Multi–state models: metapopulation and life history analyses

A. N. Arnason & E. Cam

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Multi–state models are designed to describe populations that move among a fixed set of categorical states. The obvious application is to population interchange among geographic locations such as breeding sites or feeding areas (e.g., Hestbeck et al., 1991; Blums et al., 2003; Cam et al., 2004) but they are increasingly used to address important questions of evolutionary biology and life history strategies (Nichols & Kendall, 1995). In these applications, the states include life history stages such as breeding states. The multi–state models, by permitting estimation of stage–specific survival and transition rates, can help assess trade–offs between life history mechanisms (e.g. Yoccoz et al., 2000). These trade–offs are also important in meta–population analyses where, for example, the pre–and post–breeding rates of transfer among sub–populations can be analysed in terms of target colony distance, density, and other covariates (e.g., Lebreton et al. 2003; Breton et al., in review). Further examples of the use of multi–state models in analysing dispersal and life–history trade–offs can be found in the session on Migration and Dispersal. In this session, we concentrate on applications that did not involve dispersal. These applications fall in two main categories: those that address life history questions using stage categories, and a more technical use of multi–state models to address problems arising from the violation of mark–recapture assumptions leading to the potential for seriously biased predictions or misleading insights from the models.

Our plenary paper, by William Kendall (Kendall, 2004), gives an overview of the use of Multi–state Mark–Recapture (MSMR) models to address two such violations. The first is the occurrence of unobservable states that can arise, for example, from temporary emigration or by incomplete sampling coverage of a target population. Such states can also occur for life history reasons, such as dormancy or the inability to capture non–breeders and in these cases, the rates of transition to and from the unobservable state provide life history insights. The second failure Kendall considers is the misclassification of states (for example in models involving states for age, sex, breeding condition, etc. where these cannot be determined without error). He reviews solutions for these that encompass three approaches: constraints on parameters to ensure identifiability (the least desireable solution); incorporating additional information; and the use of sub–sampling that leads to the multi–state application of the Robust design. In passing, Kendall makes reference to what are probably the 3 most significant developments in the area of multi–state models since the last Euring meeting: (1) the incorporation of tag–recovery data in addition to recapture data in MSMR models; (2) a comprehensive methodology for goodness–of–fit testing and assessing parameter identifiability in MSMR models; and (3) the development of new software to make these methods accessible. Much of (2) and (3) is based on the landmark thesis of Olivier Gimenez (Gimenez, 2003).

Two further presentations in this session followed up the plenary theme of unobservable and misclassified states. The presentation by Roger Pradel (Pradel, in press), represented in these proceedings as a brief abstract only, dealt with the problem of errors in sexing animals; an example of what Kendall refers to as bidirectional misclassification. The presentation by Marc Kéry (Kéry & Gregg, 2004) is, we think, the first

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occurrence in the Euring proceedings of an application of mark–recapture to plants. This presentation, represented in these proceedings by an extended abstract with complete references, is an example of dormancy as an unobservable state. Even though the non–dormant states are observed with probability 1, MSMR permits reliable estimation of the proportion of dormant plants in the presence of state ambiguity (dormant or dead?) and can permit assessing the influence of environmental covariates on this proportion.

The presentation by Christophe Barbraud (Barbraud & Weimerskirk, 2004), included in these proceedings as an extended abstract, takes the life–history trade–off application of MSMR models a step further by taking into account environmental and individual covariates on survival. The trade–off considered is between survival and transitions among several states describing breeding experience of long–lived petrels and how it is affected by harsh climate conditions. The study is a showcase for the powers of the new software (U–Care and M–Surge).

The paper by Senar and Conroy (Senar & Conroy, 2004) is a novel application of MSMR models to animal epidemiology. States included age, sex and infected state and the model permits estimation of survival, infection, and recovery rates for birds during an outbreak of Serin avian pox. The use of a MSMR model permits estimation of the prevalence rate unconfounded by differences in capture rates of infected and non–infected birds. Here too there is a potential for ambiguous states in that the uninfected state might include both immune post–infection animals and susceptible pre–infection animals and these groups would likely have different survival rates. The authors are able to deal with this because of the length of the study and the availability of data outside the main outbreak.

Finally, this session includes a paper by Jamieson and Brooks (Jamieson & Brooks, 2004) that appears to lie outside the MSMR theme of this session but which was included because of its relevance to metapopulation analyses. Our call for papers for this session also invited papers illustrating multi–population meta–analysis and use of Bayesian methods. By these criteria, their paper is no outlier. It addresses the longstanding question of density dependence in game bird survival; a question of great interest to theoretical biologists and of vital importance to wildlife managers. The controversy arises because the density dependence revealed in estimates may not reflect the underlying density dependence mechanism in the population parameters. The Bayesian analysis presented here circumvents this problem by fitting a 2 stage model: a time series model for the true population sizes N_t allowing for density dependence and then for the distribution of the estimates $\hat{N}_t$ given the N_t. The use of data–intensive sampling methods to fit this model neatly sidesteps the insurmountable problem for a purely frequentist (likelihood) approach of having to integrate out the N_t from the likelihood. (As a historical note, this problem confronted George Jolly when he developed the original Jolly Seber model and he handled it by simply fixing the unobservable marked pool sizes M_t a at their maximum likelihood values… a procedure that biases the s.e. of the estimates). This paper is also instructive as the Bayesian methodology provides a straightforward means of accounting for model uncertainty in parameter estimates and model predictions.

In summary, the session was a gratifying and useful mix of overview and case studies. The case studies are valuable for their sophisticated use of multi–state and Bayesian models and the subtlety and care with which inferences are drawn from the model fitting results.

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