A semi-Markov model to assess reliably survival patterns from birth to death in free-ranging populations

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Summary

1. Semi-Markov models explicitly define the distribution of waiting time duration and have been used as a convenient framework for modelling the time spent in one physiological state in previous biological studies.

2. Here, we focus on the modelling of the time spent within a life-cycle stage (e.g. juvenile, adult and old) by individuals over their lifetime from Capture–Mark–Recapture data, which are commonly used to estimate demographic parameters in free-ranging populations.

3. We propose a parametric model (1) with a semi-Markov state, (2) associated to a hazard function and (3) accounting for imperfect detection to assess reliably survival patterns from birth to death.

4. These models indeed outperform models with a linear trend or a quadratic form, often selected as the best model for survival in capture–recapture studies.

5. Moreover, our approach offers the first opportunity to estimate statistically rather than visually the age of the onset of actuarial senescence, associated with confidence intervals.

6. The application of this new approach to the detailed long-term study of survival in roe deer at Trois Fontaines (France) illustrates the relevance of semi-Markov models to assess survival patterns from birth to death.

Key-words: continuous function, Cormack–Jolly–Seber model, long-lived species, mixture, nonlinear model, Reduce Additive Weibull, Siler

Introduction

The interpretation of age-specific mortality assessed using transversal life tables and associated survival curves has led investigators to split the lifespan into several distinct life history stages. For instance, in his pioneering analyses of mammalian life tables, Caughley (1966) recognized three different stages including a juvenile stage characterized by a relatively high mortality rate, an adult stage characterized by a relatively low mortality and a senescence stage during which mortality increases, known nowadays as the U-shaped mortality curve. However, two major sets of problems could induce biases in such analyses. First, changes in population age structure (Coulson *et al.* 2004), differential variation in annual survival among age classes (Gaillard *et al.* 2000) and imperfect and variable detection of individuals (Gimenez *et al.* 2008) that occur in free-ranging animal populations cast doubt on the reliability of age-specific survival estimates obtained from transversal life tables (Menkens & Boyce 1993; Gaillard *et al.* 1994). To account for such problems, Capture–Mark–Recapture (CMR) methods offer a suitable alternative (Lebreton *et al.* 1992; Nichols *et al.* 1993). Second, the threshold ages separating the life history stages have been assessed using *ad hoc* procedures. For instance, the age at onset of senescence has been assessed using visual inspection (Péron *et al.* 2010b) or based on generalized additive models applied to individual fitness contribution (Jones *et al.* 2008), and no current method allows estimating

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the age at onset of senescence with confidence intervals (CI). Using currently available CMR methods does not improve the situation, so that formally identifying the age at which survival senescence starts still corresponds to a very difficult task.

In contrast to the numerous methods available for modelling survival from actuarial data (i.e. life tables in human or captive populations), ageing and mortality processes remain largely unknown in natural populations (Jones *et al.* 2008; Nussey *et al.* 2008). The problem is even more acute from a statistical viewpoint because only small sample sizes of old individuals are available. Thus, there clearly is a lack of statistical power towards the end of life of any species, which makes the fitting of and selection among age-dependent models a non-trivial task. However, the marked increase of the number of CMR studies (especially for vertebrate populations) has led to provide clear evidence of senescence in birds (Bennett & Owens 2002) and mammals (Gaillard *et al.* 2003) using either age classes (Gaillard *et al.* 1993a), a linear trend (Loison *et al.* 1999; Péron *et al.* 2010a) or a quadratic trend (Descamps *et al.* 2006). Gaillard *et al.* (2004) fitted an exponential increase of the cumulative hazard function by using approximations of Gompertz or Weibull laws from the age at first reproduction onwards. They showed that these approximations work well, but a threshold age from which the mortality increases is required, as these models do not allow to estimate mortality during the juvenile stage, during which the hazard function should decrease.

More adequate hazard functions have been used recently in human modelling. Bebbington, Lai & Zitikis (2007a) used a mixture of two hazard functions to fit actuarial life tables for two contrasted human populations (Canadian vs. Indonesian), which is able to represent first a decrease in mortality at young ages and then an increase in mortality at old ages. They showed the relevance of the mixture for describing mortality patterns of Indonesian populations in which the shape of infant mortality may be similar to the shape of young mortality in free-ranging populations of long-lived species of vertebrates.

We developed here a model for CMR data that allow us to model directly survival over the entire lifespan, using a specific hazard function. To do so, we used a semi-Markov framework (Guédon 2004), a continuous-time stochastic process with a specified distribution of transition times between states, which is well adapted to deal with the requirement of continuous law as well as with imperfect and variable detection. We assessed four different hazard functions: (1) the flexible Weibull model (Bebbington, Lai & Zitikis 2007b), (2) the reduced additive Weibull model (Xie & Lai 1996), (3) a mixture of the two previous models and (4) the Siler model (Siler 1979). The three former have been used to describe patterns of human mortality (Bebbington *et al.* 2007a), whereas the last one has been applied to mammalian populations (Siler 1979).

These models allowed estimating survival from birth to death using a continuous law with the adequate property that the juvenile stage is usually characterized by a rapid decrease of the hazard function, followed by an almost constant hazard function in adult period, and finally by an increase of the hazard function from the age at which senescence begins. In addition, using the continuity property of the survival function, we proposed a geometric criterion based on the curvature of the survival function to assess the timing of onset of senescence. We applied this new approach to a long-lived species, the roe deer (*Capreolus capreolus*) for which a detailed long-term CMR study was available (Gaillard *et al.* 1993a, 2003).

Age-dependent Cormack–Jolly–Seber model with a semi-Markov state

Assume we have K capture occasions and N individuals. Let the encounter history for individual i be $h_i = (\delta_{i1}, \ldots \delta_{ik})$ where δ_{ik} denotes whether individual i is observed ($\delta_{ik} = 1$) or not ($\delta_{ik} = 0$) at time k. Let e_i be the occasion where individual i is captured for the first time, at age 0, l_i the last occasion when individual i is recaptured. In the classical Cormack–Jolly–Seber model (CJS, Lebreton *et al.* 1992), it is assumed that the annual survival probability is constant among all the individuals at a given time. In our case, a mixture of young and old individuals leads to a non-homogeneous probability of survival with time. Instead of a time-dependent annual survival probability, we consider an age (time elapsed since birth)-dependent annual survival probability, with $A = K - 1$ different parameters, one for each age class. The capture probability, on the contrary, varies with calendar time. Thus, the likelihood component corresponding to individual i's encounter history is

$$L(\phi_1, \ldots, \phi_{(A-1)}, p_2, \ldots, p_K; h_i)$$
$$= \left\{ \prod_{k=e_i}^{l_i-1} \phi_{k-e_i+1} \right\} \left\{ \prod_{k=e_i+1}^{l_i} p_k^{\delta_{ik}} (1-p_k)^{1-\delta_{ik}} \right\} \chi_{e_i,l_i} \qquad \text{eqn 1}$$

where p_k is the probability of recapture at occasion k of individual i ($p_{e_i} = 1$ as the likelihood is conditional upon the first capture), ϕ_a is the probability of survival over the interval ($e_i + a - 1, e_i + a$) of individual i, and $\chi_{e,l}$ the probability that an animal born at time e and still alive at time l, is not subsequently recaptured, calculated recursively as $\chi_{e,l} = 1 - \phi_{l-e+1}(1 - (1 - p_{l+1})\chi_{e,l+1})$, with $\chi_{e,K} = 1$ (see Lebreton *et al.* 1992). Assuming independence among individuals, the likelihood is the product of the probabilities of all individual encounter histories given by $\prod_{i=1}^{N} L(\phi_1, \ldots, \phi_{(A-1)}, p_2, \ldots, p_K; h_i)$. Instead of considering A different annual survival parameters, one for each age, we use a continuous mortality model to describe the variation of survival with age over the entire lifespan. To implement the continuous function, we rewrite the CMR likelihood (eqn 1) using a statistical hidden semi-Markov model.

A hidden semi-Markov chain (Guédon 1999) is a pair of stochastic processes that we will call respectively state and observation processes. The state process is a finite-state semi-Markov chain that is composed of an embedded first-order Markov chain representing the transitions between distinct states (in our case 'Alive' and 'Dead'), and state occupancy distributions representing sojourn times in non-absorbing states (in our case the 'Alive' state, as to predict the state 'Alive', it is

not sufficient to condition on the past state as in classical first-order Markov chain: we also need to know for how long the animal has been alive). This process is not observable directly, but only indirectly through the observation process whose realizations in the CMR framework are the encounter histories of the individuals. These two processes are related by a probabilistic function or mapping (see Pradel 2005, for several hidden Markov models applied to CMR).

We associated to the state 'Alive' a survival duration time denoted d. The state 'Alive' associated with d is called a semi-Markovian state. We denote $S(d)$ the survival function (the fraction still surviving at date d) with $S(0) = 1$. By stating that $\phi_{a+1} = \frac{S(a+1)}{S(a)}$ and following Guédon (1999), we can replace Eqn (1) by the following likelihood associated to individual i:

$$L(S, p_2, \ldots, p_K; h_i) = \sum_{\text{dep}=f_i-e_i}^{K-e_i-1} (S(\text{dep}) - S(\text{dep}+1)) \prod_{k=e_i+1}^{e_i+\text{dep}} p_k^{\delta_{ik}}$$
$$\times (1-p_k)^{1-\delta_{ik}} + S(K-e_i) \prod_{k=e_i+1}^{K} p_k^{\delta_{ik}}$$
$$\times (1-p_k)^{1-\delta_{ik}}$$

<div align="right">eqn 2</div>

where $S(u) - S(u+1)$ is the probability of dying in the interval $[e_i + u, e_i + u + 1]$. The second part of the likelihood takes into account the right censoring, in the case when an animal is still alive at the last capture session. In addition to this source of right censoring, there may be a risk of mortality because catching (few individuals may die). To take this type of censoring into account, we only need to replace $S(u) - S(u+1)$ in Eqn (2) by $S(u)$. The survival function S with a constant survival rate ϕ is related to the discrete well-known geometric distribution, and $S(u-1) - S(u) = \phi^{(u-1)}(1-\phi)$ is then the probability to die at time u. In the next section, we will consider survival functions related to our case of interest.

U-shaped hazard functions

As in any modelling of actuarial data, we consider the survival function $S(a)$ at time a associated to the hazard function h:

$$h(a) = -\frac{S'(a)}{S(a)}.$$

Among all possible failure rates, Bebbington *et al.* (2007a) note that there are only two possible limiting extreme value distributions, which correspond to the Gompertz and Weibull failure laws. The authors consider the flexible Weibull (FW) and the reduced additive Weibull (RAW) survival functions, and a mixture (MIX) of both presented below. In addition, we consider the Siler (1979) function, which is a simplified version of the Heligman–Pollard function (Heligman & Pollard 1980), a mixture of three components: the first component captures juvenile mortality, the second component captures an increase in adult mortality because of accidents, and the third component captures the mortality of old individuals
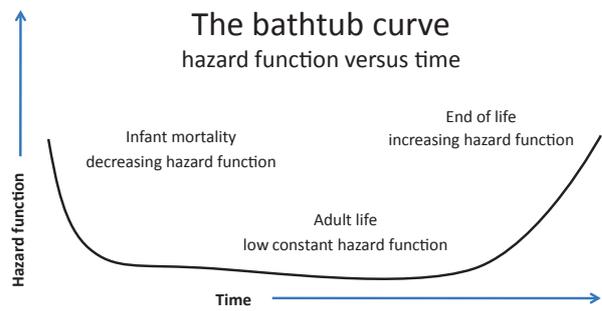
during the senescence stage. These four hazard functions have the attractive property to be able to reproduce a U-shaped curve (Fig. 1) or approaching it in the FW case, which is well adapted to model the three main life history phases.

- The FW hazard function and the associated S_{SW} are defined in Bebbington *et al.* (2007b)

$$h_{FW}(a) = \left(\alpha + \frac{\beta}{a^2}\right) \exp^{\alpha a - \frac{\beta}{a}} + \gamma$$

$$S_{FW}(a) = \exp\left(-\exp^{\alpha a - \frac{\beta}{a}} - \gamma a\right)$$

with $\alpha > 0, \beta > 0$ and $\gamma \geq 0$. h_{FW} has three parameters and is close to a U-shaped curve.

- The RAW hazard function and the associated survival function S_{RAW} are defined in Xie & Lai (1996)

$$h_{RAW}(a) = bc(ba)^{c-1} + \frac{b}{c}(ba)^{\frac{1}{c}-1} + d$$

$$S_{RAW}(a) = \exp\left(-(ba)^c - (ba)^{\frac{1}{c}} - da\right)$$

with $b > 0$, $c > 1$ and $d \geq 0$. h_{RAW} also has three parameters and has the good property for a U-shaped curve.

- The MIX hazard function and the associated survival function S_{MIX} are

$$h_{MIX}(a) = \frac{\pi h_{FW} + (1-\pi)h_{RAW}}{\pi S_{FW} + (1-\pi)S_{RAW}}$$

$$S_{MIX}(a) = \pi S_{FW} + (1-\pi)S_{RAW}$$

with π the coefficient of mixture. Instead of $d = 0$ in Bebbington *et al.* (2007a), we set $\gamma = 0$ in the mixture model to avoid redundancy.

- The SILER hazard function and the associated survival function S_{SILER} are

$$h_{SILER}(a) = b_1 \exp(-c_1 a) + b_2 + b_3 \exp(c_3 a)$$

$$S_{SILER}(a) = \exp^{\frac{b_1}{c_1} \exp(-c_1 a) - b_2 a - \frac{b_3}{c_3} \exp(c_3 a) - \frac{b_1}{c_1} + \frac{b_3}{c_3}}$$

with $b_1, b_2, b_3, c_1, c_2, c_3 > 0$.

We can easily show the equivalence of these models with nonlinear models of annual survival, using either S_{FW}, S_{RAW}, S_{MIX} or S_{SILER} in Eqn (2). Thus, these models are nested in the age-dependent model.

Fig. 1. Represents a hazard function with a U-shape (or bathtub shape) modelling the three main phases of life: infant mortality (decrease of *h*), adult life (stabilization of *h*), end of life (increase of *h*).

Materials and methods

THE DATA SET

The roe deer population of the Territoire d'Etude et d'Expérimentation of Trois Fontaines (east France) has been intensively studied for more than 30 years (Gaillard *et al.* 1993a). A total of 479 female fawns were marked as newborn during fawning time in May–June (Gaillard *et al.* 1993b) between 1985 and 2008 (i.e. belonging to 24 cohorts) and monitored over time using winter captures (a total of about 12 days of captures using net-driving are organized each year in January–February (see Gaillard *et al.* 1993a, 2003, for further details). The marked newborn fawns were thus recaptured for the first time at 8 months of age, and then on a yearly basis. To take into account unequal time intervals (length of first interval different from the next) instead of S in Eqn (2), we consider the following survival function S_{shift}

$$S_{\text{shift}}(a) = S\left(a - \frac{1}{3}\right), \quad a = 1, \ldots, K - 1,$$
$$S_{\text{shift}}(0) = S(0) = 1.$$

MODEL SELECTION

The sampling design allowed us to assign a CMR history to each marked fawn. We used these CMR histories as support for estimating age-specific survival probabilities. We considered the umbrella model $S(\text{Age})p(t)$, which fits the data. To assess the Goodness of Fit of the CJS model, we used program U-CARE (Choquet *et al.* 2009a). Only the transient component was significant suggesting an important age effect, which is taken into account by the age effect on survival probabilities (Pradel *et al.* 1997). Following previous CMR analyses in that population, we estimated capture probabilities using a model including additive effects of age (two age-classes, 8-month-olds and older, as roe deer <1 year of age have higher capture rates, Gaillard *et al.* 1997) and time (three periods, 1986–1999, 2000 and 2001–2008), as the hurricane Lothar that hit the study area in December 1999 led to a marked decrease in capture rate of roe deer (Gaillard *et al.* 2003) and the departure of highly trained people after 2000 led to a decrease in capture rate after 2000). We thus used four parameters [denoted $p(i3)$] to model the variation observed in capture probabilities during the study period. We compared the four models $[S_{\text{FW}},p(i3)]$, $[S_{\text{RAW}},p(i3)]$, $[S_{\text{MIX}},p(i3)]$, $[S_{\text{SILER}},p(i3)]$ and the model used in (Gaillard *et al.* 2004, a quadratic function of age) {model denoted $[S(\text{age} + \text{age}^2),p(i3)]$}. Finally, we also modelled survival using a five age-classes model [denoted $S(5 \text{ classes})$, $p(i3)$] including summer fawn survival, winter fawn survival, prime-age adult survival (between 2 and 8 years of age) survival of older individuals (between 8 and 13 years), and survival of individuals older than 13 years of age (Festa-Bianchet, Gaillard & Cote 2003; Gaillard *et al.* 2003, 2004). All model fitting was done using the maximum likelihood method and implemented in Matlab (The Mathworks, Natij, Massachusettes, USA). Estimates were obtained by minimizing the deviance using a quasi-Newton procedure (Dennis & Schnabel 1983). The program required for using the method will be implemented soon in the software E-SURGE (Choquet, Rouan & Pradel 2009b). As the ratio between the number of control events and the largest number of parameters of models is >40 (Burnham & Anderson 2002), we used the Akaike Information Criterion (AIC) to select the best model.

DERIVATE QUANTITIES: ESTIMATING THE ONSET OF ACTUARIAL SENESCENCE

As pointed out in Bebbington *et al.* (2007a), the bending of the curve is very difficult to interpret. As a consequence, a criterion based on the decrease of the bending is not reliable to determine the onset of senescence. We used instead the curvature quantity κ to evaluate the onset of actuarial senescence. The curvature of the survival function S is defined as

$$\kappa(a) = \frac{S''(a)}{(1 + S'(a)^2)^{\frac{3}{2}}},$$

where $S'(a)$ and $S''(a)$ are respectively the first and the second derivatives of S at a. A point with a positive maximum of κ will indicate a point of maximum slow down of decrease of S. A point with a negative minimum of κ will indicate a point of maximum speed up of decrease of S. The latter criterion was used to characterize the onset of senescence. The CI for the onset was then obtained by a nonparametric bootstrap procedure.

Results

The best model (see Table 1), as selected by AIC, not surprisingly included age (two-classes) and time (three period) effects for explaining capture probability variation. For survival, the selected model was the RAW function. We note that three of the new semi-Markov models (RAW, Mixture and Siler) performed better than $S(\text{age} + \text{age}^2)$, and that model RAW explained 94% of the survival variability with age, compared with 85% for model $S(\text{age} + \text{age}^2)$.

For the best model, we computed CI of the estimates by a nonparametric bootstrap procedure. The estimates and 95% CI are $\hat{b} = 0.0875\ [0.08; 0.093]$, $\hat{c} = 7.03\ [1.78; 8.15]$, $\hat{d} = 0.009\ [0.000; 0.055]$ (for the last interval, 0 is not included in the CI). The survival function S, the survival probabilities ϕ and the hazard function h are displayed in Fig. 2. In the panel for annual survival probabilities ϕ (the one in the middle), we represent our model ('+') and the quadratic model $S(a + a^2)$ ('o'). The panel displaying annual survival probabilities illustrates the difficulty for the quadratic model to estimate survival probabilities in early life.

The RAW hazard function is the sum of two Weibull hazard functions, each one respectively with c and $1/c$ as shape parameters. The first hazard function shows an increase at the end of life, whereas the second hazard function shows a decrease in early life. This property ensures that the RAW hazard function has a bathtub shape. For each part, b is the scale parameter, a low/large b will characterize respectively a large/short adult life duration. The parameter d characterizes infant mortality at age zero.

The curvature of the survival function is represented on Fig. 3. Applied to our data set on roe deer females at Trois Fontaines, the curvature of the survival function showed three local extrema. In Fig. 3, the negative minimum provided an estimate of the onset of actuarial senescence at 8·96 years of age (0·54 95% SE) ([7·94, 9·90] 95% CI).

After age 10, the curve of the survival function is convex, so the rate of decrease of the annual survival slows down.

Table 1. Model selection. The capture rate was modelled either as time-dependent (*t*) or as a youth effect in addition with three distinct periods and denoted in this case (*i*3). The survival was modelled as yearly constant (.), as full age-dependent (Age), with a quadratic function of age (age + age²), with five periods (5 classes), or using functions RAW, FW, MIX or SILER. The model retained according to AIC is the RAW model

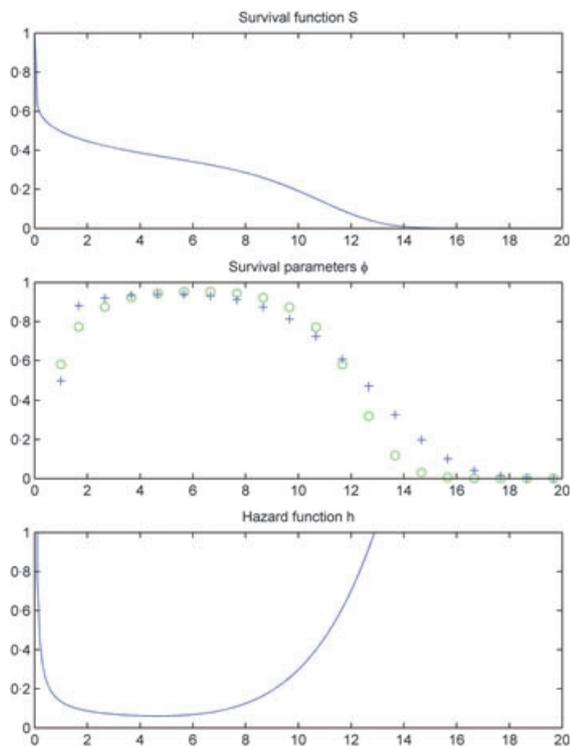| (S)	(p)	# Parameters	Deviance	Akaike Information Criterion (AIC)	ΔAIC
S_{RAW}	$p(i3)$	7	2558·70	2572·70	0
S_{SILER}	$p(i3)$	9	2559·59	2577·59	4·89
S_{MIX}	$p(i3)$	10	2557·98	2577·98	5·28
S(5 classes)	$p(i3)$	9	2565·30	2583·30	10·60
S(age + age²)	$p(i3)$	7	2571·50	2585·50	12·80
S(Age)	$p(i3)$	28	2549·57	2605·57	22·87
S_{FW}	$p(i3)$	7	2601·94	2615·98	43·28
S(Age)	$p(t)$	48	2531·66	2627·66	54·96
S(.)	$p(i3)$	5	2696·16	2706·16	133·46
S(.)	$p(t)$	25	2672·10	2722·10	149·40

Fig. 2. Shows the survival function *S* (top panel), the annual survival probabilities ϕ ('+') (middle panel) and the hazard function *h* (bottom panel) across age for model S_{RAW}, $p(i3)$. As predicted, the hazard function reproduces the three phases of life: juvenile mortality, adult life and senescence. In the middle panel, we compared ϕ ('+') with 'o' representing annual survival probabilities for the quadratic model S(age + age²), $p(i3)$.

This result must be taken with caution especially because after age 12, very few individuals remained alive.

Discussion

THE ROE DEER ANALYSIS

In this paper, we used a semi-Markov framework to incorporate continuous survival functions in the CMR likelihood. Using a unique U-shaped hazard function, we modelled, for the first time, the survival pattern from birth to death of a
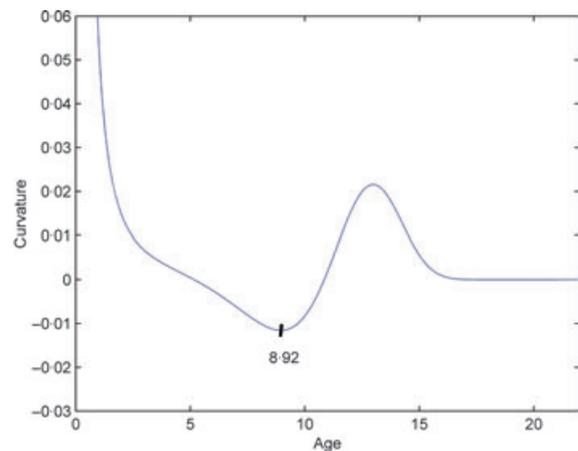

Fig. 3. Shows the curvature of the survival function *S* for model S_{RAW}, $p(i3)$. Several extrema were detected at ages 0·0300, **8·9200** and 13·3500. *S* at **8·9200** is concave. This point was retained as an estimate of the age at onset of senescence.

free-ranging population of a long-lived species, the roe deer, by taking explicitly into account imperfect detection. Semi-Markov models satisfactorily captured the complexity of the survival pattern of roe deer females, with a marked survival increase after 8 months of age (from about 0·65 to about 0·85). In his modelling of roe deer survival (at Kalo, Denmark), Siler (1979) also found that the maturity time occurred within the first year of life. After this critical time for survival, roe deer enjoy a long period of high annual survival (at about 0·92) and a decrease with increasing age towards the oldest ages. The age at onset of actuarial senescence we estimated (8·96) is close to the threshold age (8 years of age) that is usually retained from CMR analyses to separate prime-aged adults from old animals in roe deer and other medium-sized ungulates. The threshold for roe deer was initially reported for roe deer in Gaillard *et al.* (1993a)). An estimate was first based on observed patterns of tooth wear and then obtained from CMR modelling by sequential pooling of age-classes and comparison of model performance via an analysis of deviance. Interestingly, Siler did not find any evidence of senescence and concluded that senescence in roe deer is not likely to occur before 10 years

of age. This discrepancy between studies can be easily explained by considering the type of data used. Siler (1979) analysed a life table and assumed that the detection probability was 1, whereas we included a modelling of the capture probability to account for imperfect detection in the present analyses. In agreement with Gimenez *et al.* (2008)'s demonstration that accounting for imperfect detection is required to get unbiased measures of survival, we recommend focusing on longitudinal monitoring of known individuals when using semi-Markov models as performed here, and avoiding using them on data coming from life tables. Our approach has also some advantages compared to splines, another flexible method usually used to fit nonlinear relationship between time (Gimenez *et al.* 2006) or age (Viallefont in press) and survival. These models have very few parameters, have more biological meaning and are also parametric which allow us to get formally an estimate of the onset of senescence.

COMPARATIVE PURPOSE

That the use of geometrical consideration of the survival function enabled us to get an estimate of the onset of actuarial senescence along with a CI in a free-ranging population also is a derived result of the present work. However, when the estimated curvature for the survival function is only convex with age (with positive second derivative), then no estimate for the onset of senescence is available. Overall, the new semi-Markov-based approach we propose to study survival patterns from birth to death provides a suitable tool for population and evolutionary ecologists that should open the way to comparing ageing patterns among populations [e.g. between free-ranging and captive populations (Ricklefs & Cadena 2007)], between sexes (Clutton-Brock & Isvaran 2007; Bonduriansky *et al.* 2008) or to study possible trade-off between age at maturity, or age of first breeding, the onset of senescence and the speed of the senescent decline in survival (Charmantier *et al.* 2006).

LIMITATIONS

A natural limitation of this approach is the duration of the biological process under consideration. There is no interest to study 4 years of data with such models, as the main purpose of reducing the number of parameters could not be achieved in that case. In some situations, when intermediate occasions are available, it is possible to increase the duration by rescaling the time. For example, in some cases, we can use seasonal occasions instead of annual occasions. However, strong variability of survival among seasons within the year precludes the continuous requirement of the model under consideration.

The user must also keep in mind that the approach described here cannot be applied to sparse data that will not allow testing for different sources of variability. This is certainly the main limitation for studying free-ranging populations.

EXTENSIONS OF THE MODEL

As the semi-Markov models we propose here have a small number of parameters (i.e. good parsimony) and can describe a large range of patterns (i.e. high flexibility), our approach should reliably be applied to any long-lived species of birds and mammals and thereby offers a powerful method to perform comparative analyses among survival patterns. Moreover, to fit with recent increasing evidence for among-individual heterogeneities in life-history traits [see, e.g. Hamel *et al.* (2009) on large mammals, Lescroel *et al.* (2009) on seabirds], one can easily extend the models to include classes of survival heterogeneity in the estimation process. Furthermore, we can also include cohort effects to test for different sources of variability in the age at the onset of senescence. For example, an individual who has lived much of its life in good years might senesce later than an individual who has spent much of its life during bad years.

These models can also be extended to situations where the animals are captured in different sites with unequal catchability, but experience the same pattern of mortality.

More generally, this kind of model should improve the estimation of duration times in the case where the Markov process is more complex, and the data are incomplete. For example, our approach could be useful to estimate the time spent in successive biological states when studying the propagation of diseases, or the whole reproduction period.

Acknowledgements

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