M–SURGE: new software specifically designed for multistate capture–recapture models

R. Choquet, A.–M. Reboulet, R. Pradel, O. Gimenez, J.–D. Lebreton

Abstract

M–SURGE: new software specifically designed for multistate capture–recapture models.— M–SURGE (along with its companion program U–CARE) has been written specifically to handle multistate capture–recapture models and to alleviate their inherent difficulties (model specification, quality of convergence, flexibility of parameterization, assessment of fit). In its domain, MSURGE covers a broader range of models than a general program like MARK (White & Burnham, 1999), while being more user–friendly than MS–SURVIV (Hines, 1994). Among the main features of MSURGE is a wide class of models and a variety of parameterizations: (1) M–SURGE covers conditional models with probability of recapture depending on the current state (Arnason–Schwarz type models) as well as on the current and previous state (Jolly–movement type models). In both cases, age and/or time–dependence and multiple groups can be considered. (2) Combined survival–transition probabilities can be represented as such or decomposed into transition and survival probabilities. (3) Among the transition probabilities with the same state of departure, the one to be computed by subtraction can be freely picked by the user. User–friendliness is enhanced by the easiness with which constrained models are built, using an interpreted language called GEMACO. Examples of various types of multistate models are developed and presented.

Key words: Constraints, Language, Linear Model, Population dynamics.

Resumen

M–SURGE: el nuevo programa de software diseñado especialmente para los modelos multiestado de captura–recaptura.— El M–SURGE, al igual que su compañero, el programa U–CARE, se ha escrito con el propósito específico de manejar modelos multiestado de captura–recaptura, lo que a su vez permite mitigar las dificultades inherentes a los mismos (especificación de los modelos, cualidad de la convergencia, flexibilidad de parametrización, evaluación del ajuste). En su terreno, el M–SURGE abarca una gama de modelos más extensa que un programa general, como el MARK (White & Burnham, 1999), al tiempo que resulta más accesible para el usuario que el MS–SURVIV (Hines, 1994). De entre las principales características del M–SURGE, cabe destacar una amplia gama de modelos y varias parametrizaciones: (1) El M–SURGE abarca los modelos condicionales con probabilidad de recaptura según el estado actual (modelos tipo Arnason–Schwarz), y según el estado actual y anterior (modelos tipo Jolly–movement). En ambos casos, es posible examinar la dependencia de la edad y/o del tiempo, así como grupos múltiples. (2) Las probabilidades combinadas de supervivencia–transición pueden representarse como tales, o descomponerse en probabilidades de transición y supervivencia. (3) Por lo que respecta a las probabilidades de transición con el mismo estado de partida, el usuario puede elegir libremente la probabilidad que deberá calcularse por sustracción. Además de ser un programa muy accesible para el usuario, también debe subrayarse la facilidad con que permite construir modelos limitados utilizando un lenguaje interpretado denominado GEMACO. En este estudio desarrollamos y presentamos varios tipos de modelos multiestado.

Palabras clave: Limitaciones, Lenguaje, Modelo lineal, Dinámica poblacional.

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Introduction

Adequate statistical models play a central role in the ability to answer biological questions, and, as a consequence, to the development of specific fields of biology (e.g., the Generalized Linear Models (GLM), McCullagh & Nelder, 1989, and more recently generalized additive models, Hastie & Tibshirani 1990, and generalized linear mixed models, McCulloch & Searle, 2001). In practice the availability of software to fit models belonging to a well–defined class of models in a flexible way is crucial. For instance, the development of GLIM (Payne, 1986) greatly helped disseminate the use of GLM (Crawley, 1982) and promoted many different uses of categorical data analyses relevant to a variety of biological fields.

In animal population ecology, capture–recapture methods (see the overview by Seber, 1982, and the recent book by Williams et al., 2002) have been key tools over the last fifty years to estimate population size and demographic parameters such as survival, recruitment and dispersal. In the case of survival estimation, for instance, the development of family of models in the spirit of GLM (Lebreton et al., 1992) and the availability of flexible software such as SURGE (Pradel & Lebreton, 1991; Reboulet et al., 1998) and MARK (White & Burnham, 1999) "have given rise to literally hundred of papers exploiting this very powerful methodology" (Seber & Schwarz, 2002).

Recent developments in capture–recapture methodology and an increasing emphasis on spatial aspects of population dynamics and variation between individuals give a central role to multistate capture–recapture models (Lebreton & Pradel, 2002, and references therein). In multistate models, individuals are sampled on discrete occasions, at which they may be captured or not, and can die or move within a finite set of sites or states, between occasions. By considering states based on various competing events in an individual's life, one can analyze complex individual histories, dealing with accession to reproduction over several sites (Lebreton et al., 2003) or with mixtures of information such as live recaptures and dead recoveries (Lebreton et al., 1999).

We present here a general computer program, called M–SURGE, for "Multistate Survival Generalized Estimation", to fit a wide class of multistate capture–recapture models in a flexible way. M–SURGE, along with its companion program U–CARE, has been written specifically to handle multistate capture–recapture models with the ultimate concern to alleviate their inherent difficulties (model specification, quality of convergence, flexibility of parameterization, number of estimable parameters,…). In its present version, M–SURGE covers a broader range of models conditional on numbers released, than a general program like MARK (White & Burnham, 1999), while being more user–friendly than MS–SURVIV (Hines, 1994). The philosophy to define a model is to build the asso-ciated constraint matrix with a simple language (i.e. without any manipulation inside the matrix and/or any programming).

The purpose of this paper is to provide an overview of M–SURGE abilities and key features, to present the class of models covered and the language used to define models, then to present a few illustrative examples and discuss perspectives of development.

An overview of M–Surge: abilities and key features

M–SURGE covers a wide class of models and a variety of parameterizations: (1) M–SURGE covers models conditional on numbers released with probability of recapture depending on the current state (Arnason–Schwarz type models) as well as on the *current* and *previous* state (Jolly–MoVement type models) (Brownie et al., 1993). In both cases, age and/or time–dependence and multiple groups can be considered; (2) combined Survival–Transition probabilities can be represented as such or decomposed into transition and survival probabilities (Hestbeck et al., 1991); (3) among the transition probabilities with the same state of departure, the one to be computed by subtraction can be freely picked by the user.

The second main feature is that user–friendliness is enhanced by the easiness with which constrained models are built, using a language called GEMACO. This language is like those in general statistical software such as SAS or GLIM (i.e., a formula such as t+g generates a model with additive effects of time and group), thus avoiding tedious, time consuming and error–prone matrix manipulations using an editor or a spread–sheet.

Class of models covered

As SURGE and more recent programs for capture–recapture analysis, M–SURGE consider constrained models obtained by linear constraints among parameters, in the spirit of generalized linear models (Lebreton et al., 1992). The vector, θ, of parameters of direct interest to the biologist, or, for short, "biological parameters" is expressed as a linear transformation of a vector, β, of "mathematical parameters". To keep the biological parameters, which are probabilities, in–the interval [0,1], a link function f is used:

$$f(\theta) = X\beta \qquad \text{or} \qquad \theta = f^{1}(X\beta)$$

The matrix, X, is a "matrix of constraints", which can be a genuine design matrix in the case of a designed experiment. In M–SURGE, it will be built by GEMACO using the model definition language described below. Often, X will be based on a mix of 0/1 variables (for equality constraints on survival probabilities e.g.) and of external covariates (e.g.,

capture effort or weather covariates). An overview of linear constraints in single state capture–recapture models is provided by Lebreton et al. (1992).

Our presentation of multistate models will use the following general notation: s is the number of states; K is the number of occasions; k = 2,...,K is the current occasion for a recapture; i = 1,...,s is the index of the departure state; j = 1,...,s is the index of the arrival state.

All matrices of parameters are written with i as row index and j as column index.

The most general model in M–SURGE is an age and time dependent version of the JollyMoVe model (JMV) (Brownie et al., 1993). For the sake of clarity, we do not specify the occasion, the cohort and the group in this section. In JMV models, capture probabilities depend on both previous and current states. Thus, the generic set of recapture parameters is a matrix of probabilities of dimension s x s.

Models with recapture probabilities depending only on the current states are also considered, with age and/or time dependence. The generic set of recapture parameters is then a vector of probabilities $P = (p^i)$ or, using the diagonal operator D, a s x s diagonal matrix D(P). The time–dependent version of this model corresponds to the Arnason–Schwarz model (Arnason, 1972, 1973; Schwarz et al., 1993). However models presently considered in M–SURGE work conditional on releases (i.e., without estimation of population size). The time–dependent model bears then to the original Arnason–Schwarz model the same relationship as the Cormack–Jolly–Seber (CJS) model does to the full Jolly–Seber model. This class of models will then be called "Conditional Arnason–Schwarz" models (CAS). They are obtained as particular cases of JMV models obtained by dropping the dependence of probabilities of capture on the previous state.

JMV and CAS models reduce to Cormack–Jolly–Seber models (CJS) when there is a single state

(s = 1), since the matrix of survival transition–probabilities reduces to a scalar, φ, and the matrix or vector of recapture probabilities reduces to a scalar, p.

In both JMV and CAS models, survival–transition probabilities can be represented in M–SURGE in two ways:

1. Combined survival–transition probabilities. The generic set of survival–transition parameters is a matrix $\Phi = (\phi^{i,j})$ where $\phi^{i,j}$ is the probability that an animal in state i at time $k–1$ is in state j at time k. The row sums,

$$F^i = \sum_j \phi^{i,j}$$

are survival probabilities conditional on the state of departure, i, and are ≤ 1 (= 1 if and only if survival is 1).

2. Separate movement and fidelity–survival probabilities. The parameters considered are s fidelity–survival probabilities,

$$F^i = \sum_j \phi^{i,j}$$

arranged in a s x s diagonal matrix F, and the transition probabilities conditional on survival, arranged in a s x s matrix

$$\psi = \left(\psi^{i,j} = \frac{\phi^{i,j}}{\sum_i (\phi^{i,j})} \right)_{(1 \leq i, j \leq s)}$$

Once (s–1)*s parameters are known, the remaining s are obtained by difference.

The separate and combined parameterizations are related by the matrix relationship $\Phi = F * \psi$. They are further commented by Hestbeck et al. (1991). By combining the JMV or CAS recapture probability parameterizations with the separate/combined survival–transition parameterizations, one obtains four parameterizations (table 1).

M–SURGE provides thus a great amount of flexibility since only the CAS —separate survival–tran-

Table 1. Parameterizations of multistate capture–recapture models used in M–SURGE. See text for notation and further explanations.

Tabla 1. Parametrizaciones de los modelos multiestado de captura–recaptura utilizados en el M-SURGE. Para anotaciones y más detalles al respecto, consultar el texto.

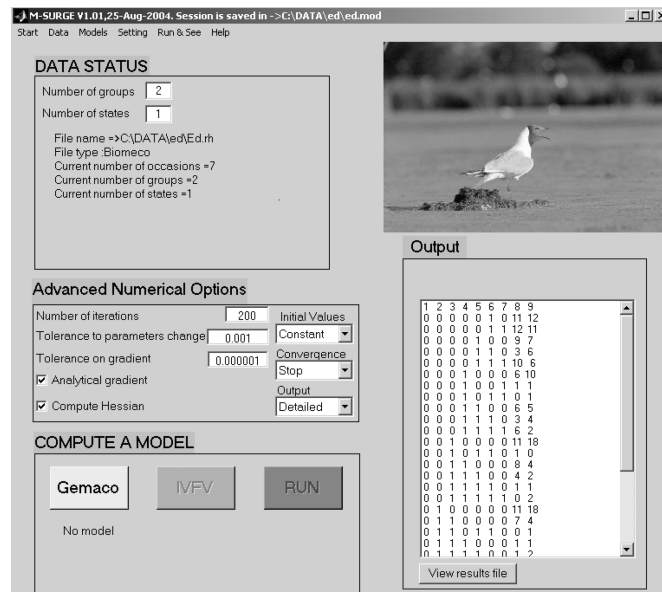| | Recapture parameters | Survival–transition parameters | |
		Combined	Separate
JMV	Matrix $P = (p^{i,j})$: depends on previous and current state	Matrix $\Phi = (\phi^{i,j})$: matrix of survival–transition probabilities	Matrix $\Phi = F * \psi$ $F = D(F^i)$: diagonal matrix of fidelity–survival $\psi = (\psi^{i,j})$: matrix of transition probabilities
CAS	Vector $P = (p^i)$: depends on current state only	Matrix $\Phi = (\phi^{i,j})$	Matrix $\Phi = F * \psi$

Fig. 1. Selection of time dependent models in the menu "Models".

Fig. 1. Selección de los modelos dependientes del tiempo en el menú "Models".

sition models were until now easily fitted, using MARK. The preferable parameterization will depend on the biological context. The JMV model appears as a natural step in testing the fit of the CAS model (Pradel et al., 2003).

In M–SURGE, the starting point for any model is an umbrella model with pre–programmed variation in parameters, later submitted to constraints. The generic sets of parameters, Φ and P or F, ψ and P, according to the parameterization chosen, may vary in different ways: (1) by group, if there are several permanent groups of individuals, such as sexes or species, or disconnected study sites; (2) between cohorts, cohort being taken in the sense of individuals first released with a mark on a same occasion; (3) over time (i.e., between occasions).

The user has to choose variation by time only, or by cohort and time as a first step in the analysis. The former models are called "time–dependent models", the latter, "time– and cohort–dependent models" (denoted "time.cohort", in relation with the Model Description Language implemented in GEMACO, see next section). The parameterization and the choice of the umbrella model (time or time.cohort) are selected by simple menus as in figure 1.

The model definition language in GEMACO

The constraint matrix, X, associated with the model, $f(\theta) = X\beta$, is obtained by describing it using a Model Definition Language (MDL). This language is interpreted in a section of M–SURGE called GEMACO (Generator of Matrices of Constraints). For the sake of simplicity, one constraint matrix has to be defined for each type of parameter (survival, capture and transition or capture and combined survival–transition depending on the particular kind of parameterization previously chosen). M–SURGE assembles the overall matrix. For instance, with matrices X_1 and X_2 for survival–transition and recapture probabilities, respectively, the overall matrix is, in block matrix notation:

$$X = \begin{pmatrix} X_1 & 0 \\ 0 & X_2 \end{pmatrix}$$

The main step in defining a matrix of constraints for one type of parameter consists of typing a phrase in the MDL that will be interpreted by GEMACO to build X automatically. The language is based on main keywords for various effects such as time (t) or group (g) and operators such as the dot (.). This language expands the tensor notation for analysis of variance models (Wilkinson & Rogers, 1973; McCullagh & Nelder, 1989) already advocated by Lebreton et al. (1992) for CJS models. GEMACO and the MDL offers very wide possibilities that make the building of nearly any biologically meaningful model a fairly easy task.

Key words for main effects

In capture–recapture modelling, several classical effects, such as time, age and group, have been widely used to explain variability in the data (Lebreton et al., 1992). In the model definition language of M–
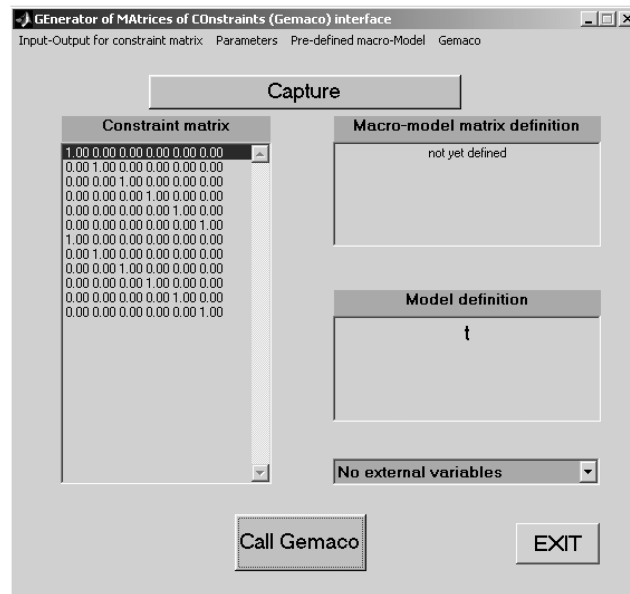
Fig. 2. Window structure of the GEMACO interface. As shown here, the recapture structure of the CJS model has just been built. The notation, "t", means that recapture probabilities vary over time as it must for the CJS model. The corresponding design matrix, automatically computed by GEMACO, has popped up in top left area. In this example, the numbers of occasions and groups are 7 and 2, respectively.

Fig. 2. Estructura en forma de ventanas de la interfaz de GEMACO. Tal y como puede observarse en la figura, la estructura de recaptura del modelo CJS acaba de construirse. La anotación "t" significa que las probabilidades de recaptura varían a lo largo del tiempo, según lo exigido por el modelo CJS. La correspondiente matriz de diseño, calculada automáticamente por GEMACO, se muestra en el área superior izquierda. En este ejemplo, los números de ocasiones y de grupos son 7 y 2, respectivamente.

SURGE, these effects are represented by reserved keywords, with synonyms to facilitate the writing of models. The effects and their associated keywords are described in table 2. In what follows, these effects are first considered by themselves (i.e., as main effects in the meaning of analysis of variance) then combined (i.e. with interaction).

As a first example of the capabilities of GEMACO, let us assume we want to run a CJS–type model with survival constant over time and varying over groups, and recapture probability varying with time only. One has only to define the structure for survival and recapture probabilities to be "g" and "t" respectively, exactly as in the tensor notation of this model (ϕ_g, p_t). The time–dependent CJS model in the strict sense is written as (ϕ_t, p_t). The phrases for model definition are typed in a specific window called "GEMACO interface" (fig. 2).

As an example, let us consider cohort and time variation in survival probability over a single state and 4 occasions (i.e., 3 intervals). The vector of parameters is written as (with the first index for cohort and the second for time):

$$\theta_1 = (\phi_{11}\,\phi_{12}\,\phi_{13}\,\phi_{22}\,\phi_{23}\,\phi_{33})' = X_1\beta_1$$

(where v' stands for the transpose of v).

Defining the model as "t" creates a matrix X with as many rows as components in θ, in the same order, with columns corresponding to the time index (second subscript):

$$X_1 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{pmatrix}$$

Defining the model as "c" (for cohort) creates a matrix X_1 with $K–1$ columns:

$$X_1 = \begin{pmatrix} 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

Effects "from" and "to" take their meaning only when there are several (s > 1) states. When "from" is applied for instance to survival–transition probabilities with 3 states, all matrices F will be equal to (rows = previous state, columns = current state):

$$\Phi = \begin{pmatrix} \beta_1 & \beta_1 & \beta_1 \\ \beta_2 & \beta_2 & \beta_2 \\ \beta_3 & \beta_3 & \beta_3 \end{pmatrix}.$$

If the structure "to" is used, the transition probability matrices will be equal to:

$$\Phi = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 \\ \beta_1 & \beta_2 & \beta_3 \\ \beta_1 & \beta_2 & \beta_3 \end{pmatrix}.$$

Further keywords are described in Choquet et al. (2003).

Combining effects with operators

Two operators can be used to combine effects to generate more complex models. Let a and b be two factors with m_a and m_b categories, respectively:

1. Dot product (.): a.b is the product column by column of a by b (i.e. the set of all combinations of categories of the factors a and b, or a model with interaction). The result, a.b, is a factor with $m_a \times m_b$ categories. This dot product is the "crossing operator" of McCullagh & Nelder (1989).

2. Sum (+): a+b joins the columns of a and b. If the intercept (constant column equal to one) is obtained as linear combination of the variables in a and in b, the first column of b is suppressed to avoid linear redundancy. The result, a+b, has then m_a+m_b-1 columns. Otherwise, all the columns of a and b are kept.

In the previous example, one obtains for t.g and t+g the respective matrices for survival:

$$X_1 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \text{ and } X_1 = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 0 & 1 & 1 \\ 0 & 1 & 0 & 1 \\ 0 & 0 & 1 & 1 \\ 0 & 0 & 1 & 1 \end{pmatrix}$$

The CJS model with several groups will be denoted as $(\varphi_{t.g}, p_{t.g})$.

The dot operator is very useful with the "from" and "to" effects when there is more than one state (s > 1): "from.to" applied to a transition probability matrix induces a variation by rows and columns (i.e.; a matrix with all elements different):

$$\Psi = \begin{pmatrix} \beta_1 & \beta_4 & \beta_7 \\ \beta_2 & \beta_5 & \beta_8 \\ \beta_3 & \beta_6 & \beta_9 \end{pmatrix}$$

with $\beta_1 = 1 - \beta_4 - \beta_7$, $\beta_5 = 1 - \beta_2 - \beta_8$, $\beta_9 = 1 - \beta_3 - \beta_6$

Several effects can be combined using these operators since in a.b and a+b, a and b can themselves be model formulae. As a consequence of these rules, the JMV model with separate transition–survival representation is generated by "from.t" for fidelity–survival F, "from.to.t" for transition y and capture p. The Conditional Arnason–Schwarz time–dependent model is generated by "from.t" for fidelity–survival F, "from.to.t" for transition y, and "to.t" for capture p. The default priority order of operations is (+ < .). This order can be changed using brackets (e.g., "[a+t].g").

External covariates

Let us assume in the previous example that a time–dependent covariate x is available as a column vector,

$$x = \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}$$

The X matrix corresponding to a linear effect of this time–dependent covariate is:

$$X = \begin{pmatrix} 1 & x_1 \\ 1 & x_2 \\ 1 & x_3 \\ 1 & x_2 \\ 1 & x_3 \\ 1 & x_3 \\ 1 & x_1 \\ 1 & x_2 \\ 1 & x_3 \\ 1 & x_2 \\ 1 & x_3 \\ 1 & x_3 \end{pmatrix}$$

which reduces to i+t*x.

Hence the matrix product of a factor by an external covariate replaces this factor by the linear effect of the covariate. The default priority order of operations is (+ < . <*), and, as above, can be changed using brackets (e.g., "[a.t]*x"). Several covariates related to different effects can be used simultaneously provided they are prepared in a file with a specific format. They are then used as x(1), x(2),etc.

Aggregation of parameters: lists

M–SURGE offers several possibilities of "grouping parameters" in the broad sense. First, one often needs to build effects less fine than time, age or any given factor. This is obtained by lumping categories. For instance in an analysis of data concerning the dipper, *Cinclus cinclus*, over 6 year intervals, Lebreton et al. (1992) described how floods impacted the survival probability in years 2

Table 2. Effects and keywords used in the Model Definition Language of M–SURGE. The sentences in this language are interpreted in GEMACO to build the matrices of constraints X.

Tabla 2. Efectos y palabras clave utilizados en el lenguaje para la definición de modelos del M-SURGE. Las frases escritas en este lenguaje se interpretan en GEMACO para construir las matrices de limitaciones X.

Effects	Keywords and abbreviations/synonyms	Comments
Constant or Intercept	intercept, i	To obtain constant parameters
Time	time, t	Categorical variation over time ("factor" with K–1 levels)
Age	ge, a	Categorical variation over age (time elapsed since first capture) ("factor" with K–1 levels). More refined age variations are introduced later
Cohort	cohort, c	Categorical variation between cohorts (batches of individuals released for the first time with a mark on a same occasion) ("factor" with K–1 levels)
Group	group, g	Categorical variation between groups
Departure state ("from") or previous state (capture)	from, f previous, p	Forces rows in j or y matrices to differ. In JMV models, forces rows in p matrices to differ Not active on p in CAS models
Arrival state("to") or current or next state (capture)	to, next, n, current	Forces columns in j or y matrices to differ Not active on F parametersIn JMV models, forces rows in p matrices to differ In CAS models forces terms in p vector to differ

and 3. The resulting X matrix is obtained by lumping years 2 and 3 on the one hand, and years 1, 4, 5, and 6 on the other. This is done in M–SURGE using lists of parameter categories, each list corresponding to a set of categories lumped together. In the dipper example, the model formula to reduce the variation over time to two levels would be "t(1 4 5 6, 2 3)". Similarly, over 7 occasions, to distinguish the first year after capture from the other ones, as two age–classes, one would use "a(1, 2 3 4 5 6 7)" or "a(1, 2:7)". The user can also define shortcuts for complex expressions (e.g. "sex" for "g(1 3, 2 4)" if groups 1 and 3 are females and groups 2 and 4 are males). Complex models using repeatedly such expressions (e.g., as "sex.t") are then written easily.

Aggregation of parameters: the aggregation operator

The lists make it possible only to aggregate parameters within a same main effect. The aggregation operator & makes it possible to aggregate parameters corresponding to categories of different effects (i.e. that cannot be handled within a same list). The syntax f(1).to(1)&to(2) applied to the combined survival transition for two states builds the following constraint $\phi_{11} = \phi_{12} = \phi_{22}$

Redundancy in the transition matrix

The transition matrix ψ is associated to a markov chain (i.e., the sum of each row is equal to one). Thus, only s x (s − 1) parameters out of the s x s parameters should be estimated. One redundant parameter has to be chosen for each row. This is open to the user's choice, based on a transition pattern matrix. This matrix is a s x s matrix made of 0's and 1's, with rows corresponding to the previous state and columns to the current state. The elements, t_{ij}, are equal to 1 except for one element per row, set equal to 0, defining the position of the redundant parameter for this row. Hence, there must be exactly one zero per row. With three states, for instance, if instead of using the parameters $\{\psi_{12}\ \psi_{13}\ \psi_{21}\ \psi_{23}\ \psi_{31}\ \psi_{32}\}$ we want to use the parameters $\{\psi_{11}\ \psi_{12}\ \psi_{21}\ \psi_{22}\ \psi_{32}\ \psi_{33}\}$, we have to change the transition pattern matrix from

$$\begin{pmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{pmatrix}$$

which is the default, to

$$\begin{pmatrix} 1 & 1 & 0 \\ 1 & 1 & 0 \\ 0 & 1 & 1 \end{pmatrix}.$$

Table 3. Correspondence between models as defined in the notation proposed by Lebreton et al. (1992) and the Model Definition Language in GEMACO: ML. Model in Lebreton et al. (1992, p. 88, 91 and 95); MGs. Model used in GEMACO for survival; MGc. Model used in GEMACO for capture.

Tabla 3. Correspondencia entre modelos, según lo definido en la anotación propuesta por Lebreton et al. (1992) y el Lenguaje para la definición de modelos en GEMACO: ML. Modelo en Lebreton et al. (1992, p. 88, 91 y 95); MGs. Modelo utilizado en GEMACO para la supervivencia; MGc. Modelo utilizado en GEMACO para la captura..

ML	MGs	MGc
ϕ_t, p_t	t	t
ϕ_t, p	t	i
ϕ_{fn}, p	t(1 4 5 6, 2 3)	i
ϕ, p	i	i
ϕ_{c^*t}, p_{c^*t}	t.g	t.g
ϕ_c, p_{c+t}	g	t+g
$\phi_{ac^*t^*s}, p_{period^*s}$	a(1,2,3:10).t.g	t(1:7,8:10).g
$\phi_{ac^*t^*s}, p_{period}$	a(1,2,3:10).t.g	t(1:7,8:10)

Table 4. Correspondence between models used in Brownie et al. (1993) in the notation proposed by Lebreton et al. (1992) and the Model Definition Language in GEMACO: MB Model in Brownie et al. (1993) (with *s* = site); MGt. Model used in GEMACO for transitions; MGc. Model used in GEMACO for capture.

Tabla 4. Correspondencia entre los modelos utilizados en Brownie et al. (1993) en la anotación propuesta por Lebreton et al. (1992) y el lenguaje para la definición de modelos en GEMACO: Mb. Modelo en Brownie et al. (1993) (con s = localidad); MGt. Modelo utilizado en GEMACO para las transiciones; MGc. Modelo utilizado en GEMACO para la captura.

MB		MGt	MGc
Φ_{s^*t}, P_{s^*t} (JMV)	f.to.t	f.to.t	
Φ_{s^*t}, P_{s^*t} (CAS)		f.to.t	to.t
Φ_s, P_{s^*t}		f.to	to.t
Φ_s, P_s		f.to	to

So, GEMACO provides an unambiguous notation to describe multistate models (table 4).

Illustrative examples

Case studies in Lebreton et al. (1992)

Pradel & Lebreton (1991) introduced program SURGE to fit single state models. Three case studies described in Lebreton et al. (1992) were analyzed with this program using the PIM (Parameter Index Matrix) approach. The main models used in these three studies are described in table 3. While some models are quite classical, some other ones are not (e.g., flood effect on survival, for which aggregation of categories was used to describe a particular variation over time).

Wintering Canada Geese

Brownie et al. (1993) introduced a routine to be used with MS–SURVIV that allows easy implementation of the JMV model and of constrained versions of this model. We show here how models considered in Brownie et al. (1993) can be implemented simply with M–SURGE (table 4).

In the notation used by Brownie et al. (1993), the first two models (JMV) and (CAS) are written in the same way, although capture parameterizations differ. In GEMACO, the sentences for recapture parameters in the two models do differ.

Discussion and perspectives

In this paper, we have presented M–SURGE and the set of models which are presently available. The set of models considered is based on: (1) the central role of JMV–type models, a large set of models for which GOF tests are now available (Pradel et al., 2003); (2) combined and separated fidelity transitions formulations; (3) a language which allows to build easily constraint matrices for multistate models.

Optimized algorithms (in particular, use of the explicit gradient of the likelihood, profile likelihood calculations) are used to fit the model and will be described in another paper.

We are continuously exploring new features with working versions. For instance, Gimenez (2003) introduced efficient starting point for quasi–Newton algorithms. We hope to use this work to improve the reliability of the results.

We only described here basic models. However GEMACO is able to generate in a straightforward fashion very complex models, such as models mixing recapture and recoveries (Catchpole et al., 1998; Lebreton et al., 1999) and multistate recruitment models (Lebreton et al., 2003). Thus, we hope that the language developed for building

constraint matrices and the fast and reliable computations in M–SURGE will help to put the emphasis on biological questions.

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