p_1 \right) p_2 \phi_2 \dots \phi_4 p_5 \chi_5 \\
 &= N_1^- (\phi_1 + f_1 - \phi_1 p_1) p_2 \phi_2 \dots \phi_4 p_5 \chi_5 \\
 &= N_1^- \left(\frac{\beta_1}{\beta_0} + \phi_1 (1 - p_1) \right) p_2 \phi_2 \dots \phi_4 p_5 \chi_5 \\
 &= \frac{N_1^-}{\beta_0} (\beta_1 + \beta_0 \phi_1 (1 - p_1)) p_2 \phi_2 \dots \phi_4 p_5 \chi_5 \\
 &= N_1 (\beta_1 + \beta_0 \phi_1 (1 - p_1)) p_2 \phi_2 \dots \phi_4 p_5 \chi_5 \\
 &= \text{'super population expectation'} \quad (\text{Schwarz } et \text{ al., 1993})
 \end{aligned}$$

2 Conceptual issues in modelling λ_i

Since $\lambda_i = \phi_i + f_i$, models involving constraints upon λ need to be considered carefully. For example, if a model is fit with time invariant λ , but time varying ϕ , then this implies a direct inverse relationship between survival and recruitment. While this may be true in a general sense, it is doubtful that the link between the two operates on small time scales typically used in mark-recapture studies.

Models where ϕ is time invariant while λ is allowed to vary over time are reasonable, as variations in recruitment are the extra source of 'variation' in λ . More complex models involving covariates have the same difficulty. Population-level covariates (e.g. weather) are interpretable, but it is potentially difficult to interpret individual-based covariates as operating on population growth. The root of the problem is that while individual covariates could apply to survival rates, the recruitment parameter is not tied to any individual—it is a population-based, average recruitment per individual in the population. What is needed is a generalization of the JS model where new entrants to a population are tied to existing members of the population, for example, if nestlings were identified with their parents.

3 Utility of retrospective analysis for prospective use

As clearly noted by Nichols & Hines, various methods exist for retrospective estimation of realized λ , which is simply the ratio of population abundance in successive years. However, retrospective analysis of variation in realized λ must be approached with considerable caution, for two reasons. First, variation in estimated population growth rate may confound changes in actual growth of the population with changes in the study design. For example, if the study area is enlarged in a given year (often done to serve other purposes in many studies), then the population will appear to have increased, such that there is a general expectation that the population will appear to have grown relative to the previous year (such that $\lambda > 1$). In many instances, especially when the study area is only a small part of the available habitat, and is not isolated, a population will be poorly defined, and thus

parameters that are function of population size (such as λ), will be difficult to interpret. Second, a clear distinction must be drawn between realized λ and asymptotic growth expectations based on the ergodic properties of the projection matrix. Clearly, both approaches rely on the same underlying vital rates, and both methods consider the effect of differences in one or more vital rates on some measure of the cumulative effect of all of the vital rates considered simultaneously—the growth of the population (either realized, or projected). The relationship between projected growth (deterministic or stochastic), the variance and covariance of the vital rates, and the observed (retrospective) variation in realized growth rate, is clearly in need of more study. However, regardless of which measure of population growth is used in a retrospective analysis, it is important to remember that such studies generally rely on analysis of a single realization of a complex set of underlying stochastic processes, which may limit the degree to which retrospective analysis may (or may not) inform prospective applications. Caswell (1989) and Renshaw (1991) have both cautioned against making prospective inferences from a single realization of the dynamics of a population; analysis of what has happened (retrospective) may not necessarily be informative about the future behaviour of a population.

In summary, we believe that the paper by Nichols & Hines will further stimulate interest in assessment of sources of variation and contributions to population growth. We anticipate that this paper will motivate further thinking about the relevant metrics for analysis of population dynamics.

REFERENCES

- CASWELL, H. (1989) *Matrix Population Models: Construction, Analysis, and Interpretation* (Sunderland, Massachusetts, USA, Sinauer).
- NICHOLS, J. D. & HINES, J. E. (2002) Approaches for the direct estimation of λ and demographic contributions to λ using capture-recapture data, *Statistical Analysis of Data from Marked Bird Populations*, *Journal of Applied Statistics*, this issue.
- PRADEL, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate, *Biometrics*, 52, pp. 703–709.
- RENSHAW, E. (1991) *Modelling Biological Populations in Space and Time* (Cambridge, UK, Cambridge University Press).
- SCHWARZ, C. J., SCHWEIGERT, J. & ARNASON, A. N. (1993) Using tag-recovery data to estimate migration rates, *Biometrics*, 49, pp. 177–194.
- SCHWARZ, C. J. & ARNASON, A. N. (1996) A general methodology for the analysis of capture-recapture experiments in open populations, *Biometrics*, 52, pp. 860–873.