ASSESSING THE RELATIVE IMPORTANCE OF DIFFERENT SOURCES OF MORTALITY FROM RECOVERIES OF MARKED ANIMALS

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Abstract. Overall mortality rates often are based upon a variety of mortality sources such as predation, disease, and accidents, and each of these sources may influence population dynamics differently. To better understand population dynamics or to derive effective conservation plans, it is thus crucial to know the frequency of specific mortality causes as well as their variation over time. However, although the mortality cause of retrieved marked animals is often known, this information cannot be used directly to estimate the frequency of a mortality cause. By calculating the ratio of the number of animals reported dead from a specific cause to the total number of retrieved animals, one does not consider the fact that the probability of finding a dead individual depends on the cause of its death. Although frequently used, such ad hoc estimates can be heavily biased. Here we present a new way of estimating the frequency of a mortality cause from ring-recovery (band-recovery) data without bias. We consider the states ''alive,'' ''dead because of mortality cause A,'' and ''dead due to all other causes'' and estimate within a multistate capture–recapture framework the transition probabilities as well as the state-specific resighting probabilities. Among the transition probabilities are the overall survival probability and the proportion of animals dying because of A. From these, the probability that an animal dies during a year due to the specific cause of interest (cause A kill rate) can easily be calculated. We illustrate this model using data from White Storks *Ciconia ciconia* ringed in Switzerland to estimate the proportion of storks that died due to power line collision. Average unbiased estimates of this proportion were 0.37 ± 0.08 (mean $\pm$ 1 SE) for juveniles, about 25% lower than ad hoc estimates, and 0.35 ± 0.09 for adults. The annual survival rate of juveniles was 0.33 ± 0.05 and of adults, 0.83 ± 0.02. Power line mortality is thus important for White Storks, with about one in four juveniles and one in 17 adults dying each year because of power line collision. We discuss advantages and disadvantages of the new model and how the results could be used to explore the link between a specific mortality cause and population dynamics.

Key words: band recoveries; Ciconia ciconia; *kill rate; mortality cause proportion; multistate capture–recapture model; population dynamics; reporting rate; ring recoveries; survival rate; White Storks.*

INTRODUCTION

Overall mortality rates are often based upon a variety of mortality sources such as predation, disease, or accidents, and each of these sources may influence population dynamics differently. While some sources of mortality can be avoided by learning, abatement in others may be unavoidable. Hence, different age cohorts of the population are more susceptible to certain sources of mortality. Compounding the complexity of the age pattern, temporal and spatial variation with respect to different sources of mortality is also likely to occur. The different proportions of mortality from multiple sources among categories of individuals, populations, or locales will eventually translate into different sur-

vival rates. As population growth rate is often highly sensitive to changes in survival rates, particularly in long-lived animals (Lebreton and Clobert 1991, Sæther and Bakke 2000, Fujiwara and Caswell 2001), differences in the proportion of mortality from multiple sources can be a main reason for differences in dynamics among populations. Thus, studying the proportion of different sources of mortality is important for understanding proximate causes of population dynamics. In particular, conservationists aim to know proportions of mortality causes so that they can effectively slow population declines and promote population increases by enhancing survival (Caswell 2000). Indeed, different sources of mortality might require different conservational actions. Hence, conservation efforts could be focused more efficiently if more were known about the contributions from different sources of mortality.

In the field of evolutionary ecology, it is the proportion of intrinsic vs. extrinsic mortality causes that is of prominent interest. For example, a key evidence for ageing is the increase in the proportion of intrinsic mortality causes with age. However, the demonstration of ageing in wild animal populations has been identified as a very difficult task (Stearns 1992), because a reliable method for estimating the proportion of intrinsic causes of mortality was lacking. The ability to estimate the proportions of intrinsic vs. extrinsic mortality causes is also relevant to studies of the evolution of age at maturity or age-specific reproductive investment (Stearns 1992). In addition, changes in the proportion of extrinsic mortality causes are likely to have consequences on individual decisions such as habitat selection or dispersal.

Unless animals are radiotagged (e.g., Heisey and Fuller 1985, Ferraras et al. 1992, Bro et al. 2001), the importance of a particular source of mortality is difficult to assess. Traditionally, crude estimates of proportions of mortality causes have been produced by taking the number of animals reported dying from a particular cause and dividing by the total number reported altogether (e.g., Riegel and Winkel 1971, Newton et al. 1999, Pennycott 1999, Hüppop and Hüppop 2002). However, these ad hoc estimates are likely to be biased by unequal detection rates: the probability of finding and reporting a dead animal may depend on the cause of mortality. Thus, the proportion of mortality causes related to humans is particularly likely to be overestimated. For example, marked individuals killed by hunters are more likely to be recovered and reported than those that died from natural causes. Consequently, the frequency of dead individuals due to a given source of mortality is not a valid estimator of the true mortality frequency.

Here we present a way of obtaining unbiased estimates of the frequency of dead individuals resulting from different sources of mortality using ring-recovery (band-recovery) data complemented with information about the mortality cause. By use of multistate capture–recapture models (Nichols et al. 1992) we undertake to estimate independently the proportion of animals that have died from a mortality cause of relevance, the overall survival rate, and the cause-specific probability of reporting a dead animal. All parameters are not always estimable and we consider use of additional information to increase estimability in multistate capture–recapture models.

We illustrate this approach by a study of the migratory White Storks *Ciconia ciconia* L. The most frequent cause of mortality observed in White Storks is collision with overhead power lines (e.g., Zink 1967, Riegel and Winkel 1971, Moritzi et al. 2001), responsible for up to 50% of recovered stork mortality. Thus, power line collisions are cited as a major source of mortality, having a significant impact on stork population dynamics (Bairlein and Zink 1979).

It is well known that dead White Storks can often be found along power lines, and there are substantial efforts to recover them there. The probability of finding a White Stork that died because of a power line collision is therefore likely to be higher than that for a White Stork that died for another reason. The importance of power line mortality is therefore likely to be overestimated by traditional ad hoc analyses. It is not, however, known how serious this overestimation is. If it were large, stork population dynamics would be much less influenced by construction of power lines than usually thought, lessening the threat of power line mortality. Using a 16-yr long data set of marked White Storks from Switzerland, we estimated the proportion of storks that died each year because of power line collisions. We discuss advantages and disadvantages of this approach over the traditional ad hoc analysis and how the results can be used to explore the link between a specific mortality cause and population dynamics.

MATERIAL AND METHODS

The basic model

Consider the fate of a marked individual over a predefined time interval. Each fate occurs with a particular probability and can be observed with another probability. We aim to estimate the unknown probabilities by using a multinomial probabilistic model. More specifically, a marked animal may survive from year i to year $i + 1$ with probability S_i, or it may die with probability $1 - S_i$ some time during the year. If it dies, this is either because of the mortality cause under scrutiny (cause A) with probability α_i or because of any other cause (cause B) with probability $1 - \alpha_i$ (Fig. 1). Conditional on the two fates, "dead because of A" and "dead because of B," the animal may be encountered with probabilities λ^A or λ^B, respectively. The probability of encountering a dead, ringed animal in a given time period (λ_i^A, λ_i^B) is defined as the probability that an animal that has died between i and $i + 1$ is found and its ring is reported, herein referred to as the recovery rate. The probabilities of the different fates and recovery rates can be estimated using a multistate capture–recapture model (Arnason 1972, 1973, Nichols et al. 1992). The different states in this model are "alive," "newly dead because of A," and "newly dead because of B." In principle, the model contains a further state "dead for at least one year," but because corpses are not usually retrieved after one year, this state is unobservable and absorbing and it is not necessary to include it explicitly (Lebreton et al. 1999). The transition matrix and the associated vector of recovery probabilities are then

$$\begin{bmatrix} S & \alpha(1-S) & (1-\alpha)(1-S) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}_t \begin{pmatrix} 0 \\ \lambda^A \\ \lambda^B \end{pmatrix}_t. \qquad (1)$$
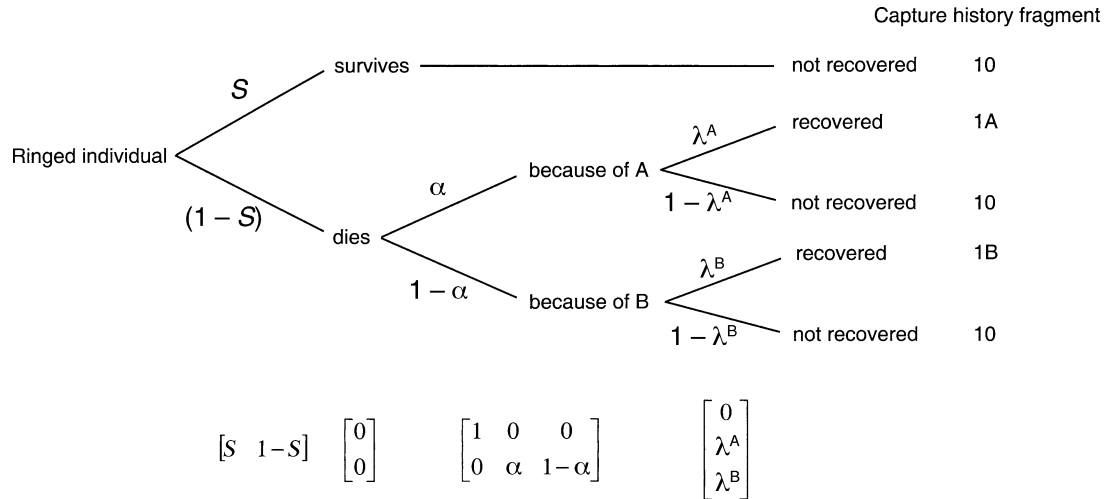
Fig. 1. Fate diagram of a marked White Stork from occasion i to occasion $i + 1$, decomposed into a succession of two simple Markovian steps. S is the survival probability, α the proportion of individual that die because of cause A, λ^A the probability that a ringed individual that died because of cause A is found and its ring is reported, and λ^B the probability that a ringed individual that died because of an unknown reason other than A is found and its ring is reported. The resulting capture history fragments from each of these possible fates are shown and coded in the same way as the input data. The matrices of transition probabilities are written below each process. The departure states are in rows, the arrival states in columns. Interspersed among transition matrices are the vectors of state-specific probability of observation.

The matrix and vector subscript t denote that the parameters are time dependent, i.e., they are different at each step of time. Unfortunately, this fully time-dependent model (alternative notation following Lebreton et al. (1992): $\{S_t, \alpha_t, \lambda_t^A, \lambda_t^B\}$) is not full rank, i.e., only the survival rates can be estimated separately. We checked the 16 possible models where between zero and all of the four parameter types are time dependent with computer algebra for identifiability (Catchpole and Morgan 1997, Catchpole et al. 2002, Gimenez et al. 2003) and found that in only two of them were all parameters separately estimable ($\{S_t, \alpha_t, \lambda^A, \lambda^B\}$, $\{S, \alpha_t, \lambda^A, \lambda^B\}$). However, nonestimable parameters of relatively simple models may become estimable when the model is generalized to incorporate additional effects (e.g., Morgan and Freeman 1989). This was the case with the White Stork example that follows, where we enlarged the basic model to include resighting data and incorporated the probability of natal dispersal and age dependency in some parameters.

The White Stork and power line collisions as a case study

We illustrate and discuss the use of the model with an example of White Storks from Switzerland that were ringed between 1984 and 1999 at 57 different locations. A total of 2912 nestlings (>90% of all nestlings born in Switzerland) and nine adults were ringed during these 16 years. Nestlings were ringed on average each year on 14 June (1 SD = 9 d); thus, we used that date as the banding date, i.e., annual survival probability and the proportion of storks that die because of power line collisions refer to the period between 14 June of year i to

13 June of year $i + 1$. We used resighting data collected on adult birds (>3 yr old) at breeding colonies between 1 March and 30 September each year. Although many different observers visited various breeding colonies, these data were not abundant (88 resightings of 61 adult White Storks), and the resighting effort was not constant from year to year. Ring-recovery data were more abundant (ring-recovery data contains information about the ring number of the individual, the location and date of the recovery as well as the cause of death), and, by 13 June 2000, 416 dead recoveries had been reported to the Swiss ringing center (Swiss Ornithological Institute, Sempach, Switzerland). Of this total, 195 (46.8%) were reported as due to power line collision ("electrocution" or "collision with thin man-made structure"). The raw proportion of recoveries resulting from power line collisions was higher in juveniles (50.1%, $n = 161$) than in adults (34.4%, $n = 34$).

For every ringed White Stork, we constructed an individual capture history which contained a "1" in years the White Stork was ringed or resighted, a "P" when it was reported dead because of power line collision, an "R" when it was reported dead because of another reason, and a "0" otherwise. These individual capture histories were the input data for the analyses.

Statistical analyses

The basic model described above was modified for the stork data. Before White Storks start to breed at age 3–4 yr (Zink 1967, Lebreton 1978) they may stay in Africa or on the Iberian peninsula, or they may return as nonbreeders to the natal sites. Because of this, the resighting probability of nonbreeding (<4 yr) White Storks during

the Swiss breeding season is not homogenous among individuals and can thus bias the survival estimates (Sandland and Kirkwood 1981). We therefore excluded all resightings of storks younger than 4 yr. Once storks start to breed, they exhibit strong philopatry to their breeding sites across breeding seasons (Zink 1967, Barbraud et al. 1999). Natal dispersal however, is much more substantial (Zink 1967). Young White Storks can disperse to breeding sites outside Switzerland, where they have no chance of being resighted. To account for this in our model, we assumed that White Storks do not emigrate from Switzerland once they have started to breed, and we included the probability of juvenile emigration (d) in our model. With natal dispersal included in the model, we also added the state "alive, but outside Switzerland." We included an age structure with two age classes (the first spanning the time from ringing as nestling up to the end of the first year of life, and the second all following years) in some of the parameter types. Because some parameters change with the age of the White Stork, we present the multistate model with three different transition matrices. One refers to juvenile storks, i.e., to the time between ringing as nestling and the end of the first year of life. The second matrix refers to subadult storks, i.e., to the time birds are between 1 and 3 yr old, and thus have dispersed, but were not resighted. The third matrix refers to adults, i.e., to all further annual time steps. The model has four states: (1) alive and in Switzerland, (2) alive, but outside Switzerland, (3) newly dead because of overhead power line collision, and (4) newly dead due any other mortality cause. The transition matrix and the associated vector of recapture and recovery probabilities referring to juveniles are then

$$
\begin{bmatrix}
S_{juv}(1-d) & S_{juv}d & (1-S_{juv})\alpha_{juv} & (1-S_{juv})(1-\alpha_{juv}) \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}_t
$$
$$
\times \begin{pmatrix} 0 \\ 0 \\ \lambda^P \\ \lambda^R_{juv} \end{pmatrix}_t. \tag{2}
$$

The annual transition matrix and the corresponding recapture/recovery vector for subadult storks are

$$
\begin{bmatrix}
S_{ad} & 0 & (1-S_{ad})\alpha_{ad} & (1-S_{ad})(1-\alpha_{ad}) \\
0 & S_{ad} & (1-S_{ad})\alpha_{ad} & (1-S_{ad})(1-\alpha_{ad}) \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}_t \begin{pmatrix} 0 \\ 0 \\ \lambda^P \\ \lambda^R_{ad} \end{pmatrix}_t. \tag{3}
$$

Then, from the age of 4 yr, the last transition matrix and its corresponding recapture/recovery vector are repeated each year. They are

$$
\begin{bmatrix}
S_{ad} & 0 & (1-S_{ad})\alpha_{ad} & (1-S_{ad})(1-\alpha_{ad}) \\
0 & S_{ad} & (1-S_{ad})\alpha_{ad} & (1-S_{ad})(1-\alpha_{ad}) \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}_t \begin{pmatrix} p \\ 0 \\ \lambda^P \\ \lambda^R_{ad} \end{pmatrix}_t. \tag{4}
$$

The subscripts of the parameters refer to age (juv, juveniles; ad, adults), the subscript t in the matrices and the vectors denotes time dependence. An alternative notation of this model is $\{S_{a2*t}, \alpha_{a2*t}, d_t, \lambda^P_t, \lambda^R_{a2*t}, p_t\}$, where subscript a2 refers to the two age classes, and subscript t to time dependence.

Our model thus includes time dependence for all parameter types and age dependence in all parameter types except for the resighting rate p (because only adult White Storks can be resighted) and for the recovery rate λ^P associated with the power line mortality. Indeed, the probability of finding and reporting a White Stork that died because of power line collision (λ^P) is unlikely to depend on its age. By contrast, λ^R is likely to depend on age as it is the combined recovery probability for many different causes of death, the frequency of which are likely to differ between juveniles and adults.

Our most general model is still not full rank as checked with computer algebra (Catchpole and Morgan 1997, Catchpole et al. 2002, Gimenez et al. 2003), meaning that some parameters are not separately identifiable. This, however, does not prevent the formulation of reduced parameter models.

We reduced the number of parameters in the general model in a two-step process. First, we focused on natal dispersal and recovery rates. We checked whether there was evidence that natal dispersal varied over time. Next, we assessed whether the recovery rate associated with power line kills varied over time and whether the recovery rate associated with other mortality causes varied over time and/or was different for the two age classes. Overall, we fit 10 models each representing a different combination of age and/or time dependence in the recovery rates. We used the Akaike Information Criterion adjusted for small sample size (AIC$_c$, calculated from the model deviance, the number of estimated parameters, and the sample size [Burnham and Anderson 2002]) to identify the most parsimonious among these 10 models. In the next step, we modeled the survival rate and the proportion of White Storks that died because of power line collision and formulated a second set of candidate models related to these parameters. As a result of the first modeling step, these models all had the same parameters for natal dispersal and recovery rates. We knew a priori that the survival rate was age dependent in White Storks (Lebreton 1978). We therefore only assessed whether survival of both age classes varied independently from each other over time (S_{a2*t}), whether the survival rates of both age classes varied in parallel over time (S_{a2+t}), or whether survival of both age classes was constant across time (S_{a2}), corresponding to a comparison of these three model structures. We had no a priori knowledge about the variation of the proportion of deaths due to power line collisions, and regarded all combinations of age and time dependence as possible (i.e., the parameter structures α_{a2*t} [α of both age classes varies indepen-

TABLE 1.　Modeling the recovery rates of Swiss White Storks associated with power line accidents (λ^P) or other mortality causes (λ^R) based on the most general model {S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2*t}, p_t} and simplifications thereof.

Model	No. parameters	Deviance	ΔAIC_c	AIC weight
S_{a2*t}, α_{a2*t}, d, λ^P, λ^R_{a2}, p_t	81	357.4	0.0	0.97
S_{a2*t}, α_{a2*t}, d, λ^P, λ^R, p_t	80	366.6	7.1	0.03
S_{a2*t}, α_{a2*t}, d, λ^P, λ^R_t, p_t	95	349.8	22.0	0.00
S_{a2*t}, α_{a2*t}, d, λ^P, λ^R_{a2+t}, p_t	96	349.6	23.9	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R, p_t	95	352.3	24.4	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2}, p_t	96	351.4	25.7	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_t, p_t	110	349.2	53.3	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2*t}, p_t	111	347.2	53.4	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2+t}, p_t	111	347.6	53.8	0.00
S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2*t}, p_t	126	345.9	84.4	0.00

Notes: For each model we report the number of estimable parameters, the deviance, the difference in the sample-size-adjusted Akaike Information Criterion between the actual and the most parsimonious model in the table ($\Delta AIC_{c_i} = AIC_{c_i} - AIC_{c_{min}}$), and the Akaike weight ($w_i = \exp(-0.5\Delta AIC_{c_i})/\Sigma\exp(-0.5\Delta AIC_{c_i})$). Subscript t refers to time dependence of a particular parameter and subscript a2 refers to age dependence.

dently from each other over time], α_{a2+t} [α of both age classes varies in parallel over time], α_{a2} [α is constant across time but different in both age classes], α_t [α is the same in both age classes but varies over time], and α [α is constant across time and the same in both age classes]). We also had no a priori knowledge about the interaction of the survival rate and the proportion of White Storks that died because of power line accidents. Therefore, the set of candidate models consisted of models with all possible combinations of these parameter structures ($3 \times 5 = 15$ models). Again, AIC_c was used to rank the models according to their support by the data.

We used the program MARK (White and Burnham 1999) for modeling and for parameter estimation. However, MARK uses a parameterization that was unsuitable to fit our models directly. We had to add a dummy occasion (a column of zeros) after each real occasion in the capture histories, except the last one. Because one real step of time was divided into two steps in this way, products of parameters in the transition matrix (e.g., [1 − S]α) could be separated into their product terms (Fig. 1, Grosbois and Tavecchia 2003). Appendices A and B provide a comprehensive description of how to implement the model with MARK. We reported model-averaged estimates from all candidate models of the second modeling step. Model-averaged estimates were based on the Akaike weights of each model (Burnham and Anderson 2002) and thus included model selection uncertainty in the estimate of a given parameter and its associated precision (SE). This method of multimodel inference enabled us to use the complete set of candidate models rather than basing conclusions on a single, best-fitting model. Standard errors (SE) for calculating 95% confidence intervals were obtained using the delta method (Seber 1982), unless they were directly available from MARK.

The goodness-of-fit test for multistate models recently developed (Pradel et al. 2003) could not be used with our data because it does not allow for nonob-servable states. In order to have an indication of whether our model-fitted the data, we performed a goodness-of-fit test of the reduced model {S_{a2}, λ_t} including only recovery data, i.e., the bulk of the data available. This model was very simple and made strong assumptions. It did not account for different mortality causes, but included age-dependent survival and time-dependent recovery rates. Most of the information for our analysis came from recoveries, which justified a goodness-of-fit (GOF) test based solely on the recovery data. This test was conducted as a comparison of the expected recovery matrices under the model with the observed data (Brownie et al. 1985), and indicated no significant lack of fit ($\chi^2_{32} = 37.11$, $P = 0.25$). Therefore we concluded that the more general model would adequately fit the data.

RESULTS

Temporal variation of natal dispersal was not important as indicated by a comparison of the two models {S_{a2*t}, α_{a2*t}, d_t, λ^P_t, λ^R_{a2*t}, p_t} (deviance = 323.2; number of parameters = 138) and {S_{a2*t}, α_{a2*t}, d, λ^P_t, λ^R_{a2*t}, p_t} (deviance = 345.9; number of parameters = 126). Including temporal variation in d in the first model entailed an increase in AIC_c of 3.2 points. Modeling of the recovery rates revealed that both (λ^P and λ^R) could be considered constant over time, and that the recovery rate associated with other mortality causes than power line accidents was age dependent (Table 1). Models with other structures in the recovery rates had no support (Akaike weights < 0.01). Modeling of the focal parameters (S and α) revealed that the survival rate of both age classes could be considered constant over time and that the proportion of White Storks that died because of power line accidents varied over time (Table 2). A model with identical proportions of power line accidents for both age classes was about 2.23 times more likely than a model with a constant difference of this proportion between the two age classes in each year, as shown by the ratio of Akaike weights (0.67:

TABLE 2. Modeling survival (S) and proportion of power line accidents (α) among all mortality causes in Swiss White Storks based on the most general model $\{S_{a2*t}, \alpha_{a2*t}, d, \lambda^P, \lambda^R_{a2}, p_t\}$ and simplifications thereof.

Model	No. parameters	Deviance	ΔAIC_c	AIC weight
$S_{a2}, \alpha_t, d, \lambda^P, \lambda^R_{a2}, p_t$	35	427.5	0.0	0.67
$S_{a2}, \alpha_{a2+t}, d, \lambda^P, \lambda^R_{a2}, p_t$	36	427.1	1.6	0.30
$S_{a2}, \alpha_{a2*t}, d, \lambda^P, \lambda^R_{a2}, p_t$	51	401.1	6.4	0.03
$S_{a2+t}, \alpha_{a2+t}, d, \lambda^P, \lambda^R_{a2}, p_t$	51	403.5	8.8	0.00
$S_{a2}, \alpha_{a2}, d, \lambda^P, \lambda^R_{a2}, p_t$	21	472.5	16.5	0.00
$S_{a2*t}, \alpha_{a2+t}, d, \lambda^P, \lambda^R_{a2}, p_t$	66	382.5	16.9	0.00
$S_{a2+t}, \alpha_t, d, \lambda^P, \lambda^R_{a2}, p_t$	50	414.0	17.2	0.00
$S_{a2}, \alpha, d, \lambda^P, \lambda^R_{a2}, p_t$	20	478.4	20.4	0.00
$S_{a2+t}, \alpha_{a2}, d, \lambda^P, \lambda^R_{a2}, p_t$	36	446.3	20.8	0.00
$S_{a2*t}, \alpha_{a2*t}, d, \lambda^P, \lambda^R_{a2}, p_t$	81	357.4	23.0	0.00
$S_{a2+t}, \alpha_{a2*t}, d, \lambda^P, \lambda^R_{a2}, p_t$	66	388.7	25.1	0.00
$S_{a2*t}, \alpha_t, d, \lambda^P, \lambda^R_{a2}, p_t$	65	396.1	28.4	0.00
$S_{a2*t}, \alpha_{a2}, d, \lambda^P, \lambda^R_{a2}, p_t$	51	428.8	32.1	0.00
$S_{a2+t}, \alpha, d, \lambda^P, \lambda^R_{a2}, p_t$	35	464.6	35.0	0.00
$S_{a2*t}, \alpha, d, \lambda^P, \lambda^R_{a2}, p_t$	50	446.8	48.0	0.00

Notes: For each model we report the number of estimable parameters, the relative deviance, and the difference in the sample size adjusted Akaike Information Criterion between the actual and the most parsimonious model ($\Delta AIC_{c_i} = AIC_{c_i} - AIC_{c_{min}}$), and the Akaike weight ($w_i = \exp(-0.5\Delta AIC_{c_i})/\Sigma\exp(-0.5\Delta AIC_{c_i})$). Subscript t refers to time dependence of a particular parameter and subscript a2 refers to age dependence.

0.30). The third ranked model, where the proportion of power line accidents of the two age classes varied independently from each other over time, had essentially no support.

The model-averaged, mean annual, survival rate (S) was 0.83 (95% CI = 0.78–0.87) for adults, and 0.33 (0.23–0.42) for juveniles. The reporting rate associated with power line collision (λ^P) was higher (mean = 0.22, 95% CI = 0.12–0.32) than that associated with the other mortality causes (λ^R; adults, mean = 0.13, 95% CI = 0.08–0.17; juveniles, mean = 0.17, 95% CI = 0.07–0.27). Natal dispersal probability was 0.44 (95% CI =

FIG. 2. Proportion of juvenile (open dots) and adult (filled dots) White Storks that died because of power line collision (α) between 1984 and 1999. The vertical lines show ±1 SE.

0.22–0.66), however its biological interpretation is difficult, as the resighting places were not distributed evenly over Switzerland. The resighting probabilities of adults varied over time (lowest in 1999 [mean = 0.04, 95% CI = 0.00–0.08]; highest in 1991 [mean = 0.37, 95% CI = 0.20–0.55]) and were on average 0.15 (0.09–0.20). The proportion of White Storks dying because of power line collisions varied remarkably over time (Fig. 2). In the year 1989–1990, the proportion was unusually high: over 80% of mortality in both age classes occurred because of power line collision. On average, the proportion was only slightly lower in adults (mean = 0.35, 95% CI = 0.17–0.54) than in juveniles (mean = 0.37, 95% CI = 0.22–0.53).

The probability that a stork died because of a power line accident (the power line kill rate) was estimated as the product of the overall mortality and the proportion of storks that died because of power line collision ($[1 - S]\alpha$). The survival rate did not vary over time, so the power line kill rates varied over time in parallel with the proportion of power line mortality. The model-averaged mean power line kill rate in adults was 0.06 (95% CI = 0.03–0.10) and 0.25 (95% CI = 0.14–0.36) in juveniles. Thus, about one in four young White Storks died because of a power line collision each year and roughly one in 17 adults died of the same cause every year.

DISCUSSION

The model for analyzing mortality causes

The method presented herein is suited to the estimation of any specific source of mortality in any population from mark–recovery data. Compared to the ad hoc estimator (i.e., the raw, observed frequency of animals reported to have died from each cause), it has
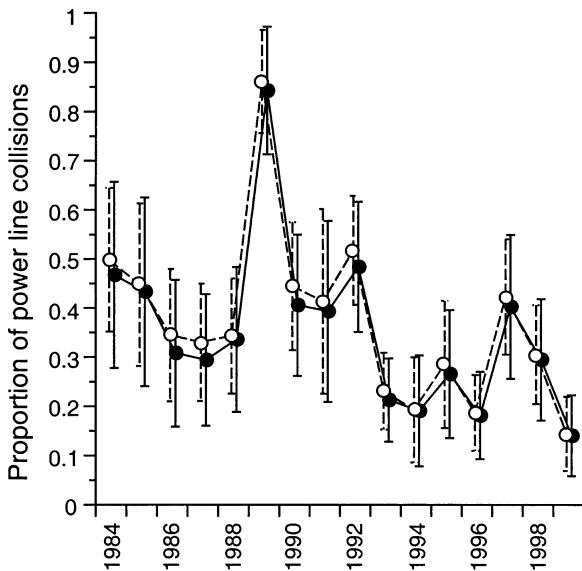
the advantage that the estimates are unbiased and that hypotheses about variation in the importance of a specific cause of mortality can be tested. More importantly, the survival rate is estimated simultaneously; hence, interactions between survival and the proportion of individuals killed because of the specific reason can be studied. Furthermore, the cause-specific kill rates can easily be calculated. This is the essential parameter for quantifying the impact of a specific cause of mortality on population dynamics. The model could also be extended to study more than one source of mortality at once, to include a larger number of age classes or to include mortality cause data obtained from telemetry.

We see various practical applications of the model. Bird ringing has been conducted for several decades, so there is a great potential of data to be used. From a population dynamics point of view, it may be interesting to test whether a specific mortality cause (e.g., hunting, collision with traffic, oil slicks and spills, drowning in fishery nets) has changed over time and is likely to explain an observed population trend. From a conservational point of view, it may be interesting to test whether the observed decrease in numbers of recoveries from hunting is due to reduced hunting activity or due to a declined readiness of the hunters to report hunted birds (McCulloch et al. 1992, Schlenker 1995). The results of such an analysis could have implications for political decisions about hunting. Furthermore, standard recovery models assume that any dead animal has the same probability of being reported (Brownie et al. 1985). When the aim is to estimate survival rates from recovery data, this model helps to reduce heterogeneity due to differential recovery rates and thus generates more accurate estimates of survival rate.

As in any modeling exercise, the limitations of the model must be considered in its application. Based on computer algebra methods, we know that some parameters in some models are not separately estimable. We checked many models for intrinsic identifiability and often found that models with variation (e.g., due to age, groups, or time) in one parameter but not in others are identifiable. Still, a nonidentifiable model can be used to test a specific working hypothesis. If such a model turns out to be the best one, the estimates of their nonidentifiable parameters can, however, not be used. In this situation, one may consider the parameter estimates of the best model in which all of the interesting parameters are identifiable (Burnham and Anderson 2002). A further, related problem is that precision, in particular of α, may be poor because of near singularity of parameters (Catchpole et al. 2001). It seems to happen specifically when temporal variation in α is low, because in most models in which α is constant across time, α is not separately estimable. Yet the topic of near-singularity is only poorly studied and warrants further investigations (Catchpole et al. 2001). Thus, we advise checking intrinsic identifiablity in any

case and advocate care in interpreting the results obtained from these models.

The method assumes that the mortality causes are diagnosed correctly, otherwise the estimated proportion of animals dying because of a specific cause can be biased. In the White Stork example, there are probably power line killed individuals that were reported without knowledge about the true cause of death, and were subsequently allocated to the mortality cause category ''others.'' We have no means to estimate the proportion of power line killed storks within the ''other mortality'' category. Since collision with power lines is a mortality cause that is rather easy to diagnose, this proportion is probably slight and therefore the bias in the estimate of the proportion of power line killed storks should be small.

Comparison with ad hoc estimates

Our analysis showed that the average proportion of juvenile White Storks dying because of collisions with power lines was about 25% lower than estimated in the ad hoc approach, whereas adult proportions were similar between methods. The magnitude of bias in the proportion of animals dying because of the specific cause in the ad hoc analysis increases as the difference in the recovery rates associated with the two opposing mortality causes increases. Besides bias, the ad hoc analysis also resulted in wrong conclusions about the sensitivity of the age classes to power line accidents. Based on the ad hoc estimates, we would have concluded that the proportion of power line killed juveniles is particularly large compared with adults. The new approach shows that the proportion is almost the same in the two age classes.

If the overall survival and the two recovery rates are constant, as in our example, the pattern of the temporal variation of the proportion of animals dying because of the specific cause is the same in both approaches. However, if there was variation in at least one of these three parameter types, the pattern of temporal variation of the proportion of dead animals due to the specific cause obtained from the ad hoc analysis would not parallel the true temporal pattern. There is no way to test for temporal variation of the survival and recovery rates using the ad hoc method. Thus, the new approach should be used for the assessment of temporal variation in α.

Perspectives

The estimates obtained from the model presented here can be used to gain deeper insights into the link between a mortality cause under scrutiny and the dynamics of the population. The first step is to study whether the mortality cause under scrutiny is totally additive to the remaining mortality, completely compensated for by other forms of mortality, or some variant in between (Williams et al. 2002). Testing these competing hypotheses is a difficult task that usually

requires an independent estimate of the killing effort (e.g., length of mid-tension power lines along the migration route in each year; Burnham and Anderson 1984). Our model provides a rigorous framework within which it can be evaluated whether the mortality cause in question acts in an additive or compensatory way, which does not require an independent estimate of the killing effort. If it would be fully additive to the remaining mortality, the overall mortality $(1 - S)$ would increase in years when the proportion of the mortality cause in question (α) increases. Thus, the covariance between $1 - S$ and α would be positive. If the mortality cause under scrutiny would be completely compensated for by other forms of mortality, the covariance between $1 - S$ and α would be zero. Of course the true process covariance between $1 - S$ and α must be considered to test these opposing hypotheses. In the present example, α varies over time, whereas the overall mortality rate does not. Thus there is evidence against the total additive hypothesis.

If the amount of compensation c (additive mortality, $c = 1$; compensatory mortality, $c = 0$), as well as the other vital rates, are known, a projection matrix model can be formulated (Caswell 2001) to estimate the effect of a change in the proportion of a mortality cause on the population growth rate. In the projection matrix model the survival rates must be replaced by the expression $1 - (1 - S)(1 - \alpha) - (1 - cx)(1 - S)\alpha$, where x is the amount by which the proportion of the mortality cause could be altered. With this replacement, the sensitivity of the population growth rate to changes in x can easily be calculated (Caswell 2001, "lower-level sensitivity"). This sensitivity assesses how much the population dynamics is influenced by the mortality cause in question, and can be important for making decisions regarding conservation or harvesting.

In conclusion, ring recovery data should only be analyzed with great care in an ad hoc way to estimate the proportion of mortality causes since the estimates may be strongly biased, increasing the risk of making incorrect inferences. Existing results based on ad hoc analyses should probably be revisited. The method presented here offers a new way to estimate the proportion of a mortality cause. In addition, much deeper insights into the significance of the mortality cause on the population dynamics can be obtained.

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APPENDIX A

An explanation of the fitting of the cause-specific mortality rates model with the MARK program is available in ESA's Electronic Data Archive: *Ecological Archives* E085-026-A1.

APPENDIX B

The parameter index matrices of the cause-specific mortality rates model used in the MARK program are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-026-A2.