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# Frailty in state-space models: application to actuarial senescence in the Dipper

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*Abstract*. Senescence, a decrease in life history traits with age, is a within-individual process. The lack of suitable methods to deal with individual heterogeneity has long impeded progress in exploring senescence in wild populations. Analyses of survival senescence are additionally complicated by the often neglected issue of imperfect detectability. To deal with both these issues, we developed state-space models to analyze capture–mark–recapture data while accounting for individual heterogeneity by incorporating random effects. We illustrated our approach by applying it to 29 years of data on breeding females in a Dipper (*Cinclus cinclus*) population. We highlighted patterns of age-related variation in annual survival by statistical comparisons of piecewise linear, quadratic, Gompertz, and Weibull survival models. The Gompertz model was ranked first in our set. It provided strong evidence for actuarial senescence with an onset of senescence estimated at about 2.3 years. The probability for this model to involve a frailty was 0.15, and the probability to involve an individual latent effect in detection was about 0.4. The estimated mean age at first reproduction was 1.2 years. The general case model described here in detail should encourage the reanalysis of actuarial senescence in cases where imperfect detection or individual heterogeneity is suspected.

*Key words: actuarial senescence; Bayesian;* Cinclus cinclus; *Dipper; frailty; individual heterogeneity; state-space models; survival.*

## INTRODUCTION

Senescence is an individual deterioration in life history traits with age caused by a progressive loss of physiological functions, translating especially into a decline in survival (e.g., Cam et al. 2002). The adaptive theory of senescence entails that it must be present in all organisms with age-structured populations (Hamilton 1966). Until quite recently, senescence in birds was in fact predicted to be either rare or absent. Due to unrealistic assumptions, analyses based on life tables provided doubtful results (Gaillard et al. 1994). Hence empirical evidence of survival senescence in the wild used to be ambiguous, partly because of methodological challenges. First, senescence can be masked by changes in extrinsic factors, especially when the study involves a small number of cohorts and all individuals of the same age also share the same environmental stresses (Nisbet and Cam 2002). Second, when an animal disperses from the study area to breed elsewhere, it is most commonly considered dead, hence only an apparent survival can be measured, which results in potential biases on senescence inference. Third, if detection probability (or resighting probability) is not accounted for, flawed inferences regarding demographic parameters (Lebreton et al. 1992) and also evolutionary processes (Gimenez et al. 2008, Keller et al. 2008) are frequent. Therefore appropriately describing actuarial senescence patterns requires at least longitudinal long-term monitoring of wild populations addressed by capture–mark–resighting (CMR) methods. Such an approach has recently become intensively used to revisit studies of actuarial senescence (e.g., Loison et al. 1999), and since then, strong empirical evidence for senescence in the wild has been accumulating in birds and mammals (e.g., Péron et al. 2010). Fourth, a major issue that needs to be accounted for in population dynamics models is that of individual variation generated by heredity, resource partitioning or other non-genetic causes (Lomnicki 1988). In particular, when CMR models ignore heterogeneity in the detection process, assumptions of independence among individuals are violated, thereby compromising further the estimation of age-specific survival trends (Lebreton et al. 1992, Pradel et al. 1997). When the population studied involves individuals with different mortality risks, individuals with lower survival rates die earlier, hence the sample composition changes with time and mean survival rate in the population increases. Due to this process of selective disappearance, described by Vaupel et al. (1979), CMR models ignoring individual heterogeneity in the survival component often fail to detect senescence (Nichols et al. 1997, Congdon et al. 2003). In order to take individual heterogeneity into account, one approach consists of using a random variable that is not directly observed (hence the terms "latent effect" or "frailty" in the case of survival

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studies), but its realizations measure the discrepancy between the statistical unit responses and the response at the population level. Presently, individual age-specific trajectories of survival have been explored in fewer than a dozen species of passerine birds (e.g., Keller et al. 2008, see comparative analyses in Jones et al. 2008). In this paper, we address the question of actuarial senescence in the White-throated Dipper (*Cinclus cinclus*, hereafter Dipper) through models involving a frailty. We modeled CMR data through state-space models (SSM) that were fit in a Bayesian framework via Markov chain Monte Carlo (MCMC; Gimenez et al. 2007). These models allow the first analysis of the survival component of senescence with both imperfect detection probability and the inclusion of a frailty. Using 29 years of data collected in this bird species with a maximum lifespan of 10 years (Marzolin 2000), our analysis reveals evidence for actuarial senescence and highlights the advantages of accounting for non-perfect detection and individual heterogeneity in both survival and detection probabilities.

## Material and Methods

### *Study species and area*

The Dipper is a relatively small passerine (about 60 g) that lives along fast-flowing streams and rivers in Eurasia all year round. Nests are built on rocky banks above water, in wall cavities under bridges, or in water mills. Typically males defend resources such as nest sites or food, while females choose breeding sites based on quality (Marzolin 2002). In this sample, 2–13% of breeding males were polygynous annually. The mean annual survival probability of breeders is around 0.5 (Loison et al. 2002, Marzolin 2002).

The sampling area (48°20′ N to 49°15′ N by 5°10′ E to 6°10′ E) is located in a hilly region of limestone cuestas (elevation from 150 to 450 m) in northeastern France (Marzolin 2002). Limited choice of secure nest sites in this study area entails strong territoriality, hence breeders of this species appear suitable for CMR methods, which, as a result, yield quite true survival estimates in contrast to apparent survival estimates. Dippers were captured as nestlings or by placing mist nets across the stream, individually color ringed and resighted as breeders in subsequent breeding seasons. We focus on the subset of 774 breeding female dippers with known birth years (see Supplement for data).

### *Model description*

In multistate models, individuals are sampled on discrete occasions and can die or move within a finite set of states between these occasions (Schwarz et al. 1993). For each occasion, these models are parameterized with a survival probability, i.e., the probability that an individual remains alive and in the sampling area at the end of the time interval, along with a probability conditional on survival that it moves from one state to another state over the interval (hereafter, a transition probability) and a state-specific detection probability. It is convenient to isolate the state, typically partially observed, of an individual in a given year from the observation made on it: observed or not observed in the case of a survival analysis. We addressed this partition between state and observation (Pradel 2005) through a state-space formulation of standard multistate CMR models (Gimenez et al. 2007), which additionally allows easy incorporation of individual random effects (Royle 2008). The state process is then a survival process, and conditional on it, the observation model is multinomial (see the Supplement for details on the implementation). In the Dipper case, we considered three states: non-breeder (NB), breeder (B), and dead. The initial state NB at birth changed once to state B, so that a transition probability $\psi(\mathrm{NB}\rightarrow\mathrm{B})$ could be estimated in relation to age, allowing an analysis of breeder recruitment. To limit the number of model parameters, we assumed that there is an age of full-breeding propensity ($x$), beyond which all individuals are in the definitive state B, so that $\psi(\mathrm{NB}\rightarrow\mathrm{B}) = 1$ for all individuals with age $\geq x$ and $\psi(\mathrm{B}\rightarrow\mathrm{NB}) = 0$. If a bird in state B skips a breeding season, it is considered as a "non-observed" breeder, hence the need for a non-observed stage. Nonbreeders cannot be detected as they are often wandering outside the study area and not established in a territory (detection probability $p(\mathrm{NB}) = 0$, resightings of non-breeders are discarded). Due to the strong territorial fidelity, before their first observed breeding in the sampling area, females were effectively non-breeders except for a few cases of total brood failure entailing returns inside the area. Since all studied birds turned into breeders, their annual survival was 1 ($\varphi(\mathrm{NB}) = 1$) before their first observed breeding year (see Appendix A: Fig. A1). These constraints made both the process and observation matrices simpler than the general case described in the Supplement. Having the state NB in our model allowed the derivation of the probability that a newborn will start breeding at age $i$ conditional on its survival to breeding (Pradel and Lebreton 1999) and the estimation of the mean age at first breeding with a credible interval.

For the regression of annual detection probability of breeders $p(\mathrm{B})$, we built an equation (see Appendix A: Eq. A.1) in which the mean detection probability $\zeta$ expressed on the logit scale, is added to $\eta$ and $\xi$, respectively time and individual normal zero mean random effects with standard deviations (SD) $\sigma_\eta$ and $\sigma_\xi$. It is common to consider time as a random rather than fixed effect, not only to restrict the large number of parameters (here, $n = 29$ years), but also to favor exchange of information among different time periods when data are unbalanced.

In a first step of the analysis, annual survival probability $\varphi(\mathrm{B})$ was regressed as a quadratic function of age (standardized) using a logit link to assess increase or decrease of survival from age 1 onwards (model $\varphi2$ in Table 1). In a second step, once a maximal annual

TABLE 1. Selection of regression models of survival on age (A) from age 1 to detect the age of maximal survival and (B) from age 2 to model senescence, in a Dipper population of northeastern France.

| Model | Deviance | DIC |
|---|---|---|
| A) Survival regression from age 1 | | |
| Quadratic (model named φ2) | 450.8 | 1890.6 |
| Eight age classes | 453.5 | 1992.4 |
| Two age classes: 1–5 and 6–8 + rd(t,i)† | 461.2 | 1993.4 |
| Two linear logit: 1–5 and 6–8 + rd(t) | 461.6 | 2053.9 |
| Two age classes: 1–5 and 6–8 | 459.5 | 2060 |
| B) Survival regression from age 2 | | |
| Gompertz + rd(t,i) | 454.6 | 1982.9 |
| Constant | 456.6 | 1993.5 |
| Two linear logit: 2–5 and 6–8 + rd(t) | 462.1 | 1999.4 |
| Extended logit‡ + rd(t) | 460.5 | 2001.6 |
| Quadratic | 454.1 | 2004.4 |
| Weibull + rd(t,i) | 460.9 | 2040 |
| Gompertz + rd(t) | 464.3 | 2100.5 |

*Note:* DIC stands for deviance information criterion.

† Time (t) or individual (i) random effect (rd).

‡ Survival of type $k/(1 + \exp[a \times \text{age} + b])$, where $a$, $b$, and $k$ are model parameters to be estimated.

survival was detected, we modeled age-specific survival trajectories starting at this onset of senescence, and using a range of distributions, namely piecewise linear, logit linear, and quadratic functions, as well as discretized versions of Weibull and Gompertz time to event models (Service 2000, Gaillard et al. 2004; see Appendix B). We added time (ε) and individual (δ) normal zero mean random effects with SD $\sigma_\varepsilon$ and $\sigma_\delta$, respectively (see Appendix A: Eq. A.2 for model φ2). All these regressions were started at the onset of senescence when survival began to decrease and were completed by survival parameters for the ages preceding this onset.

All models were run using a Bayesian approach that can quite easily deal with a combination of time and individual random effects by means of MCMC through the statistical software WinBUGS (Lunn et al. 2000; see Supplement). All parameters were assigned flat priors, $\mathcal{N}(0, 100)$ for regression parameters and U(0, 5) for SDs of the random effects. Indeed priors with bounded support yield better mixing and uniform priors appear little informative (Gelman and Hill 2007). Convergence was assessed using the Brooks, Gelman and Rubin convergence diagnostic test (Brooks and Gelman 1998), and mixing was found to be rather good (see Appendix C).

### *Model selection*

In a Bayesian framework, ranking a few dozen models is done using the deviance information criterion (DIC; Spiegelhalter et al. 2002), a Bayesian criterion with AIC-like properties. We chose this criterion despite the instability of the number of parameters in models involving hierarchical structures (Gelman and Hill 2007).

To estimate the strength of individual effects on the annual survival and resighting parameters from the onset of senescence, we checked the posterior probabilities of several models by using the method of Kuo and Mallick (1998), reviewed in O'Hara and Sillanpää (2009). These models were all submodels of a Gompertz global model (see Supplement) in which time random effects were added to φ(B) and *p*(B) and two Bernoulli-distributed indicator variables were multiplying both additive individual latent effects (Royle and Dorazio 2008). Each model of this set got the same prior probability when the prior of each indicator was fair. We could therefore estimate the posterior probabilities of each of the four submodels through the relative frequencies of each list of indicators in the set of MCMC runs.

The current state of the art of CMR goodness-of-fit (GOF) techniques (review in Pradel et al. 2005) does not allow checking the fit of a state-space model with individual heterogeneity. However we tested the fit of the multistate model without random effects using the U-CARE package (Choquet et al. 2009). This procedure essentially tests whether all animals present at any given time in the same state behave in the same manner, and especially whether their fate does not depend on their past.

## RESULTS

In the first step of our analysis, full breeding propensity at 5 years of age was determined by comparing models in which this age varied from 2 to 6 years, while survival and detection were kept equal to that of model φ2 without individual latent effects. Subsequently, a time-random effect was added to the age-dependent transition ψ(NB→B), labeled as ψ(5, t), and used in all candidate models. Model φ2 yielded a maximal annual survival at about 2.3 years (95% credible interval CR = [1.07, 2.97]). This model was better supported than models with piecewise constant survival functions whatever the number of age classes

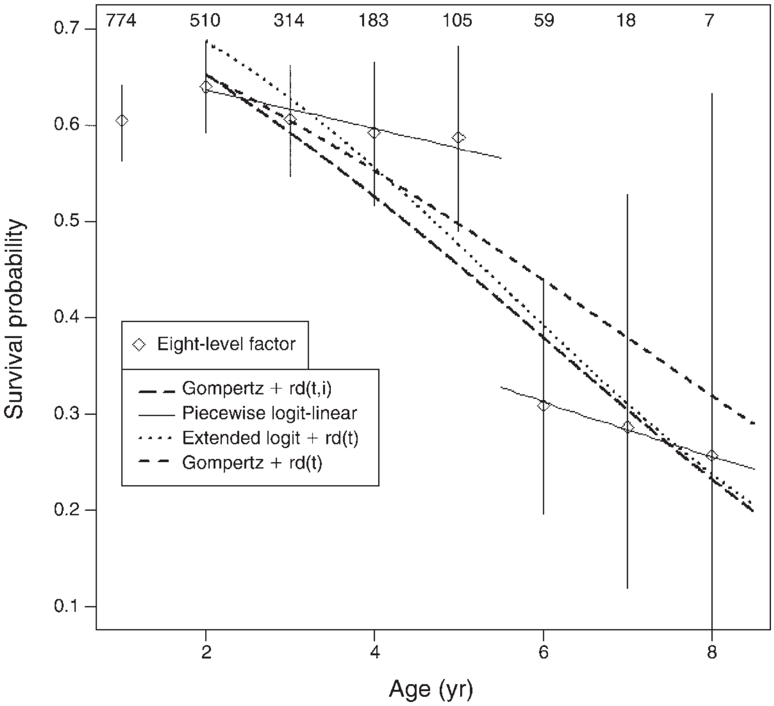

FIG. 1. Age-specific survival probability of breeding females in a Dipper population of northeastern France. Full age dependence of survival for eight age classes (open diamonds, population sample sizes at top) with 95% credible intervals. Survival senescence functions from age 2 onward were also displayed corresponding to some models of Table 1B.

considered (from two to eight, Table 1A). When an individual latent effect was added to the logit survival of this model, the onset of survival decrease was earlier, although non-significantly (1.94, CR = [0.51, 2.83]). Hence in the following analysis of senescence, all regressions of survival started at age 2 and were completed by a single parameter for age 1.

In the second step of the analysis investigating senescence patterns after age 2, we ran three Markov chains with 60 000 iterations for each regression model of survival on age to compare a set of candidate models (Table 1B).

The best model was a Gompertz model with both individual and time random effects in survival. Including an individual frailty in this model led to a clear improvement of the DIC. Models with constant survival for one, two, or seven age classes, models with piecewise logit linear regressions, as well as the Weibull model, all displayed lower performance (Table 1B, Fig. 1).

The submodel of the global model without individual random effect in $p(\mathrm{B})$ and $\varphi(\mathrm{B})$ was the best supported (Table 2). The probability for a submodel to involve an individual latent effect in $\varphi(\mathrm{B})$ and $p(\mathrm{B})$, respectively, was 0.15 and 0.42, respectively.

We plotted the relative importance of the individual random effects (Royle 2008) with their posterior densities, resulting from a model with time as fixed effects and transitions $\psi(5, \mathrm{t})$ (see Appendix A: Fig. A3). We chose a baseline $j_0$ for time (year 1988) to represent for each individual $i$: $p(\mathrm{B})[i] = \mathrm{logit}^{-1}(\zeta[j_0] + \xi[i])$ and $\varphi(\mathrm{B})[i] = \mathrm{logit}^{-1}(\alpha[j_0] + \delta[i])$, while $\alpha$, $\zeta$ are time fixed effects and $\delta$, $\xi$ are individual random effects.

Among the parameters of the global model (see Appendix A: Table A1), we note that $\sigma_\delta$ was equal to 1.67 (SD = 1.88) and $\sigma_\varepsilon$ to 2.14 (SD = 1.42). However, we found evidence of weak identifiability for the individual random effects (see Appendix C). Finally, the posterior mean age at first breeding was equal to 1.20 years (CR = [1.14, 1.26]) in this female population (see Appendix A: Fig. A2 for empirical frequencies).

As a single transition from NB to B was possible in our data set, some components of the GOF test were ruled out. The remaining ones yielded a $P$ value of 0.96, suggesting the data did not show any departure from the

TABLE 2. Probabilities of the four submodels of the global model (Gompertz type) involving time-latent effects [rd(t)] in $\varphi(\mathrm{B})$ and $p(\mathrm{B})$, in which individual random effects [rd(i)] are multiplied by Bernoulli distributed factors.

| $p(\mathrm{B})$ with | $\varphi(\mathrm{B})$ with | Relative probability |
|---|---|---|
| rd(t) | rd(t,i) | 0.076 |
| rd(t,i) | rd(t,i) | 0.069 |
| rd(t) | rd(t) | 0.509 |
| rd(t,i) | rd(t) | 0.346 |

*Notes:* Key to submodels: $p(\mathrm{B})$, annual detection probability of breeders; $\varphi(\mathrm{B})$, annual survival probability of breeders. Sum of probabilities for models with rd(i): in $\varphi(\mathrm{B})$, 0.145; in $p(\mathrm{B})$, 0.415.

hypotheses of independence underlying the different sub-components of this test.

## Discussion

Birds constitute an attractive group of organisms for comparative studies of senescence, first because they are relatively long-lived for their body sizes compared to mammals due to their slower life histories (Jones et al. 2008), and second because data on wild birds have been collected in a wide range of avian species (Vleck et al. 2007). Several studies of short-lived birds have recently shown evidence for survival senescence (e.g., Fox et al. 2006, Keller et al. 2008). Using continuous proportional hazards models, these previous studies noticed agreement with Gompertz age-dependent mortality estimates. With only two parameters, the Gompertz function provides a fairly good fit for mortality rate in a wide range of organisms (Finch 1994). Using CMR models, Gaillard et al. (2004) demonstrated a clear support of this model to female survival for two species of ungulates (*Capreolus canadensis* and *Ovis canadensis*). However, there have also recently been several case studies suggesting that non-Gompertzian models are frequently more adequate (Pletcher and Curtsinger 1998). In the Dipper study of survival from age 1 onwards, the best model in our set of candidate models was the quadratic regression which allowed us to assess the onset of actuarial senescence at age 2. When subsequently modeling senescence from that age onwards, the Gompertz model with frailty outstripped the quadratic regression and all other models. Although the collapse in survival between ages 5 and 6 (Fig. 1) needs further investigation and confirmation using larger sample sizes, this study already provides strong evidence for actuarial senescence in our dipper population.

Once the major role of individual heterogeneity was recognized in the senescence literature, several methods were developed to accommodate heterogeneity. Vaupel et al. (1979) developed Gompertz models in which each unit defines its own frailty, a $\gamma$-distributed factor multiplying the mortality risk, while Fox et al. (2006) used frailties common to maternal families. As only the general shape of the function is important, nowadays semi-parametric models for the hazard function are used. In CMR models, one makes use of finite mixtures (Pledger et al. 2003, e.g., Péron et al. 2010) in which individuals belong to hidden groups. In the absence of prior assumptions on the number of hidden groups, individual random effects can be used (Cam et al. 2002, Royle 2008, Gimenez and Choquet 2010) in which each individual has its own class of mixture. The main benefit of the state space model framework adopted here for evaluating dipper survival senescence is the straightforward implementation in WinBUGS avoiding the need to develop one's own MCMC algorithm thereby saving time to focus one's attention on concepts (Royle 2008). The choice of priors remains under debate, but due to weak identifiability we could not conform to Anderson's sentence: "I think a goal in Bayesian analysis would be to have the model priors swamped by the data" (Anderson 2008).

In our study of actuarial senescence, time random effects on detection and on survival reflected environmental variability from year to year, probably due to the availability of some nest locations ruled by river flow (Marzolin 2002). Individual heterogeneity was moderate in detection, but on survival its effect was weak as in the subset of Dipper data used by Gimenez and Choquet (2010), and less important than the effects reported by Cam et al. (2002) or Péron et al. (2010). Accounting for frailty was nevertheless sufficient to decrease the average age at onset of actuarial senescence from 2.3 to 1.9 years.

The adaptive explanation of senescence entails the prediction that mortality senescence should start soon after the reproduction outbreak (Charlesworth 1994). This is consistent with our results since the age at onset of ageing matches the mean age of first breeding in this female dipper population.

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## APPENDIX A

A table displaying the parameter estimates of the global model, an example of state transitions in the Dipper, a figure showing the empirical density of age at first breeding, a pair of density plots of individual random effects on survival and detection probabilities, and regression equations of survival and detection on age with random effects (*Ecological Archives* E092-048-A1).

## APPENDIX B

Discretization of the hazard functions in Weibull and Gompertz continuous time to event models (*Ecological Archives* E092-048-A2).

## APPENDIX C

Weak identifiability issues (*Ecological Archives* E092-048-A3).

## SUPPLEMENT

Data and WinBUGS code for the state-space formulation of multistate capture–mark–resighting models (*Ecological Archives* E092-048-S1).