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Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach

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Abstract. Whether different sources of mortality are additive, compensatory, or depensatory is a key question in population biology. A way to test for additivity is to calculate the correlation between cause-specific mortality rates obtained from marked animals. However, existing methods to estimate this correlation raise several methodological issues. One difficulty is the existence of an intrinsic bias in the correlation parameter. Although this bias can be formally expressed, it requires knowledge about natural survival without any competing mortality source, which is difficult to assess in most cases. Another difficulty lies in estimating the true process correlation while properly accounting for sampling variation. Using a Bayesian approach, we developed a state–space model to assess the correlation between two competing sources of mortality. By distinguishing the mortality process from its observation through dead recoveries and live recaptures, we estimated the process correlation. To correct for the intrinsic bias, we incorporated experts' opinions on natural survival. We illustrated our approach using data on a hunted population of wild boars. Mortalities were not additive and natural mortality increased with hunting mortality likely as a consequence of non-controlled mortality by crippling loss. Our method opens perspectives for wildlife management and for the conservation of endangered species.

Key words: Bayesian inference; cause-specific mortalities; compensatory mortality; depensatory mortality; mark–recapture; mixture of information; multistate models; ring-recoveries; wild boar.

INTRODUCTION

Disentangling the various causes of mortalities and understanding their impacts on populations is essential to address applied issues in population management (Skalski et al. 2005) or conservation (Meffe et al. 1997), and is fundamental in evolutionary biology (Stockwell et al. 2003, Metcalf and Pavard 2007). One crucial question is whether different sources of mortality are *additive*, i.e., cause-specific mortality rates are independent so that the overall mortality is the sum of all-cause specific mortality rates, *compensatory*, i.e., cause-specific mortality rates are negatively correlated so that the overall mortality is less than the sum of all cause-specific mortality rates (Errington 1946, Anderson and Burnham 1976), or *depensatory*, i.e., cause-specific mortality rates are positively correlated so that the overall mortality is more than the sum of all cause-specific mortality rates (Liermann and Hilborn 2001, Gascoigne and Lipcius 2004). Compensatory and depensatory mortality can emerge through density-dependent (and inverse-density-dependent, respectively) mechanisms and/or heterogeneous individual survival (Burnham and Anderson 1984, Boyce et al. 1999). However, whether the additivity of cause-specific mortalities is a prevailing phenomenon is still discussed (Pöysä 2004), notably in the context of exploited populations because it is a key process in determining sustainable harvesting of a population (e.g., in mallards; Nichols et al. 1995, Williams 1996).

This ongoing debate can be explained by the lack of a consensual statistical approach to disentangle additive from non-additive mortality, and by methodological issues raised by the procedures that have been used so far. Burnham and Anderson (1984) proposed a model that allows discriminating between a fully compensatory and a fully additive relationship between harvest rate and annual survival. However, besides exhibiting

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numerical instabilities (Otis and White 2004), the annual kill rate (i.e., the annual probability to be killed whether the mark is retrieved or not) and the annual band recovery rate (i.e., the annual probability that a mark is retrieved) need to be estimated separately, which requires two different monitoring schemes for the same population. To cope with this issue, Otis and White (2004) and Schaub and Lebreton (2004) suggested a two-step approach. First, time-varying cause-specific (including natural) mortalities are estimated using ring-recovery models. Second, the correlation between the two mortality time-series is estimated in a linear mixed model using a multivariate normal approximation to the ring-recovery model likelihood. Schaub and Lebreton (2004) used a standard maximum likelihood approach to estimate parameters, while Otis and White (2004) adopted a restricted maximum likelihood to reduce the bias in the estimates of variance components. Although this two-step method allows separating the true variance process from the sampling variance, the normal approximation requires large sample sizes, which is not always achievable, and some time-specific mortality rates may be estimated close or at boundary (i.e., close to one or zero), making it difficult to implement the approach. Another difficulty is the intrinsic bias in the correlation between the two mortality causes (Kimball 1969, Schaub and Lebreton 2004). Because cause-specific mortalities are competing over a non negligible time period during a year, the change over time of the numbers of individuals at risk is affected by both sources of mortality. As a consequence, a negative correlation (i.e., compensation) often occurs even when the two cause-specific mortalities are additive. This intrinsic bias can be calculated under the hypothesis of additivity (see Appendix in Schaub and Lebreton 2004), but relies on an estimate of natural survival, i.e., without any other competing source of mortality. In game species, there is often no information about survival from non-exploited populations, which makes this bias rather difficult to evaluate for exploited species.

Here, we propose a unified and flexible approach to assess in a formal way the relationship between different sources of mortality. We used a state–space modeling (SSM) approach (e.g., Buckland et al. 2004, Gimenez et al. 2007), a method that permits to disentangle the demographic process from its noisy observation, and therefore to separate the process variance from the sampling variance. More specifically, we developed a single model to estimate simultaneously two cause-specific mortality rates as well as their temporal correlation. To correct for the intrinsic bias, we included experts' opinions on natural survival in a formal way (Winkler 1981, Lipscomb et al. 1998). We adopted a Bayesian approach using Markov chain Monte Carlo (MCMC) to implement our approach. The fitting of models using MCMC simulations can be highly time consuming, which renders a model selection exercise intractable. Therefore, we first identified an appropriate model structure using maximum likelihood methods (e.g., Burnham and Anderson 2002), and second we considered an association among demographic parameters using a Bayesian approach. In this particular situation, we opted for a pragmatic combination of the Frequentist and the Bayesian paradigms rather than a philosophical choice for one framework or the other (Gimenez 2008).

As a case study, we used data from a long-term study on wild boars (*Sus scrofa scrofa*) made of physical individual recaptures (see Plate 1) and recoveries from hunting. Wild boars are widespread in Western Europe and have been increasing in numbers for the last three decades, leading to increased damage to crop and forests (Schley and Roper 2003). For instance in France, although the numbers of annually harvested wild boars increased eight-fold between 1974 and 2001, the damage to agriculture has markedly increased, and financial compensations to farmers have become very high (Guibert 2008). In this context, determining whether harvesting is compensatory to natural mortality is a key element for finding the most efficient management of the increasing wild boar populations.

METHODS

State–space modeling of cause-specific mortalities

We developed a multistate capture recapture (CR) model to combine recaptures of alive individuals and recoveries of dead individuals that were either harvested or died due to natural causes. In line with recent work by Gimenez et al. (2007) and Royle (2008), we applied a state–space formulation of this CR model that explicitly separates the demographic process of interest, i.e., being alive or dead from a specific cause of mortality, from the observations i.e., recoveries and recaptures. Then, the correlation between the cause-specific mortalities (Link and Barker 2005) is more convenient to specify in this framework. Dead-recovery models that were previously used to study compensation (Anderson and Burnham 1976, Burnham and Anderson 1984, Otis and White 2004, Schaub and Lebreton 2004) or models that combine live recaptures with dead recoveries without considering the mortality cause (Lebreton et al. 2009) can be obtained as particular cases from our model.

The four states considered were "alive," A; "newly dead by hunting," NDH; "newly dead by natural causes," NDNC; and "dead," D. We denoted $\mathbf{x}_{i,t}$, a multinomial trial taking values (1,0,0,0), (0,1,0,0), (0,0,1,0), (0,0,0,1) if, at time t, individual i is in state A, NDH, NDNC, or D, respectively. The observations were generated from these underlying states as "alive and captured," R; "dead and recovered by hunting," DR; and "not seen," NS. We denoted $\mathbf{y}_{i,t}$, a multinomial trial taking values (1,0,0), (0,1,0), (0,0,1) if, at time t, individual i is alive and captured, dead and recovered or not seen. The parameters involved in the modeling were as follows: given that individual i is alive a time t, it may survive to time $t + 1$ with probability $\phi_{i,t}$, die from hunting with probability $\mathrm{hm}_{i,t}$ or die from a natural cause (such as diseases, injuries, starvation) with probability $\mathrm{nm}_{i,t}$; the probability $p^r_{i,t}$ of detecting individual i at time t in observations r (i.e., either alive and recaptured or dead and recovered by hunting). The state–space model relies on a combination of two sets of equations, the state equations that specify the state of the individuals at time $t+1$ given their state at time t, and the observation equations, which specify the observation of the individuals at time t given their state at time t. The state–space formulation of the CR model (Gimenez et al. 2007) allowing the estimation of cause-specific mortalities is given by Eqs. 1 and 2, which are the state and the observation equations, respectively:

$$\mathbf{x}_{i,t+1} \,|\, \mathbf{x}_{i,t} \sim \text{multinomial}\,(1, \mathbf{x}_{i,t}\boldsymbol{\Psi}_{i,t}) \tag{1}$$

where

$$\boldsymbol{\Psi}_{i,t} = \begin{array}{r} \\ \text{A} \\ \text{NDH} \\ \text{NDNC} \\ \text{D} \end{array} \begin{array}{c} \begin{array}{cccc} \text{A} & \text{NDH} & \text{NDNC} & \text{D} \end{array} \\ \begin{pmatrix} \phi_{i,t} & \mathrm{hm}_{i,t} & \mathrm{nm}_{i,t} & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{pmatrix} \end{array}$$

and

$$\mathbf{y}_{i,t} \,|\, \mathbf{x}_{i,t} \sim \text{multinomial}\,(1, \mathbf{x}_{i,t}\boldsymbol{\Theta}_{i,t}) \tag{2}$$

where

$$\boldsymbol{\Theta}_{i,t} = \begin{array}{r} \\ \text{A} \\ \text{NDH} \\ \text{NDNC} \\ \text{D} \end{array} \begin{array}{c} \begin{array}{ccc} \text{R} & \text{DR} & \text{NS} \end{array} \\ \begin{pmatrix} p^{\mathrm{R}}_{i,t} & 0 & 1-p^{\mathrm{R}}_{i,t} \\ 0 & p^{\mathrm{DR}}_{i,t} & 1-p^{\mathrm{DR}}_{i,t} \\ 0 & 0 & 1 \\ 0 & 0 & 1 \end{pmatrix} \end{array}.$$

In Eq. 1, the matrix gathers the conditional probabilities of being in a state at a particular time occasion given the state at the previous time occasion. Given that an individual is alive, it can survive, die from hunting, or die from a natural cause. To ensure that these probabilities are within the interval [0, 1] and sum to 1, we used a generalized (or multinomial) logit link function to the survival and mortality parameters (Choquet 2008). In Eq. 2, the matrix gathers the conditional probability of being observed or not at a particular time occasion given the state at this current occasion. Given that an individual is alive, it can be recaptured or not. Given that an individual has just died from hunting, it can be recovered or not. We here considered that a newly dead individual due to natural causes is always non-observed (see example). However, it should be noted that this state can also be treated as being observable (e.g., Schaub and Lebreton 2004) and a probability to be observed or not as dying from natural causes, at a particular time occasion can then be estimated. Note that hereafter, the standard assumption of homogeneity between individuals in the parameters of CR models (Lebreton et al. 1992) is made, and therefore the index i for individual is dropped.

Assessing the compensatory, depensatory, or additive assumption of mortality

When the hunting mortality (hm_t) is totally additive to the natural mortality (nm_t), the two mortalities vary independently over time and the correlation between them is close to zero. On the contrary, when the hunting mortality is fully compensated by decreasing natural mortality, the correlation is equal to -1. Lastly, when depensatory mortality occurs, the correlation is positive, which means that natural mortality is also increasing when hunting mortality increases. The challenge to study compensatory, depensatory or additive mortality is therefore to estimate the correlation ρ between the two time-dependent cause-specific mortalities. To do so, we connected the time-dependent vectors of hunting and natural mortalities through a two-dimensional normal distribution with a mean vector,

$$\begin{pmatrix} \beta_{\mathrm{hm}} \\ \beta_{\mathrm{nm}} \end{pmatrix}$$

and a variance–covariance matrix,

$$\boldsymbol{\Omega} = \begin{pmatrix} \sigma^2_{\mathrm{hm}} & \rho\sigma_{\mathrm{hm}}\sigma_{\mathrm{nm}} \\ \rho\sigma_{\mathrm{hm}}\sigma_{\mathrm{nm}} & \sigma^2_{\mathrm{nm}} \end{pmatrix}$$

where σ^2_{hm} and σ^2_{nm} are the temporal variances of hunting and natural mortalities, and ρ is the correlation term of primary focus.

Schaub and Lebreton (2004) demonstrated that the two mortality rates are intrinsically negatively correlated (i.e. some process correlation occurs). A negative relationship is thus expected even in the absence of compensation. The bias of the estimated correlation ρ can be calculated as a function of the mean and variance of ϕ_0 and hm (Schaub and Lebreton 2004) where ϕ_0 is the natural survival probability, i.e., survival in the absence of any competing source of mortality. While the mean and variance of hm are directly estimated from the state–space model, ϕ_0 remains most often unknown. Schaub and Lebreton (2004) coped with this issue by using a guess estimate for ϕ_0 which could also be extracted from the literature. Incorporating a single estimate in the bias estimation precluded from incorporating any level of uncertainty associated with this value. Besides, in intensively hunted game species, in rare or elusive species, information about natural survival without any competitive source of mortality is usually lacking, making this bias difficult to evaluate. To provide a more general and flexible approach, we developed a model to incorporate experts' opinions about ϕ_0, which allowed us to estimate the distribution of ϕ_0 (Appendix A). The bias in ρ could therefore be estimated, and a bias-reduced correlation ρ' ($\rho' = \rho -$ bias) between the two cause-specific mortalities obtained. Note that because the bias lies between -1 and 0, ρ' is between -1 and 2. By inspecting the posterior distribution of the bias-reduced correlation ρ', we concluded for additivity if $\rho' = 0$ (its 95% Bayesian confidence interval includes 0), compensation if $\rho' < 0$, and depensatory mortality if $\rho' > 0$.

To assess the potential influence of the estimate of ϕ_0 on the bias, we carried out a sensitivity analysis by varying the expectation and the variance of ϕ_0 and calculated the resulting bias.

Bayesian model fitting using MCMC methods

Fitting state–space models and incorporating random effects is a rather complex task since the model likelihood involves high-dimensional integrals (Buckland et al. 2004, Gimenez et al. 2007). To overcome this issue, we used MCMC simulations in a Bayesian context (see McCarthy 2007 for an introduction). Prior distributions need to be specified for the parameters of a given model. Bayes' theorem is then used to update the priors using the likelihood and to obtain posterior probabilities of all model parameters. The MCMC algorithms then generate values from a Markov chain whose stationary distribution are the required posterior distributions. We used empirical means and 95% Bayesian confidence interval (95% BCI) to summarize posterior distributions.

To estimate the distribution of ϕ_0, each minimum value a_i and maximum value b_i given by each expert, were assumed to be the limits of uniform probability distributions. Those minima and maxima were then assumed to be drawn from normal distributions with means μ_a and μ_b and variances σ_a^2 and σ_b^2. Prior for μ_a and μ_b were uniforms while σ_a^2 and σ_b^2 were assigned inverse-gamma prior distributions with parameters 0.01 and 0.01 (see Appendix A for further explanations).

Regarding the a priori distributions for all parameters, we provided vague priors to induce little prior knowledge. Specifically, we chose uniform distributions on [0, 1] for the dead-recovery and the live-recapture probabilities, and normal distributions with mean zero and variance 100 (i.e., a precision of 0.01) for the logit of the mean hunting and natural mortalities, as commonly done to obtain a flat distribution. The prior for the variance–covariance matrix $\mathbf{\Omega}$ was chosen as an inverse-Wishart (Link and Barker 2005) with 3 degrees of freedom and a diagonal matrix (2, 2), which induced first a uniform prior on the correlation term (between -1 and 1) and second inverse-gamma distributions for the temporal variances of the two cause-specific mortalities (e.g., Link and Barker 2005). We conducted a sensitivity analysis by changing the prior on $\mathbf{\Omega}$ (Link and Barker 2005) and the results did not change.

Two MCMC chains with over-dispersed initial values were generated using 500 000 iterations with 100 000 burn-in iterations. These simulations took around seven hours on a PC (512Mo RAM, 2.6GHz CPU). Convergence was assessed using the Gelman and Rubin statistic, which compares the within- to the between-variability of chains started at different and dispersed initial values (Gelman 1996). The simulations were performed using WinBUGS (Spiegelhalter et al. 2003) and the R package R2WinBUGS (Sturtz et al. 2005) was used to call WinBUGS and export results in R. The code is available in the Supplement.

*Wild boar (*Sus scrofa scrofa*) as a case study*

To illustrate our approach, we used data from a long-term study of a hunted marked wild boar population in Eastern France. An individual encounter history was made of a mixture of physical recaptures (see Plate 1) and dead recoveries from hunting. In a previous analysis of part of the data (1982–2004), Toïgo et al. (2008) tested compensatory mortality a posteriori using a correlation test between hunting and natural mortalities. Although a weak but non-significant negative correlation was found in females between the estimated natural mortality a given year and the estimated hunting mortality the previous year (Fig. 2 in Toïgo et al. 2008), it was not possible to distinguish the true process correlation from the sampling covariance (Schaub and Lebreton 2004). This marginal relationship may thus be due to sampling correlation between the two cause-specific mortalities (Gould and Nichols 1998, Link and Barker 2005). We updated data used by Toïgo et al. (2008) by adding three years of recaptures and recoveries (1982–2007). In total, 1255 encounter histories of female wild boars from this 25-year intensive monitoring were used. As only 15 out of 1255 female wild boars were recorded as dying from natural causes, we considered that individuals dying from natural causes were consistently not observed. Using standard model selection tools, we first analyzed these data to find a parsimonious model regarding temporal variation and age structure (Appendix B). We ended up with a model specifying time-dependence on both hunting and natural mortalities probabilities and no age variation. The structure of this model was used to assess additive, compensatory, or depensatory mortality with the state–space model presented above.

To get an estimate of natural survival of wild boar in the absence of hunting mortality, we resorted to the opinion of thirteen experts with experience in population dynamics of wild boar, out of which four were co-authors of this paper. The experts were asked to give an interval for the survival probability of wild boars in natural conditions in the absence of hunting. Seven out the nine external experts responded. To these estimates, we added estimates from one study on a non-hunted population (Jezierski 1977) and on a weakly hunted population (Focardi et al. 2008). See Appendix A for further explanations.

RESULTS

The natural survival of wild boars in natural conditions in the absence of hunting given by the experts were estimated to be between $\mu_a = 0.64$ (95% BCI: 0.57–0.70) and $\mu_b = 0.87$ (95% BCI: 0.82–0.91) with their associated variance $\sigma_a^2 = 0.01$ (95% BCI: 0.01–0.03) and $\sigma_b^2 = 0.01$ (95% BCI: 0.00–0.01). See also Appendix A.

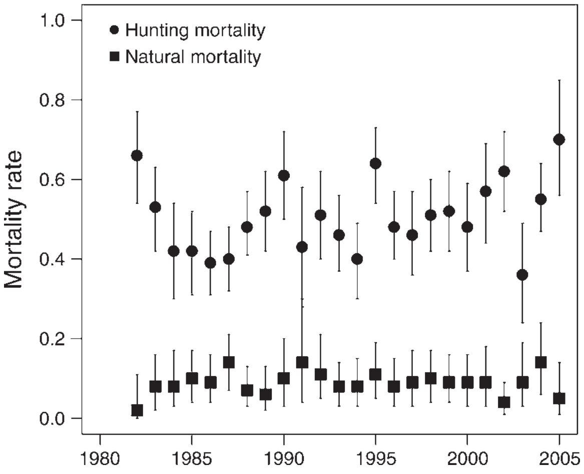

FIG. 1. Posterior annual estimates of the hunting (hm_t) and natural (nm_t) mortality probabilities in the wild boar population. Error bars show 95% Bayesian confidence intervals.

Posterior estimates of the hunting and natural annual mortalities were similar to those obtained by Toïgo et al. (2008) and to those obtained in the standard multistate analysis (Appendix B). Hunting mortalities ranged from 0.36 to 0.7, whereas natural mortalities varied between 0.02 and 0.14 (Fig. 1). Temporal standard deviations for both hunting and natural mortalities were estimated to be 0.52 (95% BCI: 0.37–0.74) and 0.66 (95% BCI: 0.14–1.03), respectively. Recapture probabilities exhibited high temporal variations and ranged from 0.03 to 0.57 (Appendix C). The probability of being recovered dead by hunting was estimated to be 0.76 (95% BCI: 0.73–0.78).

The mass of the posterior distribution of the bias-reduced correlation was clearly centered on positive values (Fig. 2), with a posterior mean of 0.75 (95% BCI: 0.30–1.28), indicating that additivity and compensatory mortalities were not supported. The relationship between the two mortalities was positive, meaning that when hunting mortality was increasing, the natural mortality was also increasing. The two cause-specific mortalities were thus depensatory. The estimate of the bias was little sensitive to different values of natural survival and its variance. The bias decreased slightly when the expectation and the variance of ϕ_0 increased (Appendix D: Table D1). In every tested case, the bias was estimated to be very close to the maximum value it could take (i.e., −1) and the bias-reduced correlation was always larger than zero (Appendix D: Table D1).

DISCUSSION

We built a state–space model to estimate hunting and natural mortalities as well as a correlation between them to evaluate whether hunting mortality is additive, compensatory or depensatory to natural mortality. The SSM approach enables to obtain more accurate results than statistical methods that do not account for sampling variation (de Valpine and Hastings 2002). Our results showed that the bias-reduced expression of the correlation was positive (Fig. 2). This depensatory population dynamics might be generated by different factors: selective hunting on individuals of higher than average quality (Coltman et al. 2003), poaching, emigration or crippling loss. In our case study, selective hunting of the best animals as often reported in trophy hunting of deer or sheep populations (Festa-Bianchet 2003) was unlikely to occur. Wild boars were hunted using drives, hunters being posted around a given hunted area, waiting for wild boars startled by beaters and flushing dogs. Wild boars were therefore shot when they were flushed out of the vegetation, leaving very few possibilities for hunters to assess the phenotypic quality of animals. Likewise, we do not expect poaching to increase with increasing hunting bags. Although data on poaching are obviously lacking, the authorized hunting bags are so large in our study site that poaching should be limited. However, wild boars living near to the forest boundary could be hunted by teams of hunters from the periphery (i.e., agricultural plain) but not reported as hunting bags in agricultural plain are smaller. Increased emigration of wild boars out of the study area with increasing hunting bags could also be discarded as hunted animals were recovered at a much larger scale than the trapping zone (8800 ha vs. ~2000 ha; see Toïgo et al. 2008 for further details). Moreover, wild boars are known to be sedentary animals, especially females (Truvé and Lemel 2003, Keuling et al. 2009). Therefore, crippling loss was most likely the factor causing increased mortality with increasing hunting bags. In a forested area like the study site, assessing with certainty the outcome of a shoot is almost impossible and some wild boars could have been wounded or killed during the hunting but never retrieved by hunters. Those wounded

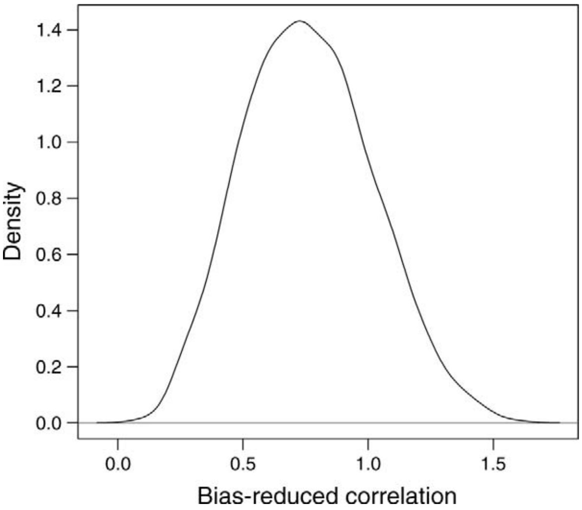

FIG. 2. Posterior distribution of the bias-reduced correlation (ρ') between the hunting mortality and the natural mortality in the wild boar population.

PLATE 1. Recapture of a wild boar female in a corral trap. Photo credit: É. Baubet.

or killed individuals would then be considered as if they have died from natural causes. While crippling loss has long been included when interpreting recoveries of waterfowl (Henny 1967), virtually no study has yet investigated or discussed the potential influence of crippling loss when hunting large mammals. Although further data are required, our results suggest that crippling loss can increase substantially the overall mortality of wild boar.

Our SSM approach is a promising approach to test whether two cause-specific mortalities are additive, depensatory, or compensatory. In management and conservation, it is important to understand whether human related mortality is additive. For instance, it would be possible to evaluate whether mortality induced by power line collision or electrocution (Schaub and Lebreton 2004, Schaub and Pradel 2004 on White Stork, *Ciconia ciconia*) or mortality induced by long-line fisheries (Awkerman et al. 2006 on Waved Albatross, *Phoebastria irrorata*) is additive or compensatory. In pest control, it can be used to test whether the reduction in numbers is additive and thus efficient. From a methodological point of view, our procedure relies on modeling a correlation between cause-specific mortalities by treating these parameters as random variables. The Bayesian paradigm, in which all quantities are treated as stochastic, is particularly relevant to deal with such models. Besides, the MCMC implementation allows coping with the complexity of SSM likelihoods. Eventually, the hierarchical structure of SSM, in which the observations are generated from an underlying hidden demographic process, is ideal to incorporate extra information. In our case, this feature was particularly useful to combine data from experts' opinions on natural survival to adjust the correlation term for some intrinsic bias.

A prerequisite of testing whether compensatory mortality or depensation occurs is that the cause-specific mortalities have to be time-dependent to estimate a correlation between them. Although parameter estimation was found to be difficult in multistate models with multiple causes of death, Schaub (2009) showed that models with mortality causes varying with time provided satisfying results in terms of bias and precision of parameter estimates. During the first step (i.e., identifying an appropriate model structure using maximum likelihood methods), parameter redundancy can occur when models are over-parameterized and consequently some parameters cannot be estimated separately. Several methods exist to obtain a diagnostic regarding parameter redundancy (Gimenez et al. 2004 for a review), in particular to determine which parameters are estimable. In a Bayesian context, a comparison between the prior and posterior distributions can inform on the identifiability of parameters (Gimenez et al. 2009).

Compared to previous methods to assess the relationship between two cause-specific mortalities, our approach can be used on data of marked animals even if a cause-specific mortality involves an unobservable state. Burnham and Anderson's approach (1984) requires different monitoring schemes for the same population, and Schaub and Lebreton's approach (2004) requires recoveries of dead individuals from another source of mortality than the focal one. As in the latter, our method requires knowledge about the natural survival. The use of a Bayesian approach enables to include in a formal way experts' opinions or existing published estimates. However, what is just as noteworthy is the fact that the bias can be highly sensitive to natural survival (Appendix D: Table D2), depending on species or populations. It is thus crucial to get a reliable natural survival estimate without any competitive mortality to be confident in the outcome and we sorely suggest performing a sensitivity analysis when it is not the case.

To conclude, we developed a state–space model to estimate cause-specific mortality rates using data on marked animals, and based on a Bayesian framework in conjunction with MCMC methods, we obtained a posterior distribution of the bias-reduced correlation between the two cause-specific mortalities. We showed that the natural mortality of female wild boars increased with hunting mortality, likely as a consequence of non-controlled mortality by crippling loss. Such a pattern could not be detected using a simple correlation between estimated hunting and natural mortalities. Investigating association among demographic parameters is of broad interest in ecology and evolution. The Bayesian state–space modeling of CR data allows estimating these correlation terms while accounting for the observation process.

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APPENDIX A

Estimating the intrinsic bias in the correlation between cause-specific mortalities: incorporating experts' opinions using a hierarchical model (*Ecological Archives* E091-130-A1).

APPENDIX B

Mark–recovery–recapture analyses of the wild boar data (*Ecological Archives* E091-130-A2).

APPENDIX C

Posterior annual estimates of alive recapture probabilities in the wild boar population (*Ecological Archives* E091-130-A3).

APPENDIX D

Sensitivity analysis of the bias when varying the expectation and the variance of the natural survival without any competitive mortality (Φ_0) (*Ecological Archives* E091-130-A4).

SUPPLEMENT

WinBUGS code for fitting the state–space formulation and obtaining the distribution of the correlation between the two causes of mortality (*Ecological Archives* E091-130-S1).