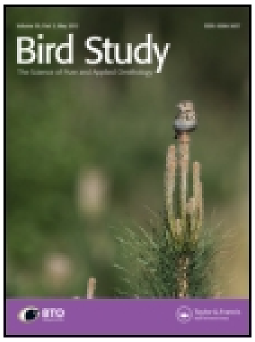

Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: https://www.tandfonline.com/loi/tbis20

Competing events, mixtures of information and multistratum recapture models

Jean-Dominique Lebreton , Tancrède Almeras & Roger Pradel

Bird Study (1999) **46** (suppl.), S39–46

Competing events, mixtures of information and multistratum recapture models

JEAN-DOMINIQUE LEBRETON*, TANCRÈDE ALMERAS *and* ROGER PRADEL *CEFE/CNRS, 1919 Route de Mende, 34 293 Montpellier Cedex 5, France*

A recent trend in the analysis of capture–recapture data, in the broad sense, is the development of survival models mixing different types of events such as live recapture and dead recoveries. These models are similar to those developed for analysing competing events and multistate life histories in human health studies, which are frequently based on Markov chains. The major difference is that, in the capture–recapture context, every event is subject to a detection probability in general lower than one. Multistratum capture–recapture models are then a natural tool. We show that models for information mixtures easily enter this framework, provided adequate, possibly non-observable, strata are defined. Similarities and differences between such models are then easy to ascertain and understand. A multistratum model for mixtures of live recaptures and dead recoveries is presented and an example of data from the literature is treated, using a prototype MATLAB *program named* M-SURGE. *Further generalizations and expected developments are discussed.*

The last 30 years have seen a rapid development in statistical methodology for the analysis of capture–recapture data in the broad sense, i.e. for the analysis of individual histories of marked animals.[1] Nevertheless, despite the great flexibility presently available,[2,3] it is fairly clear that the methodology has been lagging behind the biological questions.[4,5] One may cite as an example the *ad hoc* search for differences in demographic performance between individuals by the lifetime reproductive success school.[6] Indeed, there is much more information in data based on following individually marked animals through time than is used in classical survival analysis, for example, especially when individual covariates that may change over time such as weight, reproductive status or site are recorded at each capture. In this respect, multisite capture–recapture models[7,8] constitute a major advance especially since they can be used as multistratum or multistate models, i.e. with individual states considered as dummy geographical sites.[9,10] For the sake of generality, we speak hereafter of multistratum models. The probabilities of transitions between individual states, such as reproductive status, weight classes, etc. can then be estimated and compared efficiently. Program MS-SURVIV[9] allows one to fit multistratum models incorporating in particular constraints of equality (e.g. over time) between parameters.

A more recent trend has been the development of survival models mixing different types of events. The simplest approaches combine several sources of information such as, for example, live recapture and dead recoveries, based on independent samples.[11,12] A much more general approach consists of considering the various events which can happen to a particular individual as mutually exclusive, competing events. Typical examples of such models consider simultaneously live recapture and dead recoveries, and/or radiotracking data.[13–16] However, for such mixtures of information, there is as yet no general statistical framework for building specific models, and no general software available for analysing data.

The purpose of this paper is to show that

*Corresponding author.
Email: lebreton@cefe.cnrs-mop.fr

models mixing different types of events, in the sense given just above, are particular cases of general multistratum capture–recapture models, provided adequate strata are defined. The similarities and differences between such models will then be easy to ascertain and understand, and this will hopefully lead to software and procedures of great generality, for any type of information combination.

For the sake of clarity we proceed in three steps:

1 we reframe models for live-recapture and ring-recovery data, respectively, in the multistratum framework, introducing the idea of non-observable strata;

2 we present a straightforward multistratum model allowing the mixing of live recapture and ring recovery;

3 we look briefly at further generalizations.

All models presented were fitted using a prototype user-friendly MATLAB program for multistratum capture–recapture models, named M-SURGE,[17] which we hope to be able to make available in the future.

MULTISITE/MULTISTRATUM MODELS

The Arnason model[7] is an exact generalization of the classic time-dependent Cormack–Jolly–Seber (CJS) survival model to s strata ($s > 1$). Each survival probability is replaced by an $s \times s$ survival transition matrix, each probability of capture by an $s \times 1$ matrix (vector) of site-specific probabilities of capture (Table 1). The element in row i and column j of a survival transition matrix is the probability for an individual of being alive in stratum i at the next occasion, conditional on being alive in j at the present occasion, in accordance with the usual Markov chain notation.[18] A typical recapture history for $s = 5$ strata and $K = 8$ occasions is 01020530, in which 0 corresponds to non-capture, and the other digits to the number of the stratum where captured at the particular occasion concerned. The probability of a capture history, and in turn the likelihood of a data set, can be obtained as straightforward matrix formula generalizing those for the CJS model [9].

Arnason[7] and Schwarz *et al.*[19] obtained explicit maximum likelihood estimators of the parameters. However, the number of parameters grows very rapidly with the number of occasions K and the number of sites s.[20] For instance, with $s = 5$ strata and $K = 8$ occasions, there are 205 estimable parameters! It is thus fortunate that both particular versions (via constraints of equality) and generalizations (models with memory) of the Arnason model have appeared,[8, 9] greatly increasing its interest.

We have developed a MATLAB program called M-SURGE[17] for user-friendly fitting of multistratum models derived from the Arnason model by introducing linear constraints between parameters, and/or by fixing some parameters to predetermined values. The same general parametrization presented for the Arnason model (Table 1) applies: for instance, the survival transition matrix in Table 1 varies with time in the Arnason model, but will be the same over all intervals $k = 1, ..., K - 1$ if survival is constant over time. The generalized linear model notation for capture–recapture models[21] can be easily adapted to the multistratum context. Using capital letters to emphasize the multidimensional nature of the parameters,

Table 1. Parametrization of the Arnason[7] capture–recapture model (Φ_t, P_t) for three sites or strata. The term φ_{ij} in the survival movement matrix Φ_t ($t = 1,..., K - 1$) is the probability of being alive in site i at time $t + 1$, for an animal which was alive in site j at time t. The term p_j in the capture probability vector P_t ($t = 2, ..., K$) is the probability of being captured for an animal alive in site j at time t.

Matrix of survival-movement probabilities from time t to $t + 1$	Column vector of site or stratum-specific probabilities of capture
$\begin{bmatrix} \varphi_{11} & \varphi_{12} & \varphi_{13} \\ \varphi_{21} & \varphi_{22} & \varphi_{23} \\ \varphi_{31} & \varphi_{32} & \varphi_{33} \end{bmatrix}_t$	$\begin{bmatrix} p_1 \\ p_2 \\ p_3 \end{bmatrix}_t$

Table 2. Parametrization of the CJS model as a two-stratum model. Stratum 1, with probability of capture p, is 'Alive'. Stratum 2, not observable, is 'Dead'. φ is the probability of survival from t to $t+1$; p is the probability of capture at time t.

Matrix of survival-transition probabilities of from time t to $t + 1$	Column vector of stratum-specific capture probabilities
$\begin{bmatrix} \varphi & 0 \\ 1-\varphi & 1 \end{bmatrix}_t$	$\begin{bmatrix} p \\ 0 \end{bmatrix}_t$

the Arnason model can be denoted by (Φ_t, P_t). The model with parameters constant over time, denoted by (Φ, P), has $s^2 + s$ parameters.

In what follows, we use particular structures and fixed values for some components of the survival-transition and recapture parameter matrices of multistratum models, after having properly defined specific strata.

LIVE RECAPTURE AND DEAD RECOVERY MODELS AS A PARTICULAR MULTISTRATUM MODEL

The paradox of the CJS model is that one gets information on survival, or equivalently mortality, without ever observing dead animals. Indeed, some animals are in the state 'Dead', but this state has a probability of observation equal to 0. This leads to a straightforward representation of the CJS model as a two-stratum model (Alive = 1, Dead = 2), with a zero probability of capture in the second stratum (Table 2). This corresponds to the idea of non-observable strata. In this case, each survival transition matrix must be constrained to have the sum of each column equal to 1, i.e. to be a so-called stochastic matrix, and, as a consequence, has a single parameter identifiable. With 'Alive' = stratum 1 and 'Dead' = stratum 2 (Table 2), a typical capture history will be, for example, 00110100. No '2' ever appears in capture histories and the estimated capture probability in stratum 2 will be indeed equal to 0, and does not even have to be fixed to 0 for an iterative estimation process to work properly.

In quite a symmetrical way, with recovery data, an individual is observable only when it is dead, but not as long as it is alive. It is the knowledge of the date of death which is important, and as a consequence, one has to distinguish a stratum 'Newly dead' (stratum 2) from a stratum 'Dead' (stratum 3) to which an animal newly dead moves during the next time step[1,14] (Table 3a). Animals which are 'Alive' (stratum 1) have a probability of capture equal to 0. In the same way as the non-observable stratum 'Dead' is not needed in the CJS model, one may as well suppress the stratum 'Dead' here, and just keep the two strata 'Alive' (not observable) and 'Newly dead' (Table 3b). As above, the survival transition matrix has to be constrained. In particular, in the three strata

Table 3. Parametrization of a recovery model as a three-stratum model (a) or a two-stratum model (b). Stratum 1, not observable, is 'Alive'. Stratum 2, with probability of capture λ, is 'Newly dead'. Stratum 3, not observable, is 'Dead'.

	Matrix of survival-transition probabilities from time t to $t + 1$	Column vector of site-specific probabilities of capture
a	$\begin{bmatrix} s & 0 & 0 \\ 1-s & 0 & 0 \\ 0 & 1 & 1 \end{bmatrix}$	$\begin{bmatrix} 0 \\ \lambda \\ 0 \end{bmatrix}$
b	$\begin{bmatrix} s & 0 \\ 1-s & 0 \end{bmatrix}$	$\begin{bmatrix} 0 \\ \lambda \end{bmatrix}$

Table 4. Parametrization of a model for a mixture of live recaptures and dead recoveries as a three-stratum model (a) or a two-stratum model (b). Stratum 1, not observable, is 'Alive'. Stratum 2, with probability of capture λ, is 'Newly dead'. Stratum 3, non-observable, is 'Dead'.

	Matrix of survival-transition probabilities from time t to $t+1$	Column vector of site-specific capture probabilities
a	$\begin{bmatrix} s & 0 & 0 \\ 1-s & 0 & 0 \\ 0 & 1 & 1 \end{bmatrix}$	$\begin{bmatrix} p \\ \lambda \\ 0 \end{bmatrix}$
b	$\begin{bmatrix} s & 0 \\ 1-s & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ \lambda \end{bmatrix}$

presentation (Table 3a), it is a stochastic matrix.

With 'Alive' = stratum 1 and 'Newly dead' = stratum 2, a typical recapture history will be, for example, 010000200, for an animal marked at time 2, recovered between occasions 6 and 7, i.e. having just moved into the state 'Newly dead' at occasion 7. The competing event 'live recapture at time 7' cannot happen since the individual died during the interval between occasion 6 and occasion 7. Another typical history would be 001000000 for an animal marked at time 2, not recovered during the six time intervals after marking. Since only a single 1, (corresponding to the initial capture and release with a mark) appears in each capture-history there are no recaptures in stratum 1 and the estimated capture probability in stratum 1 will indeed be equal to 0, and does not have to be fixed to 0 beforehand.

MIXING RECAPTURES AND RECOVERIES

The next logical step is to consider that both the stratum 'Alive', as in the CJS model, and the stratum 'Newly dead', as in recovery models, are observable. A typical recapture history would be, for example, 0101102000, for an animal marked at occasion 2, recaptured (alive) at occasions 4 and 5, and found dead (recovery) in the interval between occasions 6 and 7, i.e. having moved into the stratum 'Newly dead' at time 7. In this case too, the sum of the first column of each survival-transition matrix is forced to be equal to λ. However, by now, the two probabilities of capture p and λ will have estimates in general greater than 0, recaptures taking place in both strata as in the example above. The corresponding parametrization is given in Table 4. As mentioned earlier, the parametrization of the Φ and P matrices can be used in a time-constant or time-varying context, or with more or less sophisticated constraints. An animal missed and seen again later must be in the stratum 'Alive', since it is by definition impossible to come back into the stratum 'Alive' after having left it. However, an animal never seen again may have died (i.e. moved into the stratum 'Newly dead') at any time, and have been missed at that time with probability $1 - \lambda$. The corresponding terms are automatically built into the likelihood since the multisite model likelihood takes account of all possible events for animals that are missed.[9]

For the particular case of radiotracking data, Pollock *et al.*[14] assume that dead and alive individuals have the same probability of detection, i.e. $p = \lambda$, and that there is a probability $1 - \delta$ for an individual to emigrate permanently from the study area at each time step. Based on these assumptions, one may check, for instance by writing down the likelihood, that the Pollock *et al.* model[14] is a particular case of the recapture–recovery model in Table 4, with the parametrization given in Table 5.

The 'modified Canvasback data' given by Pollock *et al.*[14] (50 individuals, 7 periods, in Table 1, p. 667 of ref. 14) have been reanalysed in the present framework, using M-SURGE. As in the original analysis, we used only the information on live recaptures (denoted as '1' in Table 1 of ref. 14) and dead individuals within the study site (denoted as '9'), i.e. animals relocated out of the study site were considered as missing. The results of our analysis are given in Table 6. In particular, we used these data as

Table 5. Parametrization of the Pollock *et al.* model[14] mixing relocations of alive and dead radiotracked animals within a given study area. Stratum 1 is 'Alive', stratum 2 is 'Newly dead'. s is the survival probability, δ is the probability of remaining in the study area, p is the probability of detection (which is equal for animals alive and dead).

Matrix of survival-transition probabilities from time t to $t+1$	Column vector of strata-specific capture probabilities
$\begin{bmatrix} s\delta & 0 \\ (1-s)\delta & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ p \end{bmatrix}$

if they were recapture–recovery data, to provide an example of our general model.

Expanding the notation slightly to emphasize that, for a particular interval or occasion, capture parameters vary across strata, one may note the standard time-dependent and stratum-dependent (i.e. $p \neq \lambda$) probabilities of capture ${}_sP_t$. This notation simply means that there is a stratum effect on the probability of capture. The time-dependent structure under the assumption $p = \lambda$,[14] i.e. with no stratum effect on the probability of capture, may then be denoted as P_t. In such models we obtain exactly the same results (Table 6) as Pollock *et al.*[14] In classical recovery models the probability of moving into the stratum 'Newly dead' is forced to be equal to $1 - s$, which makes λ identifiable. Indeed the pair of parameters (s, λ) is frequently replaced by $(s, f = (1 - s)\lambda)$[22] which is particularly useful when the recoveries are obtained from a specific cause of death (with probability $1 - s' \neq 1 - s$ which prevents one from identifying λ separately) such as hunting. In a similar way, here, δ and λ cannot be identified separately when p differs from λ: Leaving $p \neq \lambda$ and $\delta \neq 1$ does not change the deviance and the number of identifiable parameters (bottom of Table 6). Hence, it is the assumption of equal detection probabilities for animals that are alive and newly dead ($p = \lambda$) that makes s and δ separately identifiable, i.e. that makes it possible to separate death from permanent emigration in the Pollock *et al.* model.[14] This assumption may be fairly critical, as shown, in the time-constant context, by the strong difference between the estimates of p and λ (respectively 0.8780 and

Table 6. Analysis of Canvasback *Aythia valisineria* data (relocations of alive and dead radiotracked individuals analysis[14]). Same notation as Table 5.

Matrix of survival transition probabilities	*Matrix of capture probabilities*	*Relative deviance*	*Number of identifiable parameters*	MLE	AIC
$\begin{bmatrix} s\delta & 0 \\ (1-s)\delta & 0 \end{bmatrix}_t$	$\begin{bmatrix} p \\ p \end{bmatrix}_t$	306.205	17		340.205
$\begin{bmatrix} s\delta & 0 \\ (1-s)\delta & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ p \end{bmatrix}_t$	319.560	8		335.560
$\begin{bmatrix} s\delta & 0 \\ (1-s)\delta & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ p \end{bmatrix}_t$	333.188	3	$\hat{s} = 0.9453$ $\hat{\delta} = 0.9222$ $\hat{p} = 0.8780$	339.188
$\begin{bmatrix} s\delta & 0 \\ (1-s)\delta & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ \lambda \end{bmatrix}$	333.188	3	Not all separately identifiable	339.188
$\begin{bmatrix} s\delta & 0 \\ 1-s & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ \lambda \end{bmatrix}$	333.188	3	$\hat{s} = 0.8718$ $\hat{p} = 0.8780$ $\hat{\lambda} = 0.5035$	339.188

Table 7. Parametrization of Burnham's model[13] mixing live recaptures and dead recoveries, as a three-stratum model (a), which appears as a particular case of a model mixing live recaptures over two sites and dead recoveries (b). Stratum 1 is 'Alive locally', with probability of capture p. Stratum 2 is 'Alive elsewhere', with probability of capture 0 (a: Burnham's model) or q (b: general case). Stratum 3, with probability of capture λ, is 'Newly dead'.

	Matrix of survival-transition probabilities from time t to $t+1$	Column vector of site-specific capture probabilities
a	$\begin{bmatrix} sF & 0 & 0 \\ s(1-F) & s & 0 \\ 1-s & 1-s & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ 0 \\ \lambda \end{bmatrix}$
b	$\begin{bmatrix} \alpha & \beta & 0 \\ \gamma & \delta & 0 \\ 1-\alpha-\gamma & 1-\beta-\delta & 0 \end{bmatrix}$	$\begin{bmatrix} p \\ q \\ \lambda \end{bmatrix}$

0.5035) under the assumption $\delta = 1$, while under $p = \lambda$, the estimation of δ is 0.9537. In the case of the canvasback data, some animals have been relocated out of the study area,[14] implying indeed that $\delta < 1$.

MORE GENERAL MIXTURES OF INFORMATION

It is fairly clear that specific definitions of strata, whether observable or not, lead to straightforward generalizations of the previous model to any type of information mixture. As a single example, we present (Table 7a) in the multistratum framework the model mixing broad scale recoveries and local recaptures by Burnham.[13] Although the survival parameter for recoveries is the genuine survival s, the recaptures may only provide a local survival sF. F is a probability of fidelity similar to the parameter δ used by Pollock *et al.*[14] One may see that Burnham's model is a special case of a model with recaptures in two sites (Table 7b) mixed with recoveries. The first site or stratum is the area of recapture. The second site or stratum consists of the area where recoveries take place less the area where recaptures take place and is not observable. The third stratum is 'Newly dead'.

DISCUSSION

Multistratum models based on possibly not observable strata thus provide a general framework for handling mixtures of information in capture–recapture studies in the broad sense. Indeed any competing events in an individual's life that can be translated into a polytomous variable pertain to this framework, as noted for trade-off studies by Nichols *et al.*[10] Among straightforward generalizations of the examples presented here, one may cite recoveries over several sites[19] and mixtures of recaptures and recoveries over several sites. Pradel and Lebreton[27] show that models based on the strata 'Breeder' and 'Non-breeder' also provide a unifying framework for recruitment models [23] whether non-breeders are observable or not.

The models encompassed in our approach are strikingly similar in structure[1] to those developed for analysing competing events and multistate life histories in human health studies, which are frequently based on Markov chains.[24] The major difference is that, in the capture–recapture setting, every event is subject to a detection probability which is in general less than 1. The multistratum capture–recapture models thus provide a canonical structure for analysing longitudinal polytomous responses with missing data, a recurrent need in epidemiological and sociological studies.[25]

Before such models can be used widely by population biologists, several technical issues have to be solved.

The first one concerns goodness-of-fit, a critical issue for all further testing, model selection, and confidence interval calculations.[21] Although MS-SURVIV provides some goodness-of-fit testing, more refined and general tests are needed. The partitioning of the likelihood that provides the canonical goodness-of-fit tests of the CJS model[26] would be very complex and lead to many very sparse contingency table tests, and specific work is thus needed for multistratum models.

Secondly, the full usefulness of multistratum models, in particular for handling information mixtures, will also be reached when age effects will be easily handled. This need is particularly pressing for analysing recruitment by multistratum models.[27]

The third major issue concerns software: user-friendly software for multistratum models is badly needed, as noted by Barker.[16] Because the number of parameters increases rapidly with the number of strata and occasions, the ease with which constraints can be implemented will be very important. The results obtained with M-SURGE, a MATLAB program under development,[17] are encouraging. In the context of information mixtures, the fact that some strata may be non-observable raises specific identifiability problems, as seen in some of our examples. A numerical[28] or formal[29] detection of non-identifiable parameters will be very relevant.

NOTE ADDED IN PROOF

The models presented in this paper can also be fitted using recent versions of program MARK.[30]

ACKNOWLEDGEMENTS

We are grateful to B.J.T. Morgan, M.D. Smith and an anonymous referee for helpful comments on an earlier version.

REFERENCES

1. Lebreton, J.D. (1995) The future of population dynamic studies using marked individuals: a statistician's perspective. *J. Appl. Stat.*, **22,** 1009–1030.
2. Nichols, J.D. (1992) Capture recapture models. Using marked animals to study population dynamics. *Bioscience*, **42,** 94–102.
3. Pollock, K.H. (1991) Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations : past, present, and future. *J. Am. Stat. Assoc.*, **86,** 225–238.
4. Cooke, F. & Francis, C.M. (1993) Challenges in the analysis of recruitment and spatial organization of populations. In *Marked Individuals in the Study of Bird Population* (eds J.D. Lebreton & P.M. North). Birkhaüser, Basel.
5. Clobert, J. (1995) Capture–recapture and evolutionary ecology: a difficult wedding? *J. Appl. Stat.*, **22,** 989–1008.
6. Clutton-Brock, T.H. (ed.) (1988) *Reproductive Success: Studies of Individual Variations in Contrasting Breeding Systems*. University of Chicago Press, Chicago.
7. Arnason, A.N. (1973) The estimation of population size, migration rates and survival in a stratified population. *Res. Population Ecol.*, **15,** 1–8.
8. Hestbeck, J.B., Nichols, J.D. & Malecki, R. (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology*, **72,** 523–533.
9. Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H. & Hestbeck, J.B. (1993) Capture–recapture studies for multiple strata including non-Markovian transition probabilities. *Biometrics*, **49,** 1173–1187.
10. Nichols, J.D., Hines, J.E., Pollock, K.H., Hinz, R.L. & Link, W.A. (1994) A methodological framework for estimating breeding proportions and testing biological hypotheses about the cost of reproduction with capture–recapture data. *Ecology*, **75,** 2052–2065.
11. Mardekian, S.Z. & McDonald, L. (1981) Simultaneous analysis of band-recovery and live-recapture data. *J. Wildl. Manage.*, **45,** 484–488.
12. Lebreton, J.D., Morgan, B.J.T., Pradel, R. & Freeman, S.N. (1995) A simultaneous analysis of dead recovery and live recapture data. *Biometrics*, **51,** 1418–1428.
13. Burnham, K.P. (1993) A theory for combined analysis of ring recovery and recapture data. In *Marked Individuals in the Study of Bird Population* (eds J.D. Lebreton & P.M. North), pp. 199–213. Birkhaüser, Basel.
14. Pollock, K.H., Bunck, C.M., Winterstein, S.R. & Chen, C.-L. (1995) A capture–recapture survival analysis model for radio-tagged animal. *J. Appl. Stat.*, **22,** 661–672.
15. Freeman, S.N., Morgan, B.J.T. & Catchpole, E.A. (1992) On the augmentation of ring recovery data with field information. *J. Anim. Ecol.*, **61,** 649–657.
16. Barker, R.J. (1997) Joint modelling of live-recapture, tag-resight, and tag-recovery data. *Biometrics*, **53,** 666–677.
17. Almeras, T. (1996) Modèles de capture–recapture multisites: intégration de modèles contraints dans un même cadre souple et convivial, réalisation d'un logiciel de traitement de données sous Matlab. Unpublished DEA report, Montpellier II University, Montpellier.
18. Bailey, N.T.J. (1964) *The Elements of Stochastic Processes with Application to the Natural Sciences*. Wiley, New York.

19. Schwarz, C.J., Schweigert, J.F. & Arnason, A.N. (1993) Estimating migration rates using tag-recovery data. *Biometrics*, **49**, 177–193.
20. Viallefont, A. & Lebreton, J.-D. (1993) Estimation des taux de survie et de migration par capture–recapture dans des populations animales stratifiées spatialement. In *Biométrie et Analyse des Données Spatio-temporelles*. Société Française de Biométrie, Paris.
21. Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.*, **62**, 67–118.
22. Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. (1985) *Statistical Inference from Band Recovery Data – a Handbook*. Resource publication 156, US Fish and Wildlife Service.
23. Clobert, J., Lebreton, J.D., Allainé, D. & Gaillard, J.M. (1994) The estimation of age-specific breeding probabilities from recaptures or resightings of marked animals. II: Longitudinal models. *Biometrics*, **50**, 375–387.
24. Cuzick, J. (1984) A review of semi-parametric models for life histories. *IMA J. Math. Appl. Med. Biol.*, **1**, 323–332.
25. Fitzmaurice, G.M., Laird, N.M. & Liptsitz, S.R. (1994) Analysing incomplete longitudinal binary responses: a likelihood-based approach. *Biometrics*, **50**, 601–612.
26. Pollock, K.H., Hines, J.E. & Nichols, J.D. (1985) Goodness-of-fit tests for open capture–recapture models. *Biometrics*, **41**, 399–410.
27. Pradel, R. & Lebreton, J.D. (1999) Comparison of different approaches to study the local recruitment of breeders. *Bird Study*, **46** (suppl.), 74–81.
28. Reboulet, A.M., Viallefont, A., Pradel, R. & Lebreton, J.D. (1999) Selection of survival and recruitment models with SURGE 5.0. *Bird Study*, **46** (suppl.), 148–156.
29. Catchpole, E.A. & Morgan, B.J.T. (1997) Detecting parameter redundancy. *Biometrika*, **84**, 187–196.
30. White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (suppl.), 120–139.