New methodology for integrated monitoring of wild animal populations

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1. Introduction

Wild animal populations are sampled in a variety of different ways. In this paper we shall focus on two methods, one resulting in mark-recapture-recovery (mrr) data, and the other in data directly reflecting population size. We shall consider ways of analysing such data simultaneously, in an integrated manner.

The study of wild animal populations is an essential part of ecology, especially as populations vary in response to environmental change. Key demographic parameters are measures of survival and fecundity. In this paper we do not consider data on fecundity, but as we shall see, the integrated methodology proposed here extends naturally to encompass such data when they are available. For wild animals it is natural to measure survival on an annual basis. Annual survival is estimated from data on animals which are marked with unique rings or tags, which allow them to be identified when they are recaptured or resighted alive, or recovered after death. The marking process is assumed not to affect demographic parameters. Some studies focus on live recaptures, and these are typically small-scale; others concern dead recoveries, and these are often at a national level; some involve both recovery and recapture. The analysis of wild animal data is made interesting by the typically large fractions of marked animals of unknown fate each year, and sometimes the presence of emigration, which can be confounded with survival. Although originally intended to provide information on population sizes, the most recent emphasis in experiments on marked wild animals has been on estimating survival. However

Nichols and Hines (2002) review the approaches used for estimation of the population growth rate, one of which is the method of Pradel (1996), using information from marked animals.

The determination of population growth or decline may be done by means of direct observation. At the national level, information may be collected from a large number of distributed sites to form an annual index. In some cases observation may be made from the air or from the sea. Just as the analysis of marked animals has mainly focused on the estimation of survival, population size data, although naturally dependent upon survival, has played a secondary role with regard to survival. Typically, when both types of data are available for a particular species, the data from marked animals are analysed to produce survival estimates, which are then used to make predictions regarding population growth via deterministic Leslie population models (Leslie, 1945). These predictions are then compared with the direct observations on population change. Examples are provided by Burnham et al (1996) and Gauthier et al (2001). Typically the integration of diverse data has until recently been ad-hoc.

2. A simultaneous analysis

Besbeas, Freeman et al (2001) provide a methodology for the simultaneous analysis of population and mrr data. The kernel of this approach is a state-space model for the population data. Making use of a Leslie matrix, this allows us to construct a likelihood, L_c, using a Kalman Filter. Making an assumption of independence between the two data sets, we are then able to form a combined likelihood, L_j, as $L_j = L_r \times L_c$, where L_r is the ring-recovery likelihood. The L_r component is a function of survival probabilities and recovery and/or reporting rates, while the L_c component is a function of survival probabilities and parameters relating to fecundity. A further likelihood component could result from analysing fecundity data. Model parameters may vary with age and time and could if appropriate be regressed on individual and environmental covariates (see, eg., Catchpole et al, 2000). The simultaneous analysis unites methodology from the areas of population and mrr modelling, through classical model-fitting by maximum-likelihood. A drawback of the approach is that L_r may be the end-result of a complex modelling procedure, typically involving a specialised computer package such as MARK (White and Burnham, 1999), which would make the process of forming L_j complicated, if not impossible. Illustrations are provided by Catchpole et al (2000) and Gauthier et al (2001). In the former case, a specialised computer program for the analysis of integrated mrr data is used to describe the survival of the *Soay* sheep population of St. Kilda. The model selected is different for males and females, reflecting their different life-styles. Survival also varies with age, and at different ages, different covariates are found to be important; covariates also interact with each other, as well as age and sex (Coulson et al, 2001). Besbeas, Lebreton and Morgan (2001) provide a solution to this difficulty, which is based on a multivariate normal approximation to L_r, centred on the maximum likelihood parameter estimates from just modelling the mrr data alone. It is only necessary to use the parameters of interest; nuisance parameters can be ignored. Applied to data on British lapwings, *Vanellus vanellus* and grey herons, *Ardea cinerea*, the approximation is shown to perform exceptionally well. Current research focusses on making the methodology computationally straightforward and portable. In addition we are further evaluating the work in a range of applications. We shall now illustrate the application of the approximate approach to the analysis of the greater snow geese, *Chen caerulescens atlantica*.

3. The example of the greater snow goose

The paper by Gauthier et al (2000) describes a complex mrr analysis of the survival of the greater snow goose. In this case the annual survival probability, ϕ, of adult birds is modeled as: $\phi = (a - bh)r$, where h is a measure of hunting mortality, and r is a parameter describing band retention. The mrr analysis was carried out by the program SURGE (Pradel and Lebreton, 1993). In the combined analysis there are just four parameters to be estimated, viz a, b and r, and a parameter reflecting measurement error. The last parameter, c, is taken as a coefficient of variation, making use of the census data available for the species. The census data are obtained from aerial surveys, conducted in the spring, and measure the entire goose population, not just the adults. The Leslie matrix formulation involves four separate age-groups. They were found to be insensitive to assumptions made regarding fecundity estimates (not discussed here). The results are shown in Table 1.

Table 1. Maximum-likelihood parameter estimates, (i) mrr alone; (ii) approximate joint analysis. Given are the parameter estimates, together with estimated standard errors.

Parameter	(i)	(ii)
r	0.9500(0.0080)	0.9471(0.0070)
a	0.9260(0.0219)	0.9327(0.0185)
b	1.2070(0.5597)	1.2904(0.5124)
c		0.1514(0.0289)

The estimate of the coefficient of variation, $\hat{c} = 15.14\%$ is about what would be expected, given the uncertainties of the aerial survey. The model provides overall a good fit to the census data, but is unable to describe small-scale fluctuations. In addition, it is possible to judge model performance by making a comparison with a separate census of population size, taking place in the autumn. This comparison, not shown here, is also good overall, but suggests that the fecundity estimation is slightly optimistic. The detail of this study will appear in a paper in preparation, by Gilles Gauthier and the authors of this paper. We are grateful to Gilles Gauthier for his discussion of the snow goose study and his permission to use the data for this paper.

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RESUME

Des recherches récentes ont montré comment des données et des modèles séparés, décrivant des aspects distincts de la démographie de populations *in natura*, peuvent être combinés en une seule analyse. L'approche proposée est centrée sur un modèle de dynamique des populations considérant un espace d'états, et assemble des notions venant du champ de la modélisation dynamique et de celui de l'analyse des données de marquage recapture *sensu lato.* L'assemblage des différentes composantes de l'analyse conjointe est grandement facilitée par l'emploi d'approximations normales appropriées. Comme illustration, nous analysons des recensements et des données de survie de l'Oie des Neiges *Chen caerulescens atlantica.*