

Discussion comments ‘Multistate recapture models: modelling incomplete individual histories’—why are we doing all this?

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The paper by Lebreton & Pradel provides an excellent overview of what has become possible in our quest to model survival, recapture and transition rates. It is really impressive. It may, however, be useful to put this ever-growing capability into a biological perspective and ponder why we are doing all this. In these comments I will put the present capabilities into my biased perspective as a population/evolutionary ecologist.

A major challenge for population ecologists working on natural populations using organisms that are large enough to be marked and studied individually was simply to know how large the population is: how many individuals are we studying? The Jolly-Seber approach that became available in the mid 1960s was a major breakthrough, although it soon appeared that estimates tended to be rather imprecise, essentially for two reasons: for very few populations could all the conditions be met that were required to obtain an unbiased estimate, and for very few populations was it possible to maintain a sufficiently high recapture rate to obtain an accurate estimate. As a side result, the Jolly-Seber estimates also provide estimates of survival rates and of so-called births, that are actually the number of individuals recruiting into the population.

Methods to estimate survival rates from capture-recapture data began to be developed and I happened to discover SURGE as an external examiner of Jean Clobert's PhD thesis in 1981. Here the question asked no longer was ‘what is population size’, but rather ‘can we calculate survival rates and can we identify factors that cause survival rates to vary?’. To some extent, this new question was related to the fact that, in population ecology, more evolutionary (Life-history trade-off) questions were being asked, and we needed good estimates of survival.

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During the EURING conference, Ken Burnham commented that the Bayesian methods take a lot of computer time and hence other methods might be preferred. Note that when Jean Clobert gave me an early copy of SURGE I had to run each single model overnight as a batch job. Still, I needed to estimate survival rates of the tits I was studying and I had the choice of using the methods as described by David Lack, or be patient and run one analysis per night.

We have come an unbelievably long way in the past 20 years. To a large extent the intense collaboration between mathematicians/statisticians/biometricians and biologists nurtured and fostered by the EURING meetings can explain this. I have a feeling, however, that at the moment the statisticians are ahead of the biologists. They have developed the tools, but we have not often collected sufficient good quality data over a long enough time period to take full advantage of the tools. There exist, still, too many examples of papers being published today that do not use the appropriate models for analysis. I have learned (the hard way) that analysing capture-recapture data for survival analysis, even with the remarkable software that has been developed by the statisticians, cannot easily be done by biologists without help from, or training by, the people who have a complete understanding of these tools. I would even claim that help from statisticians needs to be invoked when a study to estimate survival and dispersal rates is being set up.

One of the reasons I am interested in estimating survival rates correctly is to identify the selection forces that influence them: which external variables influence survival rates, and how do they work? Do all individuals respond in the same way, and if so what determines differences in survival probabilities (age, sex, origin, previous history, development, reproductive effort, study site, etc)? Can we determine whether, and to what extent, survival is density dependent? Given the limitation of most data sets and the very large numbers of survival models that can be generated it might be helpful, in that context, to ask a number of *a priori* (biological) questions that we want to address before we begin all the calculations.

One final remark: we still need good tools to estimate population size.