Multistate recapture models: modelling incomplete individual histories

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ABSTRACT   *Multistate capture-recapture models are a natural generalization of the usual one-site recapture models. Similarly, individuals are sampled on discrete occasions, at which they may be captured or not. However, contrary to the one-site case, the individuals can move within a finite set of states between occasions. The growing interest in spatial aspects of population dynamics presently contributes to making multistate models a very promising tool for population biology. We review first the interest and the potential of multistate models, in particular when they are used with individual states as well as geographical sites. Multistate models indeed constitute canonical capture-recapture models for individual categorical covariates changing over time, and can be linked to longitudinal studies with missing data and models such as hidden Markov chains. Multistate models also provide a promising tool for handling heterogeneity of capture, provided states related to capturability can be defined and used. Such an approach could be relevant for population size estimation in closed populations. Multistate models also constitute a natural framework for mixtures of information in individual history data. Presently, most models can be fit using program MARK. As an example, we present a canonical model for multisite accession to reproduction, which fully generalizes a classical one-site model. In the generalization proposed, one can estimate simultaneously age-dependent rates of accession to reproduction, natal and breeding dispersal. Finally, we discuss further generalizations—such as a multistate generalization of growth rate models and models for data where the state in which an individual is detected is known with uncertainty—and prospects for software development.*

1 Introduction

The idea of taking account of geographical sites in capture-recapture analysis dates back to Chapman & Junge (1956) and was developed by Darroch (1961) (see

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review by Seber, 1982, p. 431 ff). The situation was that of a closed population over two dates of sampling, i.e. a generalization of the Lincoln-Petersen index to a geographically stratified population. A much more general situation was covered by Arnason (1972, 1973) with three dates, 2 and s sites in the 1972 and 1973 papers, respectively, and both time-dependent recruitment and mortality. This model, later treated in its full generality (k dates, s sites) by Schwarz *et al.* (1993) in parallel to multisite models for tag-recovery data, is thus a natural generalization of the usual one-site Jolly-Seber model (Jolly, 1965; Seber, 1965). Similarly, individuals are sampled on K discrete occasions, at which they may be captured or not. However, contrary to the one-site case, the individuals can move within a finite set of sites, or states, between occasions.

Arnason's pioneering model remained little used for a long time, probably because its interest was not fully realized, because it seemed to have limited robustness as a consequence of its large number of parameters (Viallefont & Lebreton, 1993), and because it remained difficult to use in practice in the absence of explicit estimates for $K > 3$ and of software for numerical estimation. The development of software for constrained models, such as MSSURVIV (Brownie *et al.*, 1993) and MARK (White & Burnham, 1999), permitted robust analyses, initiated by Hestbeck *et al.* (1991). Nichols *et al.* (1994) opened the way to further applications by considering individual states more generally than geographical position. To follow the traditional vocabulary for discrete dynamical models such as Markov chains, and to avoid the idea of deterministic assignment of individuals inherent in other contexts with the word stratum, the name 'multistate models' seems preferable to 'multistratum models' (Pollock, personal communication). The growing interest in spatial aspects of population dynamics (Hanski & Gilpin, 1991) and in individual variability (Clutton-Brock, 1988) is one of the main reasons that presently make multistate models a very promising tool for population biology. Nichols *et al.* (1993) and Nichols & Kaiser (1999) review further works devoted to the estimation of dispersal.

The purpose of this paper is to review the state-of-the art for multistate capture-recapture models, and the potential for further development. We will first present the basic principles of the multistate equivalent of the survival part of the Jolly-Seber model (Section 2), and then examine its biological relevance (Section 3), already well illustrated in the literature. We will go on by exploring non-standard applications (Section 4) that make multistate models a general framework for the treatment of individual recapture data. These non-standard cases comprise mixtures of information (Lebreton *et al.*, 1999) and multisite accession to reproduction (Lebreton *et al.*, in preparation). However, several numerical and statistical issues (Section 5) still have to be explored before the full potential of multistate models can be used. We then discuss further generalizations presently under study (Section 6) and some perspectives. While many of our comments will be developed for live recapture models, and will be subject to our personal bias, they apply, in general, also to tag-recovery models (Schwarz *et al.*, 1993).

2 Principles of multistate models

The multistate Arnason-Schwarz model (Arnason, 1973; Schwarz *et al.*, 1993) considers capture-recapture histories over K occasions and s sites. The capture histories can thus be represented as a series of 0 (individual not captured) and, say, integer values i ($i = 1, \ldots, s$), designating for each capture the state where it

TABLE 1. Recapture histories and typical probabilities in one-state and two-state recapture models

Situation	One state	Two-state
Basic model	Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965)	Arnason-Schwarz model (Arnason, 1973; Schwarz *et al.*, 1993)
An example of Capture history of an individual	0101100	0102200
Survival or Survival/Transition probabilities	Time dependent $\phi_1, \phi_2, \ldots \phi_{K-1}$	State (superscript) and Time (subscript) dependent $\phi_1^{11}, \phi_1^{12}, . \phi_1^{21}, \phi_1^{22}, . \phi_2^{11}, \ldots \phi_{K-1}^{22}$
Capture probabilities $(1 - p$ denoted as $q)$	Time dependent $p_2, p_3, \ldots p_K$	State (superscript) and Time (subscript) dependent $p_1^1, p_1^2, . p_2^1, p_2^2, \ldots p_K^2$
Probability of capture history	$\phi_2 q_3 \phi_2 p_4 \phi_3 p_5 \chi_5$	$(\phi_2^{11} q_3^1 \phi_3^{21} + \phi_2^{21} q_3^2 \phi_3^{22}) p_4^2 \phi_3^{22} p_5^2 \chi_5^2$ the terms χ are more involved than in the one state case

took place (Table 1). We will present the classical case of individuals surviving, and moving across states over time, conditional on initial releases, with a time dependence in parameters, i.e. the multisite generalization of the Cormack-Jolly-Seber (CJS) model.

The parameterization must take account of possible movements between the states: the survival probabilities φ_k are replaced by survival-transition probabilities φ_k^{ij}. The indices i and j ($= 1, \ldots, s$) indicate states (of arrival and departure) and the index k ($= 1, \ldots, K$) indicates occasions of capture. The recapture probabilities, which are time-dependent in the one-state case, become time and state dependent in the multistate one. When compared with the CJS model, the number of parameters jumps from $2(K - 1)$ to $s(s + 1)(K - 1)$. With ten occasions and three states, the change is from 18 to 54, with 20, from 38 to 114. It seems natural to expect more problems of stability of estimation, precision of estimates, effects of sparseness on tests and identifiability of parameters: in general, multistate models will be more demanding in terms of data than single-state models. At the same time, they may still be the only sensible approach to many biological questions.

The probability of an individual capture history must account for all possible movements, and is clearly more involved in the multistate case than in the single state one. In the example of Table 1, at time 3, the individual can be either in state 1 or in state 2.

The survival transition probabilities can be rewritten as the product of a conditional probability of survival and of transition probabilities. For instance, with survival conditional on the departure state denoted as ϕ_k^i, the survival-transition probability φ_k^{ij} is the product of the survival probability and of a transition probability ψ_k^{ij} as (Hestbeck *et al.*, 1991):

$$\varphi_k^{ij} = \phi_k^i \psi_k^{ij}$$

The ψ_k^{ij} are probabilities of movement, conditional of survival. Further ways of separating the survival and movement are developed by Joe & Pollock (this issue). Since the survival transition probabilities depend only on the last state reached by the individual, and not on the past, the movement model is Markovian. This encourages the use of matrix notation, a traditional and powerful tool for this type of model (Bailey, 1964, p. 3). The matrix $\Psi_k = [\psi_k^{ij}]$ is column stochastic, i.e. the

ψ parameters are redundant since $\Sigma_j \psi_k^{ij} = 1$. In accordance with traditional matrix notation, we assume ψ_k^{ij} is a probability of movement from j (column index) to i (row index).

The basic model presented above assumes that the fate of an individual does not depend on its past beyond the last occasion. The individuals will be considered as independent to obtain multinomial distributions. The model belongs then to the wide class of 'product-multinomial models'. As usual for many models for discrete data (McCullagh & Nelder, 1989) estimation is, in general, based on maximum likelihood, with iterative minimization of the deviance equal to minus twice the log-likelihood. Matrix notation alleviates a great part of the burden of writing down the likelihood. The likelihood is indeed an exact matrix generalization of the CJS likelihood (Brownie *et al.*, 1993), provided adequate matrices, such as $P_k = \mathrm{diag}(p_k^i)$ are used (see for example, Nichols *et al.*, 1993, p. 270). Matrix notation in the closed population model over two occasions, developed by Darroch (1961), leads also to an exact matrix generalization of the Lincoln-Petersen index (Seber, 1982, p. 433). This clearly indicates that many more existing one-state models could be generalized. The matrix notation is also very convenient for developing software for multistate models in high level languages such as Matlab (Almeras, 1996; Lebreton *et al.*, 1999). In all cases, provided the redundancy in parameters it induces is managed, one can systematically add a 'dead state' to any multistate model (Lebreton *et al.*, 1999). Even if this state is not observable, this makes the $\Phi_k = [\varphi_k^{ij}]$ matrix column stochastic. The calculation of the likelihood reduces then to products of Φ, P and I-P, the χ terms, i.e. the probabilities of never been captured again, becoming inherent in these matrix products (Caswell, 2000, pp. 138-140; Fujiwara & Caswell, in preparation). This trick is also valid for the one site CJS model, viewed as a two-state (alive-dead) model.

The similarity with the CJS model and the rapid increase in the number of parameters with the number of states and occasions (Viallefont & Lebreton, 1993) lead naturally to Generalised Linear Model (GLM) ideas (as for the CJS model; Lebreton *et al.*, 1992) to develop constrained (e.g. constant parameter) and further generalized (e.g. age dependent) models. Presently, this is the basis for the wide range of multistate models that can be fit by the maximum likelihood method using MARK (White & Burnham, 1999) which expands to a much wider class of models the philosophy developed in SURGE (Clobert & Lebreton, 1987; Pradel & Lebreton, 1991; Reboulet *et al.* 1999) for CJS models. The maximum structure for variation in ϕ, ψ, and p in MARK is a dependence by group, time and age (in the sense of the time elapsed since first capture) independently for each parameter. For each state and group, MARK will present successive triangular matrices of indices (Pradel & Lebreton 1991) (or parameter index matrices, PIMs; White & Burnham, 1999) with $(K-1)(K-2)/2$ values that describe the variation of the parameter considered over age and time. When the PIM is filled in with a single number, the corresponding parameter will be constant over time and age. This philosophy is familiar to users of SURGE and MARK. With s states and g groups, MARK will present $s \times g$ PIMs for the survival probabilities ϕ, $s \times (s-1) \times g$ PIMs for the movement probabilities ψ, and $s \times g$ PIMs for the recapture probabilities p. Further linear constraints on transformed parameters can be applied via design matrices. Only models conditional on the first release are available. More refined models can, in theory, be fitted using SURVIV (White, 1983) for which a modified version facilitating the implementation of multistate models, MSSURVIV, was developed by J. E. Hines (in Brownie *et al.*, 1993, p. 1176).

3 Biological relevance and case studies

The most direct interest of multistate models is for estimating dispersal, the very purpose for which they were developed. Lebreton & Landry (1979) applied Darroch's (1961) closed population model to study movements of Black-headed Gull *Larus ridibundus* chicks before fledging within a large colony. The landmark paper by Hestbeck *et al.* (1991) investigates exchanges of Canada geese *Branta canadensis* between three large wintering areas (Mid-Atlantic, Chesapeake, Carolinas), from one year to the next over $K = 3$ consecutive winters, based on the open population multistate models described above. The time dependent Arnason-Schwarz model has 24 parameters, some of which are non-separately identifiable. Interestingly, Hestbeck *et al.* (1991) both particularize the time-dependent model, by equality constraints between parameters, and generalize it, by considering a memory model in which birds that moved tend to come back with a greater probability to the area used just before. Particular parameter values are assumed for the interval after the initial release, since no information is available on the area used before. In a capture-recapture context, the areas consecutively used are often unknown, and a full likelihood approach raises specific difficulties (Brownie *et al.*, 1993) to which we will return later (Section 6). Taking advantage of the moderate number of capture histories (63) with only three occasions, Hestbeck *et al.* (1991) were able to compute the expected number of individuals in each capture-history, and thus provide a goodness-of-fit χ^2 test for each model fitted. This approach is unfortunately impractical for large values of K.

The Arnason-Schwarz model and constrained variants are also a natural frame-work for studying breeding dispersal (Greenwood & Harvey, 1982), i.e. dispersal between successive breeding sites. Spendelow *et al.* (1995) studied, in that way, dispersal of adult Roseate Tern *Sterna dougallii* between four colonies over 5 years, with 80 parameters for the Arnason-Schwarz model. Specific constraints, such as the effect of birth site (birds had been ringed as chicks) were investigated in a search for parsimony. However, the best fit was obtained for the fully time-dependent model. Site fidelity can be measured by the probability of coming back to the same colony, conditional on survival, i.e. ψ_k^{ii}. The estimates were, as expected, very high, the smallest being equal to 0.825, and 12 out of 16 being above 0.900. On the contrary, the capture probability varied greatly between sites.

This type of approach will certainly help to improve our understanding of dispersal, for which long-term studies of colonial birds are a very relevant biological model. In the first phase, for many data sets, one may expect fairly robust estimation from simple models with transition probabilities constant over time that will have only a few more parameters that CJS models on data pooled over the sites. In the second phase, more relevance could be achieved by modelling transition probabilities with, for example, additive effects of the origin and target population sizes and of distances between sites. The movement probabilities are the most numerous parameters, and that is where GLM ideas will be the most useful for more relevance and parsimony. Besides the logit link, various generalizations have been used (Multinomial logit: Almeras, 1996; Polychotomous logit, Fujiwara & Caswell, in preparation) to keep the column sums of the transition matrices in range. Besides a more precise evaluation of the merit of these various link functions, specific reflections on adequate constraints for the transition probabilities are a real need. Further use of multistate models to estimate dispersal will have often to account for age-effects. While this is quite practicable, taking advantage of the

PIMs in MARK, the model structure may have to be very specific, as we will see later.

The next idea is to use multistate models with states defined by individual covariates changing over time rather than geographical sites. Nichols *et al.* (1992) estimate in that way transition probabilities between body weight classes in the meadow vole *Microtus pennsylvanicus*. When the states are based on a stratification of an originally continuous covariate, one could build specific constraints to reduce the number of parameters even with a large number of states. This would lead in the limit to time series models for the continuous covariate, with missing data because of the recapture context. Defining states in relation to reproductive success, e.g. as breeder or non-breeder, provides canonical capture-recapture models for trade-off studies, as proposed by Nichols *et al.* (1994). Several case studies based on that premise concluded indeed that breeders at time *t* had a higher probability of breeding at time *t* + 1 than non-breeders (Cam *et al.*, 1998, Kittiwake *Rissa tridactyla*; Tavecchia, 1997; Flamingo *Phoenicopterus ruber*; see also Doligez & Clobert, this issue). This suggests that, as is often the case in such non-manipulative studies, differences in quality between individuals and/or microhabitats are prominent and may have masked any existing trade-offs (Nur, 1990). Capture-recapture re-analyses of existing data sets from manipulative studies, most often studied in the past based on return rates, are still badly needed (Clobert, 1995).

Even when the transition probabilities are not of direct interest, and even if survival is constant across states, it seems sensible to recommend a multistate model for improving survival estimation, as soon as recapture probability varies, e.g. as a consequence of differences in effort of recapture. A great part of the heterogeneity of capture will be removed compared to a CJS analysis over pooled data, with a limited lack of precision if constant transition probabilities can be assumed as a first approximation. This could also be advantageous in a closed population context, for which generalizations of Darroch's (1961) model to more than three occasions have still to be developed.

At this stage, the link is direct and very promising, with longitudinal studies with missing data. Fitzmaurice *et al.* (1994) provide a good example of such data. They analyse changes in weight (as two categories: obese and not obese) in a sample of 1014 children of both sexes. The study is over three occasions (1978, 1980, 1982) which correspond also to a change in age (7-9, 9-11, 12-14 years, respectively). The proportion of missing data is large since over 50% of the children have at least one missing value. Such data are amenable to a multistate capture-recapture modelling (Almeras, 1996), since the transition probabilities, such as Pr(non-Obese at *t* + 1/Obese at time *t*), give potentially a good insight into the process. A reanalysis of these data is given in Table 2. Unfortunately, Fitzmaurice *et al.* (1994)

TABLE 2. Longitudinal data (Fitzmaurice *et al.*, 1994) analysis by a multistate model: constant parameter model results

Parameter	Estimate	Standard error
Pr(Survival)	0.8709	0.0116
Pr(Recapture)	0.8997	0.0128
Pr(Non Obese/Obese)	0.1169	0.0104
PR(Obese/Non Obese)	0.2701	0.0285

develop only marginal models, i.e. models of Pr(Obese) and do not consider transitions. The dichotomy between models for longitudinal response and models for transitions is clear cut in the analysis of longitudinal data (Kosorok & Chao, 1996). Fitzmaurice *et al*.'s (1994) models can account for data missing at random (MAR: the probability that a value is missing depends on the child's category at time of sampling) or missing completely at random (MCAR: the probability that a value is missing is independent of the child's category). The counterpart in a capture-recapture setting is a state-dependent (MAR) or state-independent (MCAR) probability of capture. The increase in Pr(obese) with age observed by Fitzmaurice *et al*. (1994) (their Table 1, p. 610) is induced in the capture-recapture approach from the difference between the estimated transition probabilities (Table 2). We find, based on AIC model selection, no effect of gender on the transitions, in accordance with Fitzmaurice *et al*.'s (1994) results in which none of the z tests for gender main effects or interactions is significant. More surprisingly, the survival probability in our final model differs from 1, indicating that individuals may be leaving the study permanently: in this case the probability that a value is missing is slightly more involved than 1-Pr(capture) since it depends also on Pr(survival). However, the latter being also independent of sex and time, the missing data mechanism selected is still MCAR. The most severe inadequacy of Arnason-Schwarz models for these data is that it works conditional on the first value observed. A more adequate model would be a multistate capture-recapture model for a closed population, with the unusual feature that the population size is known, in the sense that the history '000', corresponding to children selected in the sample but for whom no obesity values were eventually available, is observed. In such a case, a refined modelling of the capture process is perhaps feasible, perhaps even more than in the usual closed population models, in which population size is, in general, unknown and is the parameter of primary interest. The analogy also suggests that heterogeneity in the missing data process in longitudinal studies could well be handled as heterogeneity of capture in closed population capture-recapture models (e.g. Chao *et al*. 1992).

In the latter example, multistate models are viewed as statistical models for Markov chains with missing data. This point of view was indeed considered by Dupuis (1995) to frame the multistate models in the hidden Markov chain context and develop Bayesian algorithms.

From the applications already available, the generality of multistate models seems thus very promising for population biology. Still, all the examples or developments cited—apart from the memory model—are in a fairly restricted framework. Some non-conventional applications open even broader perspectives.

4 A general framework?

A first step beyond existing analyses is to consider age effects in multistate models. For instance, Gaillard (unpublished) investigated accession to reproduction in the Roe deer *Capreolus capreolus* based on females marked during their first winter, using a model with two states (reproductive, and non-reproductive). As the study took place in an enclosed reserve, the immature survival was not affected by dispersal and, although the probability of capture varied with reproductive status, i.e. between states, there was no major heterogeneity of capture in a given age class. This is no longer the case when non-breeders are not observed, as often in studies of birds during the reproductive season, e.g. colonial waterbirds. Before full adult

breeding propensity is reached, each age class comprises individuals with probabilities of capture equal to 0 (the non-breeders) and greater than 0 (the breeders). Age-dependent survival capture-recapture models are thus not adapted to such data because of this intrinsic heterogeneity of capture. Clobert *et al.* (1994) developed a model that accounts for this heterogeneity, and could be fitted in the CJS framework based on a splitting of the histories in two groups. Pradel & Lebreton (1999) showed that this model could be viewed as a two-state (breeders and non-breeders) age-dependent model, with triangular transition matrices (breeders cannot come back to the state 'non-breeder'), and a probability of capture equal to zero for non-breeders.

This recruitment model admits a multisite generalisation (Lebreton *et al.*, submitted). We give here just a brief account of the main ideas. With, for example, three sites A, B, C, the total number of states is 6, since breeders and non-breeders are considered as in Clobert *et al.* (1994): breeders in A, B and C, non-breeders in the same three sites. For the sake of simplicity, these six states are denoted as A, B, C, a, b, c respectively. A typical history is, for instance, 0a0AB0, for an animal marked as young at occasion 2 in Site A, recaptured (or resighted) as a breeder in site A at occasions 4, in B at occasion 5 and not observed at occasions 3 and 6, in the latter case possibly because it is dead. When animals marked as young are considered, the first capture is always a, b or c. Since only breeders are detectable, the states for non-breeders (a, b and c) never reappear in the recapture histories, and the recapture probability vectors will always be alike ($p_a, p_b, p_c, 0, 0, 0$). Survival is considered as partly age dependent, with immature local survival from age 0 to 1, and 'adult' survival later. The stochastic movement matrices are described in block-matrix notation in Table 3. The 3×3 sub-matrix B characterizes breeding dispersal. The 3×3 sub-matrix N characterizes natal dispersal and is supposed to take place entirely in the first year of life. Intermediate movements cannot indeed be modelled and N represents transitions between birthplace and the first breeding site. Afterwards, no more movement between sites is considered for non-breeders. Accession to reproduction can then be represented by the probabilities of becoming a breeder a_{ik}, depending on site i and age k. An assumption of full breeding adult propensity, here at age 6, must be included in the model. There is no non-breeder left afterwards. After first year survival can be site-dependent, but is assumed to be the same for breeders and non-breeders, an assumption already made by Clobert *et al.* (1994). This is a key assumption of the model as will be seen later (Section 5, identifiability). This model was applied to the metapopulation of Roseate tern studied by J. A. Spendelow (Spendelow & Nichols, 1989; Spendelow 1991). Under the final model considered, the estimates of breeding and natal dispersal are given

TABLE 3. Structure of the transition between states in the multisite model of accession to reproduction, here with breeding starting at age 2, and full recruitment at age 6. The B submatrix present at all ages serves for breeders of unknown age marked in parallel to young individuals

Age	0 to 1	1 to 2	...	4 to 5	5 to 6	k to $k+1$, $k > 6$
Dispersal matrix Ψ	B 0	B diag(A_2)	...	B diag(A_5)	B I	B 0
	0 N	0 I − diag(A_2)		0 I − diag(A_5)	0 0	0 0
Remarks	Natal and breeding dispersal	Accession to reproduction at age 2	...	Accession to reproduction at age 5	Full recruitment at age 6	No more non-breeders

TABLE 4. Estimates of natal (N) and breeding (B) dispersal probabilities in the Roseate Tern example (Lebreton *et al.*, in preparation) (The probabilities do not sum exactly to 1 because of rounding error)

$\hat{N} =$	0.582	0.004	0.020	$\hat{B} =$	0.885	0.009	0.007
	0.047	0.913	0.082		0.023	0.976	0.013
	0.371	0.082	0.898		0.092	0.014	0.981

in Table 4. The a_{ik} are non-cumulative measures of accession to reproduction, which can be converted into age-specific proportions of breeders calculated for an ideal cohort in which all individuals are assumed to have survived until the age of full recruitment (Clobert *et al.*, 1994; Pradel & Lebreton, 1999). These age-specific proportions of breeders are given in Fig. 1 (after Lebreton *et al.*, submitted). As expected, the intensity of natal dispersal was stronger than that of breeding dispersal, with some degree of parallelism in the exchanges. Site A, which showed a marked decrease in numbers, has the lowest philopatry probabilities. The rate of accession to reproduction shows, however, little differences between sites (Fig. 1), with good evidence of full recruitment at age 5. Because of the clear distinction made between natal dispersal, breeding dispersal, and rate of accession to reproduction, we expect this type of model to be useful for many data sets with challenging questions on dispersal.

Multistate models also constitute a natural framework for mixtures of information (such as recoveries and recaptures) in individual history data (Lebreton *et al.*, 1999) (see also Pollock *et al.*, this issue). For instance, Reed & Gauthier (in preparation) use a multistate model for analysing the rate of collar loss in snow geese *Anser caerulescens*. The states considered are 'ringed' (R) and 'ringed + collar' (C). The transition from R to C is impossible ($\psi_{CR} = 0$), while the symmetrical transition probability ψ_{RC} corresponds to the probability that an individual loses its collar. A similar approach was developed independently by Alisauskas & Lindberg
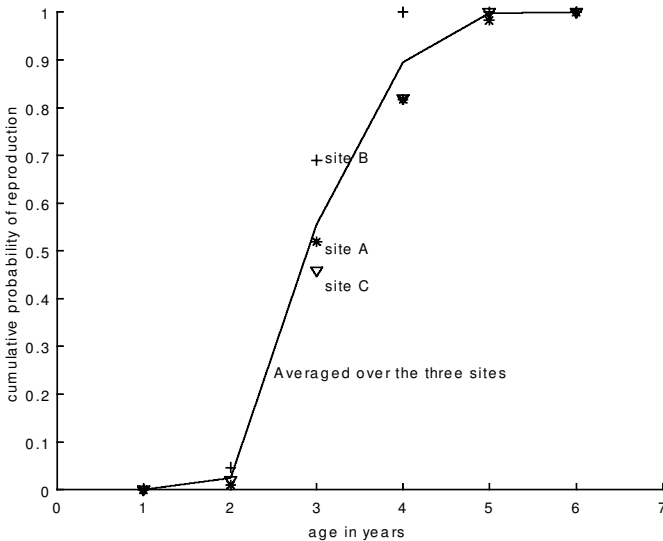

FIG. 1. Cumulative age-specific probability of breeding in the roseate tern (from Lebreton *et al.*, in preparation, final model).

(this issue). Although Barker's (1997) general model does not seem to enter this framework, many interesting mixtures of information can be looked at in that way, such as mixtures of recoveries and resightings with geographical stratification, in which local immature survival could be compared to true immature survival. Another possibility would be to mix recoveries to a single-site recruitment model based on resightings of breeders for improving the robustness of survival estimates, and in turn estimates of other parameters, in particular recruitment parameters (Torcel, in preparation). Mixing telemetry data with other types of registration is another useful possibility than can be framed in the multistate context.

More robustness can also be achieved by using a robust design approach (with primary and secondary recapture occasions) to multistate recapture observations (Nichols *et al.*, 1994). This approach has clear links with the development of multistate closed population models that could be used for the secondary occasions within each primary one.

From the possibilities just mentioned, it seems clear that much more can be done. A first direction is a more imaginative building of states, by combining several categorical covariates defined at the individual level, by mixing such individual covariates with geographical sites, by using unobservable states etc. Secondly, more imaginative field designs could be used. Thirdly, more complex statistical models need to be developed: a few foreseeable developments will be mentioned in the discussion.

5 Numerical and statistical difficulties

Multistate models are recent and, despite the exciting prospects they raise for population biology (Clobert, 1995), it is not surprising that several numerical and statistical difficulties have to be solved. Although the points we review here are fairly technical, they are of great importance.

The complexity of the likelihood and the often-large number of parameters in multistate models, when compared with single-state models, are expected to raise more numerical and statistical problems. At least three problems are common: boundary estimates, identifiability problems, and problems of local minima, sometimes in combination.

Even when estimates of probabilities are constrained to be in range by a link function, many estimates will tend to hit a boundary. The effect on model selection is poorly known. In practice, most of us will count such parameters as identifiable in the calculation of AIC or of degrees of freedom in LRT tests. However, the asymptotic results that serve as a justification for this are valid only for parameters not on a boundary. Monte-Carlo simulation is the more straightforward approach to explore this issue, e.g. by using parameter values close to a boundary, and to see how distributional properties of the deviance are affected by estimates on a boundary. Results would be beneficial to many other models, such as recovery models.

We will illustrate identifiability problems using expected values generated in a simple case for Clobert *et al.*'s (1994) recruitment model. As mentioned earlier, this model can be represented as a model with two states (breeders and non-breeders), the latter being non-observable, and age dependence in survival and transition probabilities (Pradel & Lebreton, 1999). When the probabilities of survival of after-first-year breeders and non-breeders are left unconstrained, the
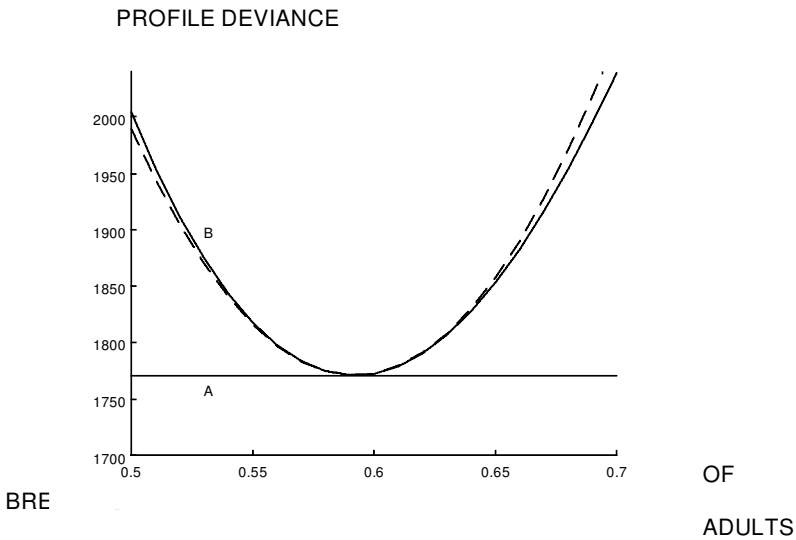
PROFILE DEVIANCE

FIG. 2. An illustration of identifiability problems in multistate models: profile deviance in a recruit-
ment model applied to simulated data as a function of the probability of survival of breeding adults.
A: Horizontal solid line: survival of breeders and non-breeders vary independently: the deviance does
not change with the survival of breeders; in the absence of a minimum, the parameters are not
identifiable. B: Continuous curved line: the probability of survival of breeders and non-breeders are
forced to be equal, which makes the parameters identifiable. The dotted line is the parabolic approxi-
mation to the profile deviance.

parameters in the model are not separately identifiable, as illustrated (see Fig. 2)
by the profile deviance as a function of the probability of survival of the after-first-
year non-breeders. The profile deviance, i.e. the deviance as a function of a focal
parameter and simultaneously minimized with respect to the other parameters
(Fig. 2) will be constant in the case of identifiability problems. In our example, as
soon as the non-breeders are assumed to have the same probability of survival as
breeders (Fig. 2), the parameters become identifiable. The detection of non-
identifiability by numerical approaches presently does not seem totally reliable (see
the comments on numerical rank by Viallefont *et al.*, 1998). A formal detection
(Catchpole & Morgan, 1997) is made difficult by the complexity of the likelihood,
although it can be used with success in some cases (Gimenez & Choquet,
unpublished results). Because of the risk of widespread non-identifiability in
complex multistate models, we recommend profile deviance plots be systematically
examined in any data analysis.

   In maximum likelihood estimation by iterative minimization, there is always the
risk of converging to a local minimum of the deviance (Fletcher, 1987). The only
formal insurance is to have a convex deviance. This is not even sure for the CJS
model, although there is no report of convergence to a local minimum reported,
and the deviance looks convex in simple examples (e.g. Reboulet *et al.*, 1999,
Fig. 2). Several people besides us (Dupuis, personal communication, White:
MARK Forum, Summer 2000) have independently detected local minima of the
deviance of multistate Arnason-Schwarz models with some data sets. In Fig. 3, we
show such an example, using again the profile deviance, for female roe deer data
over two states (with fawn, without fawn) obtained by J. M. Gaillard (see for
example, Gaillard *et al.*, 1997). The quasi-Newton methods in SURGE and MARK
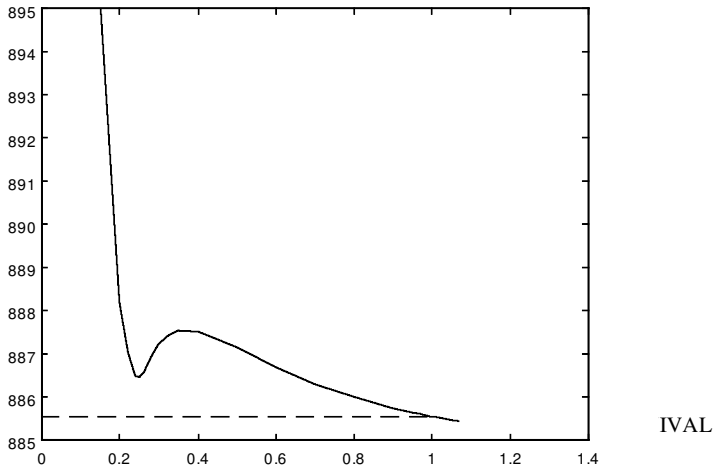
PROFILE DEVIANCE

FIG. 3. An illustration of local minima in multistate models: profile deviance of a two-state model applied to roe deer data as a function of the probability of survival φ. While the Maximum Likelihood Estimate is equal to 1 (boundary estimate, corresponding to the overall minimum of the deviance over the interval [0,1] equal to 885.547, horizontal dotted line), the deviance presents a local minimum equal to 886.454 in $\varphi = 0.2476$.

offer limited protection against convergence to a local minimum by line search at different distances in the direction chosen at the current iteration in the parameter space (Fletcher, 1987, p.33 ff). The ease with which examples of convergence to local minima appeared tells us that this protection is insufficient in the case of multistate models. Before more sophisticated algorithms (Brooks & Morgan, 1994) or improved initial values (Gimenez, in preparation) are developed, we recommend systematically checking the results by picking up a few different sets of initial values, well apart from each other, and checking differences in the deviance obtained. In our experience, any sharp change in estimates, in particular of the ψs and ps between models with similar structure could also be an indication of the lack of global convergence in one of the models. It is unclear to us whether the existence of local minima is only a by-product of sparseness or lack of adequacy of the model, i.e. they will disappear asymptotically for data generated from the model, or if they are more structural. Hence, there is here a clear need and room for further statistical and numerical research.

A final unrelated issue, Goodness of fit presently raises large difficulties for multistate models. Statisticians have kept repeating that goodness-of-fit is critical for adequate statistical model selection (e.g. Kendall & Stuart, 1961, p. 420). Within a set of models in which none fits the data, all differences in deviance between models tend to be inflated. Model selection using the deviance, as in LRT or AIC-based model selection will tend thus to give unreliable results. The toolbox for checking model fit for multistate models is presently inadequate. A first solution when K and s are small is to enumerate all capture histories, to calculate expected values under the final model and estimates, and use a χ^2 test (Hestbeck *et al.*, 1991). The number of capture histories is equal to $(s+1)^{K-1} - 1$ if there are releases in all states at all occasions, and is rapidly prohibitive: $s = 5$ and $K = 11$ produces 60 466 175 capture histories! Even when this approach is practical, the

low expected numbers in many cells raise a problem of sparseness. The χ^2 distribution under H$_0$ (the model fits the data) is known to be shrunk towards zero with sparse data, as well as that under H$_1$ (the model does not fit the data). As a consequence, the power of the goodness of fit decreases to an unknown degree. Resampling and simulation techniques offer an alternative to determining the distribution of a goodness-of-fit statistic such as the deviance under H$_0$. This is the principle of the Monte-Carlo simulation (or parametric bootstrap, Buckland & Garthwaite, 1991) test provided in MARK. The existing literature on the distribution of χ^2 statistics under sparseness assumptions (e.g. Zelterman, 1987) has not yet been fully exploited and could prove useful. These comments are relevant to the calculation of the over-dispersion factor as well, and also apply often to single-site capture-recapture models.

Unfortunately, the deviance, as a test statistic, is omnibus, in the sense that it is not sensitive to specific alternatives of interest (Cox & Hinkley, 1974, p.68). At least one test for specific alternatives is available, concerning memory models (Brownie *et al.*, 1993). There is nothing comparable to the optimal decomposition into interpretable components of the Goodness-of-fit tests of the time-dependent Cormack-Jolly-Seber model (Pollock *et al.*, 1985) as implemented in RELEASE (Burnham *et al.*, 1987). In fact, the technique used to obtain these components does not work with multistate models (Wintrebert, 1998) because individuals alive but not captured are in an unknown state. Further research pending, if we keep in mind the criticality of the goodness-of-fit issue, only a series of ad hoc procedures may be recommended: (a) run the goodness-of-fit tests on data reduced to a single state, or based on capture-recaptures within each state (Lebreton *et al.*, in preparation); (b) use parametric bootstrap (Buckland & Garthwaite, 1991) (implemented in MARK only for single state model); (c) use specific tests such as the test for a memory effect (Brownie *et al.*, 1993). Given these unresolved goodness-of-fit issues and the complexity of the multistate models, a step-up approach starting from a simple model and moving to more complex models can be a good strategy, at least until more sophisticated tools will make it possible to proceed in a step-down procedure from a model of which the fit has been duly checked, or to broadly apply model selection criteria.

To stimulate further analyses, some multistate data sets (together with single-site capture-recapture data sets) are made available with commented treatments at the following address: ftp://ftp.cefe.cnrs-mop.fr/biom/Soft/CR (file Case-Studies. Zip).

6. Discussion

Despite the numerical and statistical difficulties just mentioned, the progressive generalizations examined above open the way to much broader generalizations of a multistate approach. Here are two further generalizations presently under study: multistate growth rate models and models with uncertainty on individual state.

Pradel's (1996) growth rate model (Nichols & Hines, this issue), based on a simultaneous estimation of probabilities of survival φ and seniority γ, can be generalized to a stratified population (Lebreton *et al.*, in preparation). In a forward multistate analysis, one can estimate survival-transition matrices Φ_i, and in a separate backward analysis, diagonal seniority matrices Γ_{i+1}, e.g. in a time-dependent context. The basic idea for a multistate model of population growth is that population size vectors N_i and N_{i+1} are related through the vector of the

numbers of individuals present in the population, both at times i and $i + 1$, classified according to their state at time $i + 1$, denoted as S_{i+1}:

$$S_{i+1} = \Phi_i N_i = \Gamma_{i+1} N_{i+1}$$

Hence, the vectors of population sizes are related as:

$$N_{i+1} = \Gamma_{i+1}^{-1} \Phi_i N_i = \Lambda_i N_i$$

The set of matrices Λ_i could then be submitted to some ergodic and/or spectral analysis, under a variety of assumptions (constancy, constancy + random time effect etc), in order to develop further links with matrix models in a fixed or random environment (Caswell, 2000; Tuljapurkar, 1990). A likelihood approach considering simultaneously the backward and forward analysis, generalising thus that of Pradel (1996), can be developed (Lebreton *et al.*, in preparation).

Often, even when an animal is observed, its true state is known with some uncertainty. For instance, a bird observed on a breeding colony may be a non-breeding prospector and the status breeder/non-breeder is known with uncertainty. Similarly, the sex judged in the field from behaviour may be subject to error. Still another example is that of a bird seen, thus known to be alive, with no record of its reproductive status. Those situations, although fairly common, are not amenable to traditional multistate models, which suppose that the state of an observed animal is identified without error. The solution seems to go through the consideration of an intermediate level, that of the possible events of observation which are subsets of the set of original states (Pradel, in preparation). These events are then related to the true underlying states by a matrix of conditional probabilities, which can be seen as a generalisation of capture probabilities:

$$\pi = \begin{bmatrix} prob\,(event\ 1/state\ 1) & \dots & \dots & prob\,(event\ 1/state\ n) \\ prob\,(event\ 2/state\ 1) & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots \\ prob\,(event\ m/state\ 1) & \dots & \dots & prob\,(event\ m/state\ n) \end{bmatrix}$$

The capture probabilities still appear in the cells along with other parameters. Here is such a matrix for the problem of the identification of sex:

$$\pi = \begin{pmatrix} p_x x & p_y(1-y) & 0 \\ p_x(1-x) & p_y y & 0 \\ 1-p_x & 1-p_y & 1 \end{pmatrix}$$

The columns correspond to the true states: female, male and dead, the rows to the possible events: 'judged female', 'judged male' and 'not encountered'. x (respectively y) is the probability to correctly identify a female (respectively a male), p_x (respectively p_y) is the probability of encountering a female (respectively a male). The combination of transition matrices between true states and of π-matrices permits us to write the likelihood. Although potentially important, those multievent models are likely to suffer from identifiability problems. Fujiwara & Caswell (in preparation) develop similar models. The memory model enters also this framework. With two states A and B, the probability of transition will differ between individuals with earlier histories, say, AAA and ABA, respectively. An individual with earlier history A0A can have been in either state at time 2, i.e. its

state at time 2 is uncertain. As mentioned earlier, this difficulty has precluded up to now a full likelihood approach to the memory model, which becomes possible in the multievent framework.

This is but a few examples of what we can expect in the future. Nearly all generalizations of one-state models can be looked at, including probably a variety of models for closed populations, with an interest on transition rates rather than on population size. We expect in most cases that matrix notation will greatly facilitate model development. The gain in relevance for many biological issues dealing with individual variability is expected to be especially high, in particular in relation with the development of remote-monitoring of individual characteristics by electronic devices (Croxall, 1998), which bridges longitudinal data analysis with missing data and traditional capture-recapture analysis. The cost in terms of parsimony may be partly alleviated by the systematic use of generalized model ideas to develop constrained models. The main difficulties will be for handling the statistical and numerical issues we reviewed (identifiability, local maximums, goodness-of-fit). Hopefully, general procedures and development of software will help in solving these difficulties. Because of their generality and of the variety of biological questions they can uniquely address, we expect a multistate model to play a growing role in the development and application of capture-recapture methodology.

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