Modelling mortality causes in longitudinal data in the presence of tag loss: application to raptor poisoning and electrocution

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Summary

1. A first step for the effective management of vulnerable populations is to identify population threats and measure their relative impact on population fluctuations. The relative importance of proximate causes of mortality can be calculated from longitudinal data using capture–mark–recapture models. If marks are lost or cease to function, survival is underestimated.

2. We provide an analytical framework based on conditional probabilities to obtain a robust estimate of the contribution of multiple sources of mortality while accounting for tag loss and imperfect detection.

3. We applied this approach to radiotracking and wing tags-resighting data of red kites *Milvus milvus* to estimate the impact of illegal poisoning and the mortality by electrocution on power lines in the island of Mallorca (Spain).

4. Illegal poisoning was responsible for 53% of the total mortality and electrocution on power lines for 12%. Results indicated that poisoning-related mortality was higher in immature birds, probably due to their more wide-ranging prospective behaviour.

5. Assuming the two human-related mortalities are additive, the survival probability of kites would increase by 17% (from 0·76 to 0·91) if both threats were removed.

6. *Synthesis and applications.* We present a new approach to estimate the contribution of different sources of mortality accounting for tag loss, state uncertainty and detection failures in wildlife populations. Our results will allow the demographic consequences of human-related mortality in threatened populations to be refined. The approach is suitable for the study of multiplicative latent processes in a vast range of applied conservation studies such as, for example, wildlife epidemiology.

Key-words: capture–recapture, electrocution, multi-event, poisoning, radiotracking, red kite

Introduction

Measuring the relative contribution of different mortality causes in wildlife populations provides an insight in the proximal causes of population changes and can help to prioritize management actions (Williams, Nichols & Conroy 2002). Typically, this measure is expressed as the proportion of individuals found dead or injured because of a particular cause (i.e. Newton 1979 p. 152; Martínez-Abraín *et al.* 2009). However, this proportion cannot be easily related to a mortality probability because the number of individuals at risk, i.e. susceptible to death, is unknown. Robust estimates of mortality probability

can be obtained through analysis of longitudinal data of marked individuals through capture–mark–recapture or – recovery models, that account for imperfect detection and tag reporting probability (Brownie *et al.* 1985; Burnham *et al.* 1987; Williams, Nichols & Conroy 2002). However, incorporating the information on different causes of mortality in these models is not straightforward. In recovery models, for example, the probability of dying from a particular cause covaries with the recovery rate because different causes of mortality lead to different probabilities of finding and reporting a tag (Brownie *et al.* 1985; Tavecchia 2000; Schaub 2009). Schaub & Pradel (2004) proposed a model based on conditional probabilities able to separate the reporting rate of white storks *Ciconia ciconia* into its two components: the probability that a stork died

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because of power line collision and the probability, conditional upon death, that the tag is reported. Here, we present a new approach that extends Schaub & Pradel's work on recovery to include live encounters when studying multiple sources of mortality. Moreover, we use the flexibility of the approach to account for marks loss, a common problem in capture–mark–recapture or –recovery studies, which violates an important assumption of the statistical models (Williams, Nichols & Conroy 2002). When tags are lost, no longer visible or in the case of radiotransmitter, no longer functioning, the survival probability is biased downward reflecting tag retention rather than individual survival probability. Tag loss cannot be incorporated explicitly within capture–recapture or capture–recovery models, and classically, it is either ignored or survival estimates are corrected *a posteriori* using an 'external' measure of tag loss (Nichols *et al.* 1992; Diefenbach & Alt 1998; but see Nichols & Hines 1993; Cowen & Schwarz 2006). The problem arises from the fact that individuals become unobservable or more difficult to detect once they lose their tags. As a consequence, the encounters that precede tag loss occur with a different probability than the subsequent ones. Similarly to the problem of multiple sources of mortality, tag loss can be viewed as a problem of conditional probabilities, in which there are two sets of parameters, one conditional on tag retention, and a second conditional on tag loss (Juillet *et al.* 2011). Multi-state models (Arnason 1973) for the analysis of stratified capture–recapture data allow transition across states to occur along the encounter histories. A reformulation of these models (Schwarz, Schweigert & Arnason 1993) permits explicit estimation of across-sites movements conditional on survival. Grosbois & Tavecchia (2003) first used this formulation to allow for unobservable transitions and the estimation of successive conditional probabilities. Recently, Pradel (2005) has proposed a general framework to relate observable and unobservable states to the observable events in longitudinal data. This framework, primarily thought to model longitudinal data under state uncertainty (Pradel 2009), can be used to join external information on individual state and to model unobservable processes (Sanz-Aguilar *et al.* 2011). Juillet *et al.* (2011) first used this multi-event framework to account for tag losses in a study of double-tagged greater snow geese *Chen caerulescens atalantica*. In their formulation, a first set of encounters, i.e. observable events, corresponded to the encounter history conditional on tag retention and another set corresponded to the events recorded after the loss of one of the principal marks. In this way, they successfully decomposed the survival and recapture processes conditional on tag retention. Here, we build on their work and incorporate the conditional formulation of Schaub & Pradel (2004) to provide a new analytical framework for the study of multiple causes of mortality in the presence of tag losses. The formulation can be easily extended to multiple types of tag, reformulating the mixed information models of Freeman, Morgan & Catchpole (1992) and Burnham (1993).

We applied this model to assess the magnitude of different sources of mortality of an endangered raptor, the red kite *Milvus milvus* on the island of Mallorca (Spain). Over the last two centuries, human persecution has led to a drastic decrease in the number of birds of prey and much effort has been devoted to preventing the local population from going extinct in many parts of the world (Newton 1979). Despite their protected status, many natural and introduced populations of raptors, worldwide, are still threatened by causes directly or indirectly related to human activities, such as illegal hunting (Smart *et al.* 2010), primary and secondary poisoning (Whitfield *et al.* 2003), habitat destruction (Tilman *et al.* 1994), prey depletion, collisions with cars, windmills and electrocution on power lines (Sergio *et al.* 2004; Lehman, Kennedy & Savidge 2007; Schaub *et al.* 2010). The red kite is a medium-sized raptor with little size dimorphism distributed only in the western Palearctic, mainly in Europe and North Africa (del Hoyo, Elliott & Sargatal 1996). Since the 19th century, the species has declined throughout the whole European continent, and many of its populations are nowadays considered endangered (IUCN 2010). The species is vulnerable to secondary or direct contact with poisonous baits, used primarily to control predators of game species (Evans & Pienkowski 1991; Whitfield *et al.* 2003; Smart *et al.* 2010). In Spain, nearly all red kite populations have declined and some have disappeared because of illegal hunting, poisoning and electrocution (Viñuela, Martí & Ruiz 1999). On the island of Mallorca in the archipelago of Balearics (Spain), the population was reduced to only 7–8 pairs in the year 2000 (Adrover, Muñoz & Riera 2002). Thanks to the effort of local environmental agencies, the species has slowly increased its number, and in 2010, has reached nineteen breeding pairs (J. Adrover, unpublished data). Cases of direct and indirect poisoning are still common on the island, and the exact magnitude of the different human-related sources of mortality is not known. Here, we use the data on resighting and recovery of individually marked fledglings collected since the year 2000. We applied a new analytical approach based on conditional probabilities, (i) to estimate the age-dependent mortality of marked birds, (ii) to estimate the incidence of tag loss and the relative magnitude of different sources of mortality, and (iii) to assess whether their influence differs according to the age-class considered.

Materials and methods

LONGITUDINAL DATA AND TAG LOSS

Since 2000, 142 fledglings have been equipped with a radiotransmitter (Biotrack TW-3) mounted on a backpack harness. Birds were tagged as chicks just before leaving the nest. Transmitters had a range of 20–30 Km, a life expectancy of *c*. 3–4 years and weighed < 5% of bird body weight. In addition to the radio tag, all chicks were marked using PVC wing tags with a unique alpha-numeric code, one on each wing. This primary tag was used to assess the loss of the radio signal for mechanical or electrical reason. Wing tags are occasionally lost, but their life span is longer than that of the radiotransmitter. We never observed the loss of both types of tags, and all dead animals, found with or without the radiotransmitter, had retained at least one wing tag. Furthermore, it is not uncommon to see a 7–10-year-old kite with both wing tags. Nevertheless, we cannot rule out the simultaneous loss of both wing tags after the loss of the radio signal. In this case, the survival probabilities of birds more than 3 years old (i.e. the average life
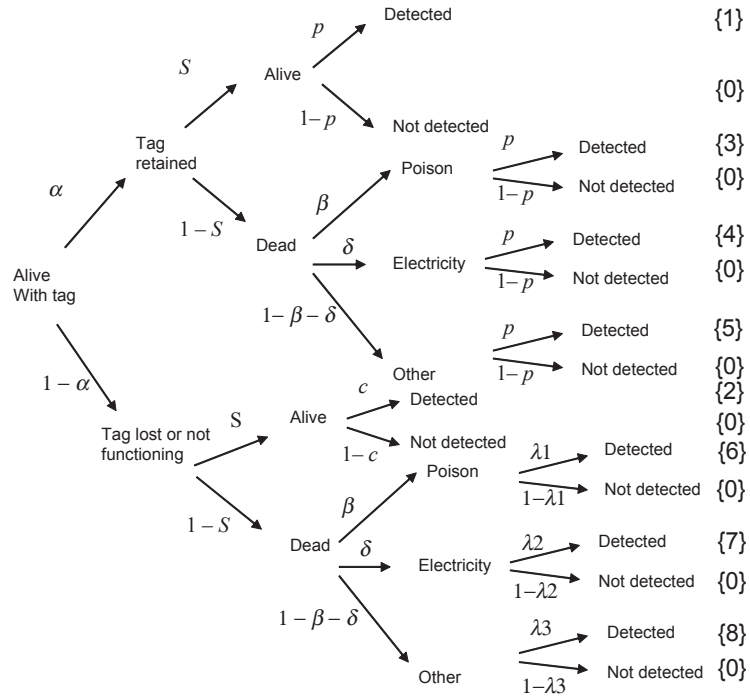
Fig. 1. Graphical representation of the possible events and the corresponding probabilities in the encounter histories. The numbers between brackets are the codes used. For instance, an encounter history such as 011206000000 corresponds to a bird marked at the second occasion, whose radio signal has been lost at the fourth occasion and which has been found newly dead by poison at the sixth occasion. Note that the probability of detection differs among mortality causes when the radio is no longer functioning (it is assumed the wing tag is retained).

span of the radio signal) might be underestimated. Note that the relative differences across mortality causes and ages remain unchanged because the loss of tags is independent from the cause of death and no birds had lost their wing tags before the radio signal was lost. Observations of marked birds were performed by active search throughout the whole island, by car or, occasionally, helicopter. When the signal was stationary, we actively searched for the radiotransmitter to confirm whether the animal was stationary, dead or had lost its radio tag. All carcasses found were sent to the laboratory for a post-mortem analysis. In addition to radio locations, we carried out observations at feeding places (dump sites and artificial feeding stations), territories and roosting sites to record the presence of birds for which we could no longer detect a radio signal. We restricted the analysis to observations of live birds recorded from April to June, to reduce problems linked with pooling data from a long time period (Hargrove & Borland 1994).

A MODEL FOR INDIVIDUAL STATES AND OBSERVED EVENTS

The observations of live and dead birds, together with the information on tag loss, formed the set of observable events from

which we estimated the proportion of birds that died by poisoning, electrocution or by other (natural) causes. This was performed by specifying a probabilistic model that linked the observed events to transitions between possible alternative individual states (Fig. 1). We considered that individuals can move across four main states: alive (noted 'A'), death by poison ('DP'), death by electrocution ('DE') and death from other (unknown) causes ('DO'). Given that individuals can lose their radiotransmitter, we considered the above states for birds with and without a functioning radio (noted with the superscript '+' and '−', respectively). As in Lebreton, Almeras & Pradel (1999), we included an additional dead state (noted '†') that corresponded to an unobservable dead state. This might be seen as 'dead for some time' in contrast with the observable state 'newly dead', corresponding to recovery of a corpse. This differentiation assumes that corpses are found soon after death and allows us to estimate the reporting rate associated with the observable dead states and the probability of dying from different causes (Schaub & Pradel 2004).

The full transition matrix, Φ, from the state at t (in line) to the state at $t + 1$ (in column) can be written as

$$
\Phi = \begin{pmatrix}
 & A^+ & A^- & DP^+ & DE^+ & DO^+ & DP^- & DE^- & DO^- & \dagger \\
A^+ & \alpha S & (1-\alpha)S & \alpha\beta(1-S) & \alpha\gamma(1-S) & \alpha(1-\beta-\gamma)(1-S) & (1-\alpha)\beta(1-S) & (1-\alpha)\gamma(1-S) & (1-\alpha)(1-\gamma-\beta)(1-S) & 0 \\
A^- & 0 & S & 0 & 0 & 0 & \beta(1-S) & \gamma(1-S) & (1-\beta-\gamma)(1-S) & 0 \\
DP^+ & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DE^+ & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DO^+ & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DP^- & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DE^- & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
DO^- & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\dagger & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}
$$

where

    S: the annual survival probability.

    α: the probability of radio signal retention.

    β: the probability of death because of poisoning given that an animal has died.

    γ: the probability of DE given that an animal has died.

    The matrix, Φ, can be decomposed into three successive matrices to single out the parameters related to each process, i.e. tag toss, survival and causes of mortality, respectively (Appendix S1, Supporting information).

    At any given time, we can observe nine types of mutually exclusive events (here arbitrarily coded with numbers from 0 to 8; Fig. 1). The first possible event (coded '0') is a non-encounter, i.e. the radio signal cannot be heard and the animal cannot be seen. This is the only ambiguous event as it may correspond to any underlying state. For example, the animal may have lost the radio or be carrying one that ceased to function, or it may be dead having lost the radio and remaining undetected. Each of the other events can happen only with one state. The events coded '1' and '2' refer to encounters of individuals alive, with respectively a functioning (the animal is then in state 'A^+' of matrix Φ) or not functioning radio (state 'A^-' of matrix Φ). The remaining six events correspond to animals found dead. In our case, we considered six cases of 'newly dead' encounters relating to three death causes and two radio states (3×2 combinations). Specifically, '3' and '6' code for birds found poisoned with and without a functioning radio respectively (states 'DP^+' and 'DP^-' of matrix Φ respectively). Similarly, '4' and '7' are for birds electrocuted with and without a functioning radio respectively (states 'DE^+' and 'DE^-' of matrix Φ). Finally, '5' and '8' refer to those birds that have been found dead but from unspecified causes with and without a functioning radio respectively (states 'DO^+' and 'DO^-' of matrix Φ, Fig. 1). Note that '2', '6', '7' and '8' code for birds encountered without a functioning radio. These codes do not distinguish whether the radio was physically lost or not functioning. If needed, these situations can further be distinguished by including additional states in the matrix Φ; however, here, we have opted not to do so for the sake of simplicity.

    Between any time interval, individuals might change state according to the transitions in Fig. 1. For example, the encounter history of a bird marked at the first occasion, for which the radio signal was lost at the third occasion, and was found electrocuted at the fifth occasion, would be 11207000000. Here, we are interested in estimating, from the observed events, the probabilities associated with each state-to-state transition. This is possible because some events arise more easily when the bird is in one state rather than in another. The matrix $\mathbf{E}$ links the states to the observations by specifying the probability of each event (in columns) conditional on each state (in rows):

$$\mathbf{E} = \begin{pmatrix} & 0 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 \\ 1 & 1-p & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 2 & 1-c & 0 & c & 0 & 0 & 0 & 0 & 0 & 0 \\ 3 & 1-p & 0 & 0 & p & 0 & 0 & 0 & 0 & 0 \\ 4 & 1-p & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 \\ 5 & 1-p & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 \\ 6 & 1-\lambda_1 & 0 & 0 & 0 & 0 & 0 & \lambda_1 & 0 & 0 \\ 7 & 1-\lambda_2 & 0 & 0 & 0 & 0 & 0 & 0 & \lambda_2 & 0 \\ 8 & 1-\lambda_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \lambda_3 \\ \dagger & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

where

    p: the probability of encounter of an animal with a functioning radio.

    c: the probability of encounter of an animal alive without the radio signal.

    λ_1: the probability of encounter of an animal dead by poisoning and without the radio signal.

    λ_2: the probability of encounter of an animal dead by electrocution and without the radio signal.

    λ_3: the probability of encounter of an animal dead by other causes and without the radio signal.

    The model was built and fitted to the data using the software program E-SURGE (Choquet, Rouan & Pradel 2009). It could also be fitted as a state-space model.

MODEL DEFINITION AND MODEL SELECTION

We wanted to investigate whether tag loss depended on the age of the tag, and whether the three different sources of mortality had a contrasting age pattern. To do this, we compared models built under different alternative hypotheses using the AICc value (Burnham & Anderson 2002). The model with the lowest AICc value should be seen as the best compromise between deviance explained and number of parameters in the model. Given the relatively small number of animals marked, we did not consider a possible variation of parameters over time. The assumption of constant parameters is unrealistic, but in our case, it is necessary to avoid models with more parameters than data. The model selection procedure consisted of progressively decreasing model complexity one parameter at a time (Grosbois & Tavecchia 2003). After eliminating irrelevant effects from one parameter at a time, a consensual model was built using the best structure selected independently for each parameter. This consensual model is then used to re-test for previously unrestrained factors in a more parsimonious environment (Grosbois & Tavecchia 2003). In addition, we calculated model probability, e.g. Akaike weight, w, as a measure of model plausibility (Anderson 2007). Parameter estimates were derived from the retained model by maximum likelihood, and final estimates were obtained by averaging the estimates from all models that followed the consensual one (Anderson 2007). In model notation, we specified each parameter in matrix Φ (see also Appendix S1, Supporting information), separated by the symbol '/'and the effects considered for are noted in brackets. Red kites commonly begin breeding at 3 years old or later (del Hoyo, Elliott & Sargatal 1996), although in Mallorca, some birds bred at their second birthday. As in Smart *et al.* (2010), we have considered three age classes, 1, 2, and $\geq$3 years old, respectively. This reflects the life cycle of the bird and avoids estimates based on those few birds that might reach old ages (Sergio *et al.* 2010). In contrast, radio signal retention was modelled as a function of radio age, i.e. time elapsed from marking, using five age classes because batteries were expected to last c. 3–4 years. In addition, we fitted a model in which radio signal was assumed to be a quadratic function of the radio age to reflect the progressive decay of the batteries. In model notation, the age effect was noted 'a' when considered as a factor and 'A' when considered as continuous variable. The symbol '.' indicates a constant parameter. Hence, a model in which all parameters are assumed to be constant would be noted: $\alpha(.)/S(.)/\beta(.)/\gamma(.)/p(.)c(.)\lambda_1(.)\lambda_2(.)\lambda_3(.)$. The reporting probabilities, λ_1, λ_2 and λ_3 were always considered age independent because of the small number of birds found dead without the tag.

Results

Fifty-one (36%) of the 142 radio-tagged birds were found dead. Post-mortem examination revealed that 53% (27) of these birds had died of poisoning and 12% (6) had been electrocuted. The remaining 18 kites died of unknown reasons.

Only two birds (4%) were found dead after their radio signal was lost (events coded 6 and 7, respectively). The first steps of the model selection suggested a strong effect of age on radio life span and a weaker effect on survival and poisoning probability. As expected, the probability of detecting radio failure, i.e. the loss of the signal, varied according to the age of the radio because this included the end of the battery life. The first consensual model assumed an effect of age in these parameters (model 8, Table 1). We used this simpler model to re-assess the importance of age in all other parameters and to model signal life span, α, as a linear function of the radio age. The latter model had the lowest AICc value (model 13; Table 1 and Fig. 2). It is worth noticing that α in first-year birds was 0.89 ± 0.03 (estimate $\pm$ standard error), which suggested that about 10% of radios were lost, or ceased functioning, within the first year after marking. According to model 13, the detection probability, p, of a functioning radio was very high, 0.99 ± 0.008, and did not vary with bird age. In contrast, the probability, c, of detecting a bird without a radio tag was associated with age, being higher in first year (0.95 ± 0.24) and lower during the second and subsequent years (0.37 ± 0.14 and 0.57 ± 0.09, respectively). The average value of survival for red kites in Mallorca in the age-independent model (model 8) was 0.76 ± 0.025. The models indicated a small difference among the three age classes considered (from model 9: 0.72 ± 0.08, 0.82 ± 0.09 and 0.79 ± 0.09 for yearlings, immature and adults, respectively). This difference was not supported by the AICc values, and averaged estimates were very similar (0.76 ± 0.03, 0.77 ± 0.03 and 0.77 ± 0.03 for yearlings, immature and adults, respectively). Among the three components of mortality, the most important was poisoning (0.53 ± 0.07), while only 0.10 ± 0.04 was because of electrocution (estimates from model 11; Table 1 and Table S1, Supporting information).
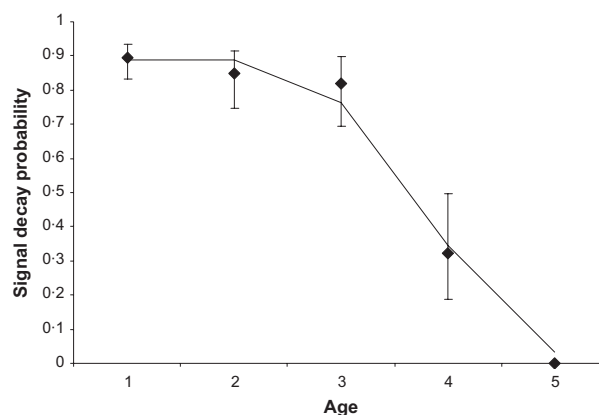

Fig. 2. Radio tag retention as a function of tag age, i.e. time elapsed since marking (dots; model 8). The solid line joins the estimates from the model assuming a progressive decay of the signal (model 13).

The results suggested that mortality because of poisoning changed with age, peaking just before the age at which most birds begin to breed (Fig. 3). However, the model without an age effect (model 11) had a similar AICc value. This was probably due to the large standard errors of the age-dependent values of mortality because of poisoning (Fig. 3). The two models describe the data equally well, but model weight indicated that the model including an effect of age was more plausible. Also, model-averaged estimates of age-dependent proportions of poisoned birds, among the birds estimated to be dead, were different (0.44 ± 0.09, 0.76 ± 0.05 and 0.63 ± 0.17 for yearlings, immature and adults, respectively). In contrast, bird age was not associated with the probability of DE, and it was poorly supported at all steps of the analysis (Table 1). As a consequence, the age-dependent estimates for

Table 1. Modelling tag retention, α, survival, S, and sources of mortality (β and γ), as a function of age. The effect of age was tested independently on one parameter at a time (models 1–7; see text for detailed on model selection strategy)

Model	T1/	T2/	T3/	E	d.f.	Deviance	AICc	ΔAICc	w
Towards a consensual model									
1	$\alpha(a)$	$S(a)$	$\beta(a)\gamma(a)$	$p(a)c(a)$	22	810·32	857·06	8·1	0·0058
2	$\alpha(a)$	$S(a)$	$\beta(a)\gamma(a)$	$p(a)c(.)$	20	816·86	859·12	10·16	0·0021
3	$\alpha(a)$	$S(a)$	$\beta(a)\gamma(a)$	$p(.)c(a)$	20	812·68	854·94	5·98	0·0167
4	$\alpha(a)$	$S(a)$	$\beta(a)\gamma(.)$	$p(a)c(a)$	20	810·98	853·24	4·28	0·0390
5	$\alpha(a)$	$S(a)$	$\beta(.)\gamma(a)$	$p(a)c(a)$	20	815·80	858·05	9·09	0·0035
6	$\alpha(a)$	$S(.)$	$\beta(a)\gamma(a)$	$p(a)c(a)$	20	813·48	855·74	6·78	0·0112
7	$\alpha(.)$	$S(a)$	$\beta(a)\gamma(a)$	$p(a)c(a)$	18	872·93	910·76	61·8	0·0000
8	$\boldsymbol{\alpha(a)}$	$\boldsymbol{S(.)}$	$\boldsymbol{\beta(a)\gamma(.)}$	$\boldsymbol{p(.)c(a)}$	**16**	**816·60**	**850·04**	**1·08**	**0·1931**
After the consensual model									
9	$\boldsymbol{\alpha(a)}$	$\boldsymbol{S(a)}$	$\boldsymbol{\beta(a)\gamma(.)}$	$\boldsymbol{p(.)c(a)}$	**18**	**813·34**	**851·17**	**2·21**	**0·1100**
10	$\boldsymbol{\alpha(a)}$	$\boldsymbol{S(.)}$	$\boldsymbol{\beta(a)\gamma(a)}$	$\boldsymbol{p(.)c(a)}$	**18**	**815·99**	**853·82**	**4·86**	**0·0292**
11	$\boldsymbol{\alpha(a)}$	$\boldsymbol{S(.)}$	$\boldsymbol{\beta(.)\gamma(.)}$	$\boldsymbol{p(.)c(a)}$	**14**	**821·68**	**850·79**	**1·83**	**0·1327**
12	$\boldsymbol{\alpha(a)}$	$\boldsymbol{S(.)}$	$\boldsymbol{\beta(a)\gamma(.)}$	$\boldsymbol{p(.)c(.)}$	**14**	**821·79**	**850·90**	**1·94**	**0·1256**
13	$\boldsymbol{\alpha(A + A^2)}$	$\boldsymbol{S(.)}$	$\boldsymbol{\beta(a)\gamma(.)}$	$\boldsymbol{p(.)c(a)}$	**14**	**819·85**	**848·96**	**0**	**0·3320**

Model notation: 'a' = age as a factorial effect (three levels except in T1 where five levels were considered, see text), 'A' = continuous effect of age (1–5), '.' = constant. 'p' = probability to encounter an animal that retained the radio signal, 'c' = probability to encounter a live kite that has lost its signal. In all models, reporting rates for birds found dead without a functioning radio (λ_1, λ_2 and λ_3) were kept constant (not shown). Models in bold were used to obtained averaged estimates.
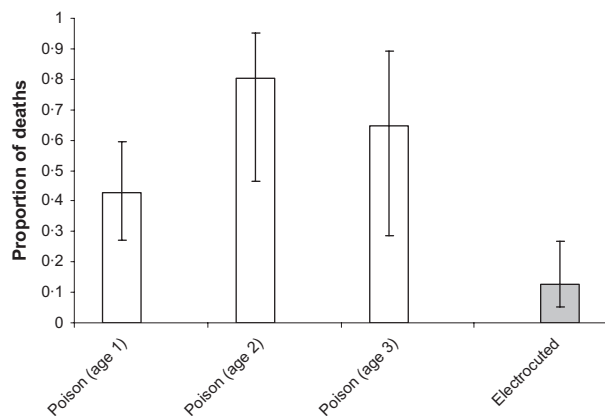
Fig. 3. Human-induced causes of mortality. The impact of illegal poisoning varies as a function of age, while the mortality because of electric power line is constant over age. Estimates are from the retained model (model 13).

this parameter derived by model averaging were very similar: 0.121 ± 0.05, 0.120 ± 0.05 and 0.119 ± 0.05 for yearlings, immature and adults, respectively.

The estimates of S and β from models 8 and 11 can be combined to calculate the expected (age-independent) survival probability in the absence of illegal poisoning and/or electrocution. This would be of 0.89 ± 0.029 $[= 1 - 0.24 \times (1 - 0.53)]$, corresponding to *c.* 14% increase in survival probability. As expected, removing mortality because of electrocution would lead to a smaller increase in survival probability, from 0.76 to 0.79 ± 0.047 (*c.* 3%). Note that standard errors of the combined estimates were calculated using the δ-method (Morgan 2000). Assuming the two human-related mortalities are additive, the survival probability of red kites would be of 0.91 ± 0.025 if both were controlled (an overall increase of 17% in average survival).

Discussion

The relative importance of proximate causes of mortality is typically expressed as the proportion of birds found dead or admitted to wildlife rehabilitation centres for a particular cause. This approach gives an indication of the relative importance of different causes of mortality, but it implicitly assumes that the probability of detecting a corpse or an injured bird is the same, regardless of the cause of death or of injury. This assumption is unlikely to be met in natural populations as the reporting rate of dead birds covaries with the cause of mortality (Brownie *et al.* 1985; Tavecchia 2000; Schaub 2009; Schaub *et al.* 2010). Thus, the proportion of animals dying from a particular cause cannot be expressed as a mortality probability, and the importance of each cause cannot be related to an absolute mortality measure. We have provided an analytical framework based on conditional probabilities that allow to assess the contributions of human-related causes of mortality in the red kite. We found that poisoning was responsible for 53% of red kite deaths in Mallorca. Moreover, our results indicated that this was higher for 2-year-old birds, probably

reflecting their wide-ranging prospective behaviour (J. Adrover, unpublished data). Age differences in poison-related mortality have been reported in other studies and, generally, immature birds are more affected by poison than adults although this might depend on the species and the geographic location. In the United Kingdom, Smart *et al.* (2010) reported that 38% of radio-tagged red kites died because of poisoning, the majority of these during their first year; the illegal use of poison decreased kite survival by 31%, 8% and 5% for 1-, 2- and 3-year-old birds, respectively. Margalida *et al.* (2008) found that 18 (86%) of 21 radio-tagged bearded vultures *Gypaetus barbatus* died of poisoning, but they did not find differences between immature and adult birds. Similarly, González *et al.* (2007) reported that 25% of 52 radio-monitored Spanish Imperial Eagles *Aquila adalberti* died of poisoning. However, none of these studies directly estimated mortality from encounter histories or accounted for different reporting rate or tag loss. In this respect, a comparison of the age pattern can be misleading as it might reflect differences in the probability of finding the corpses.

In contrast to poison-related mortality, we found that DE accounted for 12% of the overall mortality and did not vary with the age of the bird. Once again, the impact of power lines and its age-dependent pattern differs among species. In the eagle owl, *Bubo bubo* electrocution was found to be the most important cause of mortality in 17 of 25 studies of causes of mortality, and it peaked during the dispersal period of juvenile owls (Sergio *et al.* 2004). However, even if the relative importance of poison and electrocution differs across species, the most important cause of mortality tends to affect the immature more than the adults. This emergent feature of human-related mortality in raptors can have important consequences in population dynamics and management.

A MODEL BASED ON CONDITIONAL PROBABILITIES

By building on previous work by Schaub & Pradel (2004) using counts of dead birds and by Juillet *et al.* (2011) on tag loss, we have provided a general model for the analysis of death processes in the presence of tag loss and imperfect detection. Our model can be used to test hypotheses on the probability of dying of a specific cause. For instance, we found that kites of different ages were affected by poisoning to different degrees, while the likelihood of death because of power lines was not affected by the age of birds. A limitation of our analysis is that we did not include a temporal effect in the parameter variations, but that was because of the relatively small sample size and is not a limitation of the approach itself. Nevertheless, the comparatively narrow standard errors associated with each parameter in our analysis suggest that temporal variability is small.

Recovery models in which survival and recovery or reporting rates are age-dependent include parameters that are not estimable, e.g. first age survival and recovery rate (Lakhani & Newton 1983; Tavecchia *et al.* 2002; Schaub & Pradel 2004). Schaub & Pradel (2004) also reported that the proportion of birds that have died from a particular cause cannot be

estimated separately from the recovery rate because this latter depends on the cause of death. By including live resightings, we have avoided parameter identifiable problems (Freeman, Morgan & Catchpole 1992). Moreover, the detection probability of finding dead birds with a working radio tag was independent of the cause of mortality.

The presence of two types of marks made it possible to consider the probability of tag loss. This is rarely taken into account in capture–mark–recapture studies, especially in those that use radiotransmitters. Radiotracking is often considered to be a method by which fully comprehensive data on presence-absence of wild animals can be obtained, as it is assumed to have a probability detection of 1 (White & Burnham 1999; Williams, Nichols & Conroy 2002). We found a very high detection probability (0·99) for those birds that retained a functional radio tag, but note that 11% of the radios were lost or stopped functioning within the first year of use. Without the presence of a secondary mark, these radio signal failures would be erroneously confounded with mortality. Radio malfunction and radio-loss are common features of many radiotracking studies and they usually result in data loss. Our approach can be used to include these data by considering conditional probabilities.

Our model is suitable for the study of latent (unobservable) multiplicative processes and has a wide range of application in conservation studies. For example, in wildlife epidemiology, the infectious state of an individual can be treated as an uncertain state and transitions between alternative states can be estimated via a state-space model similar to the one proposed here. More generally, the approach presented is flexible enough to be extended to any added conditional process, i.e. the loss of secondary marks, movements between sites, breeding proportion or temporal emigration (Pradel 2009; Sanz-Aguilar *et al.* 2011).

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT OF WILDLIFE POPULATIONS

Conservation practitioners often base their decision on the trade-offs between cost, effort and expected positive outcome (pay-off) of a given management action. For red kite conservation, therefore, it is important to estimate the relative contribution of each cause of mortality and to know whether these are additive or compensatory (Tavecchia *et al.* 2001; Schaub & Lebreton 2004). Mortality because of poisoning is by far the most important cause of mortality in our population (Fig. 3), although at present, we do not know how much of this is additive to other sources of mortality. A part of this mortality must be compensatory because it affects principally immature birds. Also, its impact on population growth rate is not clear. On one hand, this impact is mitigated by the fact that immature birds have a low reproductive value (but see Sergio *et al.* 2010). On the other hand, these birds represent the pool of future breeders that might fill vacant territories and sustain population growth (Prugnolle *et al.* 2003; Sergio *et al.* 2004). For the red kite population in Mallorca, the impact of poisoning might be higher than expected because some birds begin to breed at

2 years old. In addition, poison is generally used to control predators in areas where there is a high density of prey (Whitfield *et al.* 2003). These areas might play the role of population sinks thereby accelerating population extinction (Delibes, Gaona & Ferreras 2001).

The average survival of red kites in Mallorca during our study was 0·76 ± 0·025. This estimate might be negatively biased because some birds could have lost both wing tags after the loss of the radio signal and would have become undetectable unless recovered dead. Although we never observed such a case, we cannot rule out this possibility. Yet, this bias would only be relevant in old birds because the probability of losing the radio signal *and* both wing tags before the age of 3 is very small. The loss of wing tags can be incorporated into the model as a new event, but in our case, the corresponding parameters would be estimated at zero as this event was never observed. Contrary to the lower survival of adult kites, survival during the first year of life was higher than that reported for the UK (Smart *et al.* 2010). This is probably a result of artificial feeding stations on the island (Adrover 2002) that tend to enhance immature survival, reduce dispersal and increase average productivity (Oro *et al.* 2008; Martinez-Abrain *et al.* 2011). It might also reflect the low permanent emigration because of insularity. The high survival of first-year birds seems to partially compensate for the low survival of adults because the population in Mallorca is slowly increasing. However, population growth could also be a consequence of the high productivity of the population because of supplementary feeding (González *et al.* 2006). At present, we do not have enough information to separate these hypotheses.

Our results emphasise the high susceptibility of the red kite to primary and secondary poisoning (Smart *et al.* 2010). This human-related mortality is higher than natural mortality and represents a serious threat to the persistence of red kites in Mallorca. Indeed, the relative importance of stochastic factors in the extinction probability is expected to increase in isolated populations where the chances of a 'rescue effect' by individuals immigrating from other areas are small. Further research should focus on the additive vs. compensatory nature of human-related mortality (Servanty *et al.* 2010), and on perturbation analyses (Igual *et al.* 2009) to investigate their impact on population dynamics.

Finally, we have identified illegal poisoning as the most important source of mortality in Mallorca especially for young kites just before the establishment of their territory. The use of poison to control predators is illegal in Spain but it is often difficult to prove where poisoned baits have been used. We recommend an increase in the radiotracking effort of 2-year-old kites to promptly locate the areas in which poison is in use so that appropriate action can be taken.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Estimates for model averaging.

Appendix S1. Decomposing mortality processes and model implementation in E-SURGE.

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