

1 Running title: Mortality processes in longitudinal data

2 **MODELLING MORTALITY CAUSES IN LONGITUDINAL DATA**  
3 **IN THE PRESENCE OF TAG LOSS: APPLICATION TO RAPTOR**  
4 **POISONING AND ELECTROCUTION.**

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10

11 **ABSTRACT:**

- 12 1. A first step for the effective management of vulnerable populations is to identify  
13 population threats and measure their relative impact on population fluctuations. The  
14 relative importance of proximate causes of mortality can be calculated from  
15 longitudinal data using capture-mark-recapture models. If marks are lost or cease to  
16 function, survival is underestimated.
- 17 2. We provide an analytical framework based on conditional probabilities to obtain a  
18 robust estimate of the contribution of multiple sources of mortality while  
19 accounting for tag loss and imperfect detection.
- 20 3. We applied this approach to radio-tracking and wing-tags resighting data of red  
21 kites *Milvus milvus* to estimate the impact of illegal poisoning and the mortality by  
22 electrocution on power lines in the island of Mallorca (Spain).
- 23 4. Illegal poisoning was responsible for 53% of the total mortality and electrocution on  
24 power lines for 12%. Results indicated that poisoning-related mortality was higher

25 in immature birds, probably due to their more wide-ranging prospective  
26 behaviour.

27 5. Assuming the two human-related mortalities are additive, the survival probability of  
28 kites would increase by 17% (from 0.76 to 0.91) if both threats were removed.

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

35

36 *Key words: radio-tracking, poisoning, Red kite, electrocution, multi-event, capture-*  
37 *recapture.*

38

## 39 INTRODUCTION

40 Measuring the relative contribution of different mortality causes in wildlife populations,  
41 provides an insight in the proximal causes of population changes and can help to  
42 prioritize management actions (Williams, Nichols & Conroy 2002). Typically this  
43 measure is expressed as the proportion of individuals found dead or injured due to a  
44 particular cause (i.e. Newton 1979 p. 152; Martínez-Abrain et al. 2009). However, this  
45 proportion cannot be easily related to a mortality probability because the number of  
46 individuals at risk, i.e. susceptible to death, is unknown. Robust estimates of mortality  
47 probability can be obtained through analysis of longitudinal data of marked individuals  
48 through capture-mark-recapture or -recovery models, that account for imperfect  
49 detection and tag reporting probability (Brownie et al. 1985; Burnham et al. 1987;  
50 Williams et al. 2002). However, incorporating the information on different causes of  
51 mortality in these models, however, is not straightforward. In recovery models, for  
52 example, the probability of dying from a particular cause covaries with the recovery rate  
53 because different causes of mortality lead to different probabilities of finding and  
54 reporting a tag (Brownie et al. 1985; Tavecchia 2000; Schaub 2009). Schaub & Pradel  
55 (2004) proposed a model based on conditional probabilities able to separate the  
56 reporting rate of white storks *Ciconia ciconia* into its two components: the probability  
57 that a stork died due to power line collision and the probability, conditional upon death,  
58 that the tag is reported. Here we present a new approach that extends Schaub &  
59 Pradel's work on recovery to include live encounters when studying multiple sources of  
60 mortality. Moreover, we use the flexibility of the approach to account for marks loss, a  
61 common problem in capture-mark-recapture or -recovery studies, which violates an  
62 important assumption of the statistical models (Williams et al. 2002). When tags are  
63 lost, no longer visible or in the case of radio-transmitter, no longer functioning, the

64 survival probability is biased downward reflecting tag retention rather than individual  
65 survival probability. Tag loss cannot be incorporated explicitly within capture-  
66 recapture or capture-recovery models, and classically, it is either ignored or survival  
67 estimates are corrected *a posteriori* using an ‘external’ measure of tag loss (Nichols et  
68 al. 1992; Diefenbach & Alt 1998; but see Nichols & Hines 1993; Cowen & Schwarz  
69 2006). The problem arises from the fact that individuals become unobservable or more  
70 difficult to detect once they lose their tags. As a consequence, the encounters that  
71 precede tag loss occur with a different probability than the subsequent ones. Similarly  
72 to the problem of multiple sources of mortality, tag loss can be viewed as a problem of  
73 conditional probabilities, in which there are two sets of parameters, one conditional on  
74 tag retention, and a second conditional on tag loss (Juillet et al. 2011). Multi-state  
75 models (Arnason 1973) for the analysis of stratified capture-recapture data allow  
76 transition across states to occur along the encounter histories. A reformulation of these  
77 models (Schwarz, Schweigert, & Arnason 1993) permits explicit estimation of across-  
78 sites movements conditional on survival. Grosbois & Tavecchia (2003) first used this  
79 formulation to allow for unobservable transitions and the estimation of successive  
80 conditional probabilities. Recently, Pradel (2005) has proposed a general framework to  
81 relate observable and unobservable states to the observable events in longitudinal data.  
82 This framework, primarily thought to model longitudinal data under state uncertainty  
83 (Pradel 2009), can be used to join external information on individual state and to model  
84 unobservable processes (Sanz-Aguilar et al. 2011). Juillet *et al.* (2011) first used this  
85 multi-event framework to account for tag losses in a study of double-tagged greater  
86 snow geese *Chen caerulescens atalantica*. In their formulation, a first set of encounters,  
87 i.e. observable events, corresponded to the encounter history conditional on tag  
88 retention and another set corresponded to the events recorded after the loss of one of the

89 principal marks. In this way they successfully decomposed the survival and recapture  
90 processes conditional on tag retention. Here we build on their work and incorporate the  
91 conditional formulation of Schaub & Pradel (2004) to provide a new analytical  
92 framework for the study of multiple causes of mortality in the presence of tag losses.  
93 The formulation can be easily extended to multiple types of tag, reformulating the  
94 mixed information models of Freeman et al. (1992) and Burnham (1993).

95         We applied this model to assess the magnitude of different sources of mortality  
96 of an endangered raptor, the red kite *Milvus milvus* on the island of Mallorca (Spain).  
97 Over the last two centuries, human persecution has led to a drastic decrease in the  
98 number of birds of prey and much effort has been devoted to preventing the local  
99 population from going extinct in many parts of the world (Newton 1979). Despite their  
100 protected status, many natural and introduced populations of raptors, worldwide, are  
101 still threatened by causes directly or indirectly related to human activities, such as  
102 illegal hunting (Smart et al. 2010), primary and secondary poisoning (Whitfield et al.  
103 2003), habitat destruction (Tilman et al. 1994), prey depletion, collisions with cars,  
104 windmills and electrocution on power lines (Sergio et al. 2004; Lehman, Kennedy, &  
105 Savidge 2007; Schaub et al. 2010). The red kite is a medium-sized raptor with little size  
106 dimorphism distributed only in the western Palearctic, mainly in Europe and North  
107 Africa (del Hoyo, Elliott, & Sargatal 1996). Since the 19th century, the species has  
108 declined throughout the whole European continent, and many of its populations are  
109 nowadays considered endangered (IUCN 2010). The species is vulnerable to secondary  
110 or direct contact with poisonous baits, used primarily to control predators of game  
111 species (Evans & Pienkowski 1991; Whitfield et al. 2003; Smart et al. 2010). In Spain,  
112 nearly all red kite populations have declined and some have disappeared due to illegal  
113 hunting, poisoning and electrocution (Viñuela, Martí, & Ruiz 1999). On the island of

114 Mallorca in the archipelago of Balearics (Spain) the population was reduced to only 7-8  
115 pairs in the year 2000 (Adrover, Muñoz, & Riera, 2002). Thanks to the effort of local  
116 environmental agencies, the species has slowly increased its number, and in 2010 has  
117 reached nineteen breeding pairs (J. Adrover *unpublished. data*). Cases of direct and  
118 indirect poisoning are still common on the island, and the exact magnitude of the  
119 different human-related sources of mortality is not known. Here we use the data on  
120 resighting and recovery of individually marked fledglings collected since the year 2000.  
121 We applied a new analytical approach based on conditional probabilities, 1) to estimate  
122 the age-dependent mortality of marked birds, 2) to estimate the incidence of tag loss and  
123 the relative magnitude of different sources of mortality, and 3) to assess whether their  
124 influence differs according to the age-class considered.

125

## 126 **MATERIALS AND METHODS**

### 127 *Longitudinal data and tag loss*

128 Since 2000, 142 fledglings have been equipped with a radio-transmitter (Biotrack TW-  
129 3) mounted on a backpack harness. Birds were tagged as chicks just before leaving the  
130 nest. Transmitters had a range of 20-30KM, a life expectancy of c. 3-4 years and  
131 weighed less than 5% of bird body weight. In addition to the radio tag, all chicks were  
132 marked using PVC wing-tags with a unique alpha-numeric code, one on each wing.  
133 This primary tag was used to assess the loss of the radio signal for mechanical or  
134 electrical reason. Wing-tags are occasionally lost, but their lifespan is longer than that  
135 of the radio transmitter. We never observed the loss of both types of tags, and all dead  
136 animals, found with or without the radio-transmitter, had retained at least one wing-tag.  
137 Furthermore, it is not uncommon to see a 7-10 years old kite with both wing-tags.  
138 Nevertheless, we cannot rule out the simultaneous loss of both wing-tags after the loss

139 of the radio-signal. In this case the survival probabilities of birds more than 3 years old  
140 (i.e. the average lifespan of the radio signal) might be underestimated. Note that the  
141 relative differences across mortality causes and ages remain unchanged because the loss  
142 of tags is independent from the cause of death and no birds had lost their wing tags  
143 before the radio-signal was lost. Observations of marked birds were done by active  
144 search throughout the whole island, by car or, occasionally, helicopter. When the signal  
145 was stationary we actively searched for the radio-transmitter to confirm whether the  
146 animal was stationary, dead or had lost its radio tag. All carcasses found were sent to  
147 the laboratory for a post-mortem analysis. In addition to radio locations, we carried out  
148 observations at feeding places (dump sites and artificial feeding stations), territories and  
149 roosting sites to record the presence of birds for which we could no longer detect a radio  
150 signal. We restricted the analysis to observations of live birds recorded from April to  
151 June, to reduce problems linked with pooling data from a long time period (Hargrove &  
152 Borland 1994).

153 *A model for individual states and observed events*

154 The observations of live and dead birds, together with the information on tag loss,  
155 formed the set of observable events from which we estimated the proportion of birds  
156 that died by poisoning, electrocution or by other (natural) causes. This was done by  
157 specifying a probabilistic model that linked the observed events to transitions between  
158 possible alternative individual states (Fig. 1). We considered that individuals can move  
159 across four main states: alive (noted 'A'), death by poison ('DP'), death by  
160 electrocution ('DE') and death from other (unknown) causes ('DO'). Given that  
161 individuals can lose their radio transmitter, we considered the above states for birds  
162 with and without a functioning radio (noted with the superscript '+' and '-',  
163 respectively). As in Lebreton *et al.* (1999), we included an additional dead state (noted

164 ‘†’) that corresponded to an unobservable dead state. This might be seen as ‘dead for  
 165 some time’ in contrast with the observable state ‘newly dead’, corresponding to  
 166 recovery of a corpse. This differentiation assumes that corpses are found soon after  
 167 death and allows us to estimate the reporting rate associated with the observable dead  
 168 states and the probability of dying from different causes (Schaub and Pradel, 2004).

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

171

$$172 \quad \Phi = \begin{pmatrix} & A^+ & A^- & DP & DE & DO & DP & DE & DO & \dagger \\ A^+ & \alpha S & (1-\alpha)S & \alpha\beta(1-S) & \alpha\gamma(1-S) & \alpha(1-\beta-\gamma)(1-S) & (1-\alpha)\beta(1-S) & (1-\alpha)\gamma(1-S) & (1-\alpha)(1-\beta-\gamma)(1-S) & 0 \\ A^- & 0 & S & 0 & 0 & 0 & \beta(1-S) & \gamma(1-S) & (1-\beta-\gamma)(1-S) & 0 \\ DP & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DE & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DO & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DP & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DE & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DO & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \dagger & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

173

174 where

175  $S$  : is the annual survival probability.

176  $\alpha$  : is the probability of radio signal retention.

177  $\beta$  : is the probability of death due to poisoning given that an animal has died.

178  $\gamma$  : is the probability of death by electrocution given that an animal has died.

179 The matrix,  $\Phi$ , can be decomposed into three successive matrices to single out the

180 parameters related to each process, i.e. tag loss, survival and causes of mortality,

181 respectively (Appendix S1 in Supporting Information).

182 At any given time, we can observe nine types of mutually exclusive events (here

183 arbitrarily coded with numbers from 0 to 8; Fig. 1). The first possible event (coded ‘0’)

184 is a non-encounter, i.e. the radio-signal cannot be heard and the animal cannot be seen.



185 This is the only ambiguous event as it may correspond to any underlying state. For  
186 example, the animal may have lost the radio or be carrying one that ceased to function,  
187 or it may be dead having lost the radio and remaining undetected. Each of the other  
188 events can happen only with one state. The events coded '1' and '2' refer to encounters  
189 of individuals alive, with respectively a functioning (the animal is then in state 'A<sup>+</sup>' of  
190 matrix  $\Phi$ ) or not functioning radio (state 'A<sup>-</sup>' of matrix  $\Phi$ ). The remaining six events  
191 correspond to animals found dead. In our case, we considered six cases of 'newly dead'  
192 encounters relating to three death causes and two radio states (3x2 combinations).  
193 Specifically, '3' and '6' code for birds found poisoned with and without a functioning  
194 radio respectively (states 'DP<sup>+</sup>' and 'DP<sup>-</sup>' of matrix  $\Phi$  respectively). Similarly, '4' and  
195 '7' are for birds electrocuted with and without a functioning radio respectively (states  
196 'DE<sup>+</sup>' and 'DE<sup>-</sup>' of matrix  $\Phi$ ). Finally, '5' and '8' refer to those birds that have been  
197 found dead but from unspecified causes with and without a functioning radio  
198 respectively (states 'DO<sup>+</sup>' and 'DO<sup>-</sup>' of matrix  $\Phi$ , Fig. 1). Note that '2', '6', '7' and '8'  
199 code for birds encountered without a functioning radio. These codes do not distinguish  
200 whether the radio was physically lost or not functioning. If needed, these situations can  
201 further be distinguished by including additional states in the matrix  $\Phi$ , however here we  
202 have opted not to do so for the sake of simplicity.

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

210 specifying the probability of each event (in columns) conditional on each state (in  
 211 rows):

212

213

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

214 where

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

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

217  $\lambda_1$  : the probability of encounter of an animal dead by poisoning and without the  
 218 radio signal.

219  $\lambda_2$ : the probability of encounter of an animal dead by electrocution and without the  
 220 radio signal.

221  $\lambda_3$ : the probability of encounter of an animal dead by other causes and without the  
 222 radio signal.

223 The model was built and fitted to the data using the software program E-SURGE

224 (Choquet, Rouan, & Pradel 2009). It could also be fitted as a state-space model.

225 *Model definition and model selection*

226 We wanted to investigate whether tag loss depended on the age of the tag, and  
 227 whether the three different sources of mortality had a contrasting age-pattern. To do  
 228 this, we compared models built under different alternative hypotheses using the AICc  
 229 value (Burnham & Anderson 2002). The model with the lowest AICc value should be

230 seen as the best compromise between deviance explained and number of parameters in  
231 the model. Given the relatively small number of animals marked, we did not consider a  
232 possible variation of parameters over time. The assumption of constant parameters is  
233 unrealistic, but in our case it is necessary to avoid models with more parameters than  
234 data. The model selection procedure consisted of progressively decreasing model  
235 complexity one parameter at a time (Grosbois & Tavecchia 2003). After eliminating  
236 irrelevant effects from one parameter at a time, a consensual model was built using the  
237 best structure selected independently for each parameter. This consensual model is then  
238 used to re-test for previously unrestrained factors in a more parsimonious environment  
239 (Grosbois & Tavecchia 2003). In addition we calculated model probability, e.g. Akaike  
240 weight,  $w$ , as a measure of model plausibility (Anderson 2007). Parameter estimates  
241 were derived from the retained model by maximum likelihood, and final estimates were  
242 obtained by averaging the estimates from all models that followed the consensual one  
243 (Anderson 2007). In model notation we specified each parameter in matrix  $\Phi$  (see also  
244 Appendix S1 Supporting Information), separated by the symbol “/” and the effects  
245 considered for, are noted in brackets. Red kites commonly begin breeding at 3 years old  
246 or later (del Hoyo et al. 1996), although in Mallorca some birds bred at their second  
247 birthday. As in Smart *et al.* (2010), we have considered three age classes, 1, 2, and  $\geq 3$   
248 years old, respectively. This reflects the life cycle of the bird and avoids estimates  
249 based on those few birds that might reach old ages (Sergio et al. 2010). In contrast,  
250 radio signal retention was modelled as a function of radio age, i.e. time elapsed from  
251 marking, using five age classes because batteries were expected to last c. 3-4 years. In  
252 addition, we fitted a model in which radio signal was assumed to be a quadratic function  
253 of the radio age to reflect the progressive decay of the batteries. In model notation, the  
254 age effect was noted ‘a’ when considered as a factor and ‘A’ when considered as

255 continuous variable. The symbol ‘.’ indicates a constant parameter. Hence, a model in  
256 which all parameters are assumed to be constant would be noted:  
257  $\alpha(\cdot)/S(\cdot)/\beta(\cdot)\gamma(\cdot)/p(\cdot)c(\cdot)\lambda_1(\cdot)\lambda_2(\cdot)\lambda_3(\cdot)$ . The reporting probabilities,  $\lambda_1$ ,  $\lambda_2$  and  $\lambda_3$  were  
258 always considered age independent due to the small number of birds found dead without  
259 the tag (see below).

260

## 261 **RESULTS**

262 Fifty-one (36%) out of the 142 radio tagged birds were found dead. Post-mortem  
263 examination revealed that 53% (27) of these birds had died of poisoning and 12% (6)  
264 had been electrocuted. The remaining 18 kites died of unknown reasons. Only 2 birds  
265 (4%) were found dead after their radio signal was lost (events coded 6 and 7,  
266 respectively). The first steps of the model selection suggested a strong effect of age on  
267 radio lifespan and a weaker effect on survival and poisoning probability. As expected,  
268 the probability of detecting radio failure, i.e. the loss of the signal, varied according to  
269 the age of the radio because this included the end of the battery life. The first  
270 consensual model assumed an effect of age in these parameters (model 8, Table 1). We  
271 used this simpler model to re-assess the importance of age in all other parameters and to  
272 model signal lifespan,  $\alpha$ , as a linear function of the radio-age. The latter model had the  
273 lowest AICc value (model 13; Table 1 and Fig. 2). It is worth noticing that  $\alpha$  in first-  
274 year birds was  $0.89 \pm 0.03$  (estimate  $\pm$  standard error), which suggested that about 10%  
275 of radios were lost, or ceased functioning, within the first year after marking. According  
276 to model 13, the detection probability,  $p$ , of a functioning radio was very high,  
277  $0.99 \pm 0.008$ , and did not vary with bird age. In contrast, the probability,  $c$ , of detecting a  
278 bird without a radio tag was associated with age, being higher in first-year ( $0.95 \pm 0.24$ )  
279 and lower during the second and subsequent years ( $0.37 \pm 0.14$  and  $0.57 \pm 0.09$ ,

280 respectively). The average value of survival for red kites in Mallorca in the age-  
281 independent model (model 8) was  $0.76 \pm 0.025$ . The models indicated a small difference  
282 among the three age classes considered (from Model 9:  $0.72 \pm 0.08$ ,  $0.82 \pm 0.09$  and  
283  $0.79 \pm 0.09$  for yearlings, immature and adults, respectively). This difference was not  
284 supported by the AICc values and averaged estimates were very similar ( $0.76 \pm 0.03$ ,  
285  $0.77 \pm 0.03$  and  $0.77 \pm 0.03$  for yearlings, immature and adults, respectively). Among the  
286 three components of mortality, the most important was poisoning ( $0.53 \pm 0.07$ ), while  
287 only  $0.10 \pm 0.04$  was due to electrocution (estimates from model 11; Table 1 and Table  
288 S1 in Supporting Information). The results suggested that mortality, due to poisoning  
289 changed with age, peaking just before the age at which most birds begin to breed (Fig.  
290 3). However, the model without an age effect (Model 11) had a similar AICc value.  
291 This was probably due to the large standard errors of the age-dependent values of  
292 mortality due to poisoning (Fig. 3). The two models describe the data equally well, but  
293 model weight indicated that the model including an effect of age was more plausible.  
294 Also, model-averaged estimates of age-dependent proportions of poisoned birds, among  
295 the birds estimated to be dead, were different ( $0.44 \pm 0.09$ ,  $0.76 \pm 0.05$  and  $0.63 \pm 0.17$  for  
296 yearlings, immature and adults, respectively). In contrast, bird age was not associated  
297 with the probability of death by electrocution and it was poorly supported at all steps of  
298 the analysis (Table 1). As a consequence the age-dependent estimates for this parameter  
299 derived by model averaging were very similar:  $0.121 \pm 0.05$ ,  $0.120 \pm 0.05$  and  $0.119 \pm 0.05$   
300 for yearlings, immature and adults, respectively.

301 The estimates of  $S$  and  $\beta$  from models 8 and 11 can be combined to calculate the  
302 expected (age-independent) survival probability in the absence of illegal poisoning  
303 and/or electrocution. This would be of  $0.89 \pm 0.029$  ( $=1 - 0.24 * (1 - 0.53)$ ), corresponding  
304 to c. 14% increase in survival probability. As expected, removing mortality due to

305 electrocution would lead to a smaller increase in survival probability, from 0.76 to  
306  $0.79 \pm 0.047$  (c.3%). Note that standard errors of the combined estimates were calculated  
307 using the  $\delta$ -method (Morgan 2000). Assuming the two human-related mortalities are  
308 additive, the survival probability of red kites would be of  $0.91 \pm 0.025$  if both were  
309 controlled (an overall increase of 17% in average survival).

## 310 **DISCUSSION**

312

313 The relative importance of proximate causes of mortality is typically expressed  
314 as the proportion of birds found dead or admitted to wildlife rehabilitation centres for a  
315 particular cause. This approach gives an indication of the relative importance of  
316 different causes of mortality, but it implicitly assumes that the probability of detecting a  
317 corpse or an injured bird is the same, regardless of the cause of death or of injury. This  
318 assumption is unlikely to be met in natural populations as the reporting rate of dead  
319 birds covaries with the cause of mortality (Brownie et al. 1985; Tavecchia 2000; Schaub  
320 2009; Schaub et al. 2010). Thus, the proportion of animals dying from a particular  
321 cause cannot be expressed as a mortality probability, and the importance of each cause  
322 cannot be related to an absolute mortality measure. We have provided an analytical  
323 framework based on conditional probabilities that allows to assess the contributions of  
324 human-related causes of mortality in the red kite. We found that poisoning was  
325 responsible for 53% of red kite deaths in Mallorca. Moreover, our results indicated that  
326 this was higher for 2-year-old birds, probably reflecting their wide-ranging prospective  
327 behaviour (J. Adrover *unpublished data*). Age differences in poison-related mortality  
328 has been reported in other studies and, generally, immature birds are more affected by  
329 poison than adults although this might depend on the species and the geographic  
330 location. In the United Kingdom, Smart *et al.* (2010) reported that 38% of radio-tagged

331 red kites died due to poisoning, the majority of these during their first year; the illegal  
332 use of poison decreased kite survival by 31%, 8% and 5% for one-, two- and three-year  
333 old birds, respectively. Margalida *et al.* (2008) found that 18 (86%) out of 21 radio-  
334 tagged bearded vultures *Gypaetus barbatus* died of poisoning, but they did not find  
335 differences between immature and adult birds. Similarly, González *et al.* (2007)  
336 reported that 25% of 52 radio-monitored Spanish Imperial Eagles *Aquila adalberti* died  
337 of poisoning. However, none of these studies directly estimated mortality from  
338 encounter histories or accounted for different reporting rate or tag-loss. In this respect,  
339 a comparison of the age pattern can be misleading as it might reflect differences in the  
340 probability of finding the corpses.

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

### 351 *A model based on conditional probabilities*

352 By building on previous work by Schaub & Pradel (2004) using counts of dead  
353 birds and by Juillet *et al.* (2011) on tag loss, we have provided a general model for the  
354 analysis of death processes in the presence of tag loss and imperfect detection. Our  
355 model can be used to test hypotheses on the probability of dying of a specific cause.

356 For instance, we found that kites of different ages were affected by poisoning to  
357 different degrees, while the likelihood of death due to power lines was not affected by  
358 the age of birds. A limitation of our analysis is that we did not include a temporal effect  
359 in the parameter variations, but that was due to the relatively small sample size and is  
360 not a limitation of the approach itself. Nevertheless, the comparatively narrow standard  
361 errors associated with each parameter in our analysis suggest that temporal variability is  
362 small.

363 Recovery models in which survival and recovery or reporting rates are age-  
364 dependent include parameters that are not estimable, e.g. first age survival and recovery  
365 rate (Lakhani & Newton 1983; Tavecchia et al. 2002; Schaub & Pradel 2004). Schaub  
366 & Pradel (2004) also reported that the proportion of birds that have died from a  
367 particular cause cannot be estimated separately from the recovery rate because this latter  
368 depends on the cause of death. By including live resightings we have avoided  
369 parameter identifiable problems (Freeman et al. 1992). Moreover, the detection  
370 probability of finding dead birds with a working radio tag was independent of the cause  
371 of mortality.

372 The presence of two types of marks made it possible to consider the probability  
373 of tag loss. This is rarely taken into account in capture-mark-recapture studies,  
374 especially in those that use radio-transmitters. Radio-tracking is often considered to be  
375 a method by which fully comprehensive data on presence-absence of wild animals can  
376 be obtained, as it is assumed to have a probability detection of 1 (White & Burnham  
377 1999; Williams et al. 2002). We found a very high detection probability (0.99) for those  
378 birds that retained a functional radio-tag, but note that 11% of the radios were lost or  
379 stopped functioning within the first year of use. Without the presence of a secondary  
380 mark, these radio signal failures would be erroneously confounded with mortality.



381 Radio malfunction and radio-loss are common features of many radio-tracking studies  
382 and they usually result in data loss. Our approach can be used to include these data by  
383 considering conditional probabilities.

384 Our model is suitable for the study of latent (unobservable) multiplicative  
385 processes and has a wide range of application in conservation studies. For example, in  
386 wildlife epidemiology the infectious state of an individual can be treated as an uncertain  
387 state and transitions between alternative states can be estimated via a state-space model  
388 similar to the one proposed here. More generally, the approach presented is flexible  
389 enough to be extended to any added conditional process, i.e. the loss of secondary  
390 marks, movements between sites, breeding proportion or temporal emigration (Pradel  
391 2009; Sanz-Aguilar et al. 2011).

#### 392 *Implications for conservation and management of wildlife populations*

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

406 expected because some birds begin to breed at 2-years-old. In addition, poison is  
407 generally used to control predators in areas where there is a high density of prey  
408 (Whitfield et al. 2003). These areas might play the role of population sinks thereby  
409 accelerating population extinction (Delibes, Gaona & Ferreras 2001).

410         The average survival of red kites in Mallorca during our study was  $0.76\pm 0.025$ .  
411 This estimate might be negatively biased because some birds could have lost both wing-  
412 tags after the loss of the radio signal and would have become undetectable unless  
413 recovered dead. Although we never observed such a case, we cannot rule out this  
414 possibility. Yet, this bias would only be relevant in old birds because the probability of  
415 losing the radio signal *and* both wing-tags before the age of 3 is very small. The loss of  
416 wing-tags can be incorporated into the model as a new event, but in our case, the  
417 corresponding parameters would be estimated at zero as this event was never observed.  
418 Contrary to the lower survival of adult kites, survival during the first year of life was  
419 higher than that reported for the UK (Smart et al. 2010). This is probably a result of  
420 artificial feeding stations on the island (Adrover 2002) that tend to enhance immature  
421 survival, reduce dispersal and increase average productivity (Oro et al. 2008; Martinez-  
422 Abbrain et al. 2011). It might also reflect the low permanent emigration due to  
423 insularity. The high survival of first-year birds seems to partially compensate for the  
424 low survival of adults because the population in Mallorca is slowly increasing.  
425 However, population growth could also be a consequence of the high productivity of the  
426 population due to supplementary feeding (González et al. 2006). At present, we do not  
427 have enough information to separate these hypotheses.

428         Our results emphasise the high susceptibility of the red kite to primary and  
429 secondary poisoning (Smart et al. 2010). This human-related mortality is higher than  
430 natural mortality and represents a serious threat to the persistence of red kites in

431 Mallorca. Indeed, the relative importance of stochastic factors in the extinction  
432 probability is expected to increase in isolated populations where the chances of a  
433 ‘rescue effect’ by individuals migrating from other areas are small. Further research  
434 should focus on the additive *vs* compensatory nature of human-related mortality  
435 (Servanty et al. 2010), and on perturbation analyses (Iguar et al. 2009) to investigate  
436 their impact on population dynamics.

437 Finally, we have identified illegal poisoning as the most important source of  
438 mortality in Mallorca especially for young kites just before the establishment of their  
439 territory. The use of poison to control predators is illegal in Spain but it is often difficult  
440 to prove where poisoned baits have been used. We recommend increasing the radio-  
441 tracking effort during the second years of kites to prompt locate the areas in which  
442 poison is in use.

443

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652 **Supporting Information**

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

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

655 SURGE

656 **Table S1.** Estimates for model averaging

657

658

659



Table 1: Modelling tag retention,  $\alpha$ , survival,  $S$ , and sources of mortality ( $\beta$  and  $\gamma$ ), as a function of age. The age effect was first modelled on each parameter at a time (models 1 to 7 ; see text for detailed on model selection strategy). Model notation: ‘a’ = age as a factorial effect (3 levels except in T1 where 5 levels were considered, see text), ‘A’= continuous effect of age (1 to 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 ( $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_3$ ) were kept constant (not shown). Models in bold were used to obtained averaged estimates.

Model	T1 /	T2 /	T3/	E	df	Deviance	AICc	$\Delta$ AICc	w
<i>Toward a consensual model</i>									
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
<b>8</b>	<b><math>\alpha(a)</math></b>	<b><math>S(.)</math></b>	<b><math>\beta(a)\gamma(.)</math></b>	<b><math>p(.)c(a)</math></b>	<b>16</b>	<b>816.60</b>	<b>850.04</b>	1.08	<b>0.1931</b>
<i>After the consensual model</i>									
<b>9</b>	<b><math>\alpha(a)</math></b>	<b><math>S(a)</math></b>	<b><math>\beta(a)\gamma(.)</math></b>	<b><math>p(.)c(a)</math></b>	<b>18</b>	<b>813.34</b>	<b>851.17</b>	2.21	<b>0.1100</b>
<b>10</b>	<b><math>\alpha(a)</math></b>	<b><math>S(.)</math></b>	<b><math>\beta(a)\gamma(a)</math></b>	<b><math>p(.)c(a)</math></b>	<b>18</b>	<b>815.99</b>	<b>853.82</b>	4.86	<b>0.0292</b>
<b>11</b>	<b><math>\alpha(a)</math></b>	<b><math>S(.)</math></b>	<b><math>\beta(.)\gamma(.)</math></b>	<b><math>p(.)c(a)</math></b>	<b>14</b>	<b>821.68</b>	<b>850.79</b>	1.83	<b>0.1327</b>
<b>12</b>	<b><math>\alpha(a)</math></b>	<b><math>S(.)</math></b>	<b><math>\beta(a)\gamma(.)</math></b>	<b><math>p(.)c(.)</math></b>	<b>14</b>	<b>821.79</b>	<b>850.90</b>	1.94	<b>0.1256</b>
<b>13</b>	<b><math>\alpha(A+A^2)</math></b>	<b><math>S(.)</math></b>	<b><math>\beta(a)\gamma(.)</math></b>	<b><math>p(.)c(a)</math></b>	<b>14</b>	<b>819.85</b>	<b>848.96</b>	0	<b>0.3320</b>

## FIGURES LEGENDS

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).

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).

Fig 3. Human induced causes of mortality. The impact of illegal poisoning varies as a function of age, while the mortality due to electric power line is constant over age. Estimates are from the retained model (model 13).

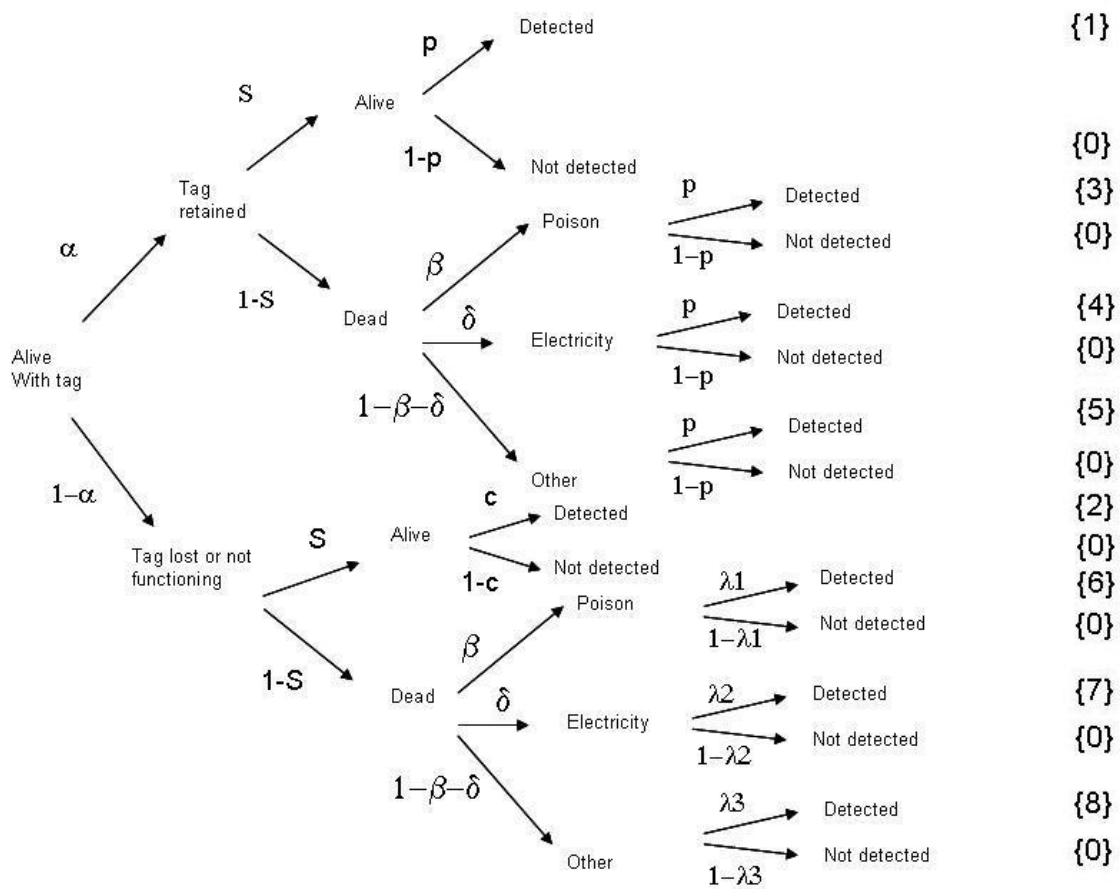


Fig.1

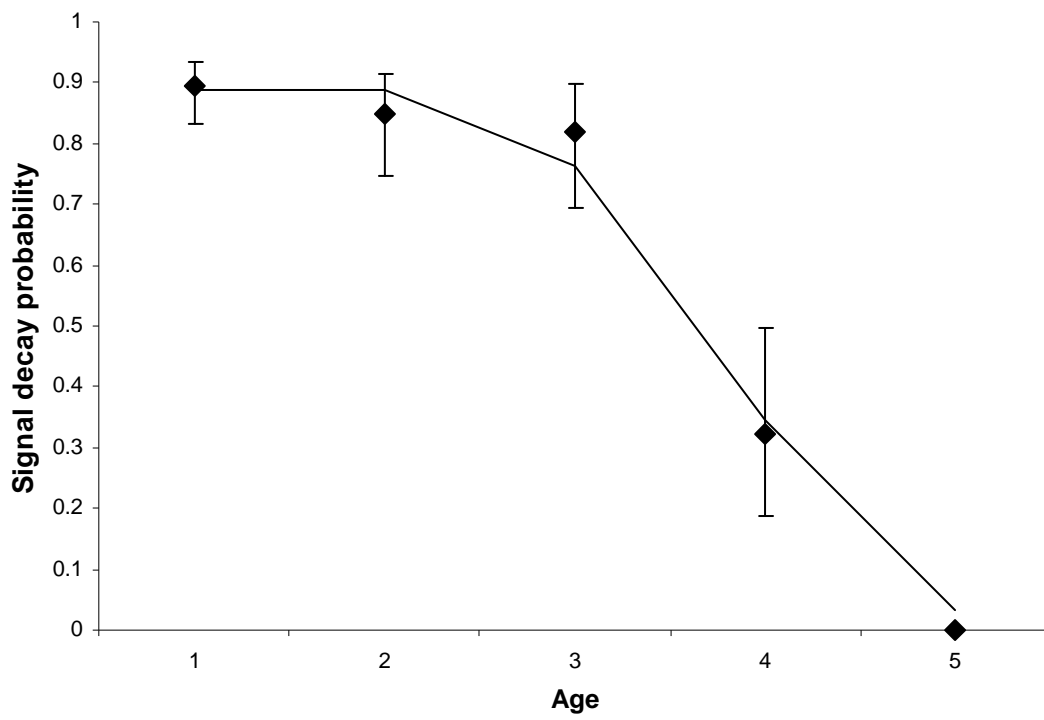


Fig 2

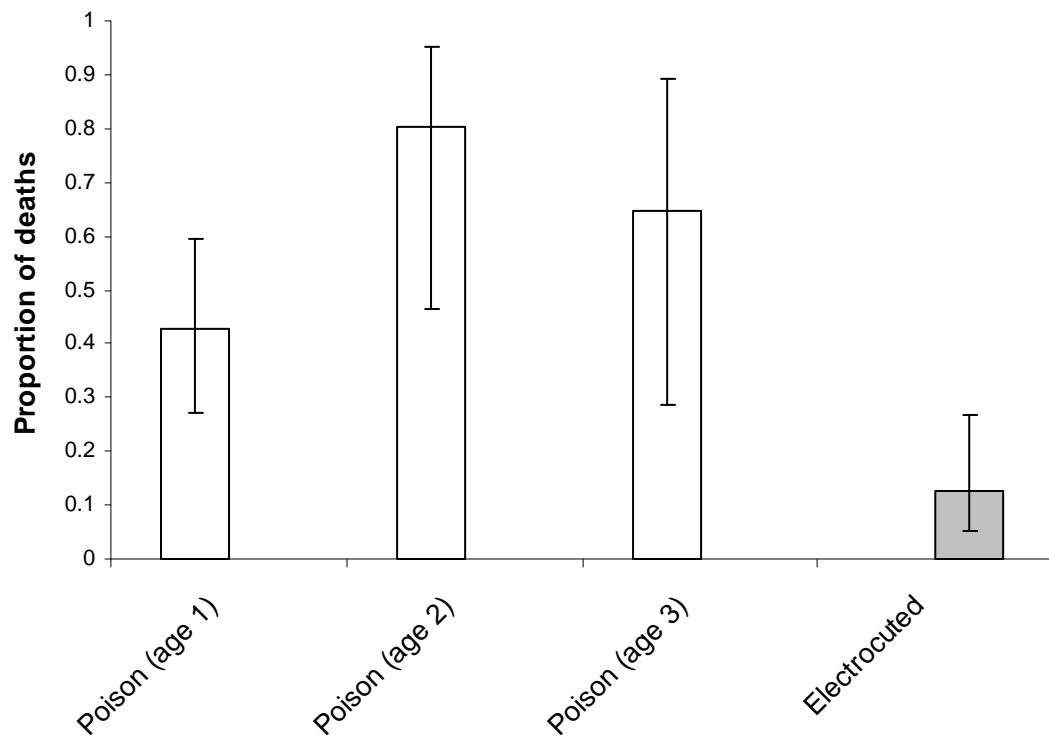


Fig. 3

## SUPPORTING INFORMATION

### APPENDIX SI: *Decomposing mortality processes and model implementation*

The transition matrix  $\Phi$  (see text) can be decomposed into three matrices, **T1**, **T2** and **T3**, each describing a specific process, or step, of the transition across states so that  $\Phi = \mathbf{T1} * \mathbf{T2} * \mathbf{T3}$ . The first matrix, **T1**, contains the probability of tag loss (i.e. the loss of the radio signal). Because we assume that dead birds are retrieved immediately or never, the probability to lose the radio signal during the time interval  $t, t+1$ , concerns only birds alive at  $t$  (in rows):

$$\mathbf{T1} = \begin{pmatrix} & \begin{array}{c} A^+ \\ A^- \\ DP^+ \\ DE^+ \\ DO^+ \\ DP^- \\ DE^- \\ DO^- \\ \dagger \end{array} & \begin{array}{cc} A^+ & A^- \\ \hline \alpha & 1 - \alpha \\ 0 & 1 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{array} & \begin{array}{c} \dagger \\ 0 \\ 0 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{array} \end{pmatrix}$$

The following matrix describes the survival process:

$$\mathbf{T2} = \begin{pmatrix} & \begin{array}{c} A^+ \\ A^- \\ \dagger \end{array} & \begin{array}{cccc} A^+ & A^- & D^+ & D^- \\ \hline S & 0 & 1-S & 0 \\ 0 & S & 0 & 1-S \\ 0 & 0 & 0 & 0 \end{array} & \begin{array}{c} \dagger \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{array} \end{pmatrix}$$

Note that in our models, we considered that the presence of a radio transmitter did not influence survival. Alternatively, we could consider different survival parameters for

birds that have lost the tag. Also, in **T2** the dead events are not stratified according to the different causes of mortality. This is done in the last matrix, **T3**, which describes the process associated with the cause of death:

$$\mathbf{T3} = \begin{pmatrix} & \text{A}^+ & \text{A}^- & \text{DP}^+ & \text{DE}^+ & \text{DO}^+ & \text{DP}^- & \text{DE}^- & \text{DO}^- & \dagger \\ \text{A}^+ & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{A}^- & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \text{D}^+ & 0 & 0 & \beta & \gamma & 1-\beta-\gamma & 0 & 0 & 0 & 0 \\ \text{D}^- & 0 & 0 & 0 & 0 & 0 & \beta & \gamma & 1-\beta-\gamma & 0 \\ \dagger & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

The matrices **T1** and **T2** are equivalent to the model proposed by Juillet et al. (2011), while the third matrix accounts for the different causes of death as in Schaub and Pradel (2004).

When implementing the model in E-SURGE, one should specify a matrix with the initial conditions, a 3-steps transition matrix for survival (**T1**, **T2**, and **T3** in the text) and a matrix with the detection probability of each event (**E** in the text). The matrix pattern and the syntax for the parametrization of the corresponding matrices to implement the model in software E-SURGE were as follow (the electronic version of this script is available from the authors and can be uploaded directly into E-SURGE):

Syntax for step 1 : i

Pattern matrix :

\* - - - - - - -

Number of step for transition : 3

Syntax for step 1 : a

Pattern matrix :

a \* -  
 - \* -  
 - - \*  
 - - \*  
 - - \*  
 - - \*  
 - - \*

- - \*

- - \*

Syntax for step 2 : i

Pattern matrix :

s - \* - -

- s - \* -

- - - - \*

Syntax for step 3 : to(3 6).a(1,2,3:5)+to(4 7)

Pattern matrix :

\* - - - - - - -

- \* - - - - - -

- - b g \* - - -

- - - - - b g \* -

- - - - - - - \*

Number of step for encounter : 1

Syntax for step 1 : firste+nexte.f(1 3 4 5)+nexte.f(2).a(2,3,4:6)+nexte.f(6,7,8)

Pattern matrix :

\* s - - - - - - -

\* - c - - - - - - -

\* - - s - - - - - - -

\* - - - s - - - - - - -

\* - - - - s - - - - - - -

\* - - - - - l - - - - - - -

\* - - - - - - l - - - - - - -

\* - - - - - - - l - - - - - - -

\* - - - - - - - - - - - - -



Table S1: Estimates used in model averaging (models 8 to 13 ; see Table 1 in the text).

For parameter notation see Table 1. In all models reporting rates for birds found dead

without a functioning radio ( $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_3$ ) were kept constant.

Parameter	Age	Matrix	Model 8	Model 9	Model 10	Model 11	Model 12	Model 13
$\alpha$	1	T1	0.898	0.898	0.898	0.898	0.897	0.889
$\alpha$	2	T1	0.841	0.841	0.841	0.841	0.842	0.888
$\alpha$	3	T1	0.823	0.822	0.823	0.823	0.823	0.763
$\alpha$	4	T1	0.324	0.324	0.324	0.324	0.324	0.347
$\alpha$	5	T1	0	0	0	0	0	0.035
S	1	T2	0.765	0.719	0.765	0.765	0.765	0.765
S	2	T2	0.765	0.825	0.765	0.765	0.765	0.765
S	3	T2	0.765	0.788	0.765	0.765	0.765	0.765
$\beta$	1	T3	0.426	0.426	0.425	0.531	0.425	0.426
$\beta$	2	T3	0.803	0.802	0.812	0.531	0.805	0.804
$\beta$	3	T3	0.648	0.646	0.640	0.531	0.651	0.648
$\gamma$	1	T3	0.125	0.125	0.115	0.102	0.125	0.125
$\gamma$	2	T3	0.125	0.125	0.084	0.102	0.125	0.125
$\gamma$	3	T3	0.125	0.125	0.065	0.102	0.125	0.125
c	1	E	0.944	0.999	0.948	0.948	0.567	0.942
c	2	E	0.367	0.342	0.366	0.367	0.567	0.370
c	3	E	0.571	0.540	0.571	0.571	0.567	0.572
p	1	E	0.992	0.992	0.992	0.992	0.993	0.992
p	2	E	0.992	0.992	0.992	0.992	0.993	0.992
p	3	E	0.992	0.992	0.992	0.992	0.993	0.992
$\lambda_1$	-	E	0.040	0.043	0.04	0.048	0.038	0.040
$\lambda_2$	-	E	0.327	0.332	0.334	0.251	0.346	0.327
$\lambda_3$	-	E	0	0	0	0	0	0