

Electrocution threatens the viability of populations of the endangered Bonelli's eagle (*Aquila fasciata*) in Southern Europe



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ABSTRACT

Electrocution on power lines negatively affects a wide range of groups of birds. Nevertheless, the overall demographic consequences of electrocution are still poorly understood. Typically, little demographic data is available for endangered species and so approaches aimed at guiding conservation measures that bear in mind this uncertainty are urgently required. In the present study, we develop a procedure based on population modeling that is useful both for obtaining unbiased estimates of mortality caused by electrocution and for estimating the mitigation effort required to restore threatened populations – even if uncertainty regarding parameter estimates exists. We used as a case study the Bonelli's eagle (*Aquila fasciata*) population in the NE Iberian Peninsula. Firstly, we used multievent models to estimate mortality while accounting for imperfect detection and uncertainty in state assignment. The fraction of mortality caused by electrocution (α) was not directly estimable from the multievent models and so to estimate this parameter we developed a method that used in addition basic monitoring information. Accordingly, α was estimated at 0.26 and 0.62 for, respectively, territorial and non-territorial individuals in the period 2008–2014. Secondly, we applied viability analysis to gauge the effort that would be required to mitigate electrocution and guarantee population self-sustainability. Our results highlight the fact that even low levels of electrocution can drive a local population to extinction. Overall, our study establishes a framework for estimating the demographic effects of electrocution and provides conservation managers with information on the effort needed to mitigate human-induced mortality and restore threatened populations.

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1. Introduction

Electrocution on overhead power lines causes the death every year of thousands of birds from a wide range of avian groups that commonly include Ciconiiformes, Falconiformes, Strigiformes and Passeriformes (Bevanger, 1994, 1998; Bayle, 1999; Janss and Ferrer, 2001; APLIC, 2006; Rubolini et al., 2005; Lehman et al., 2007; Tintó et al., 2010; Dwyer et al., 2014). This conservation problem has serious economic repercussions for human societies in the form of power failures, the loss of revenue, the need for repairs to infrastructures and the cost of legal compliance (APLIC, 2006; Lehman et al., 2007).

Researchers and practitioners currently have a good understanding of the basic causes of electrocution, that is, the type of pylons and poles that increase the risk of electrocution and the specific factors pertaining to habitat, behavior, age, sex, population and species that also affect the possibilities of electrocution (Janss, 2000; Real et al., 2001; Tintó et al., 2010; Guil et al., 2011, 2015; Dwyer et al., 2014). Technical modifications to electricity poles have been shown to be an effective way to mitigate the frequency of electrocution (Tintó et al.,

2010; Kaluga et al., 2011). However, despite important advances, few reliable estimates exist of the magnitude of mortality caused by electrocution in given species and/or populations. Thus, most estimates are based on records of individuals found dead, data from ringed birds or surveys of power lines (Ferrer et al., 1991; Harness and Wilson, 2001; Lehman et al., 2007). In these cases, mortality caused by electrocution is usually estimated as a raw proportion, which ignores the fact that different causes of death may have distinct encounter probabilities leading to biases in the estimates of mortality caused by electrocution (but see Schaub and Pradel, 2004; Tavecchia et al., 2012). This gap in our knowledge means that the effect of electrocution on shaping the population dynamics for any given species – a pre-requisite for providing evidence-based conservation guidance – is still poorly understood (Bevanger, 1994, 1998; Lehman et al., 2007; Loss et al., 2014; but see Schaub et al., 2010; López-López et al., 2011).

Raptors are very susceptible to electrocution due to their large size and the fact that many habitually use power line pylons to perch, rest, roost or even nest (Lehman et al., 2007). Additionally, many raptor species have unfavorable conservation statuses (BirdLife International, 2004; IUCN, 2015). Electrocution has an impact on the populations of many raptor species in Europe (Real et al., 2001; López-López et al., 2011; Guil et al., 2015), America (Bevanger, 1994; Lehman et al.,

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2010; Harness and Wilson, 2001), Africa (Kruger et al., 2004; Boshoff et al., 2011; Angelov et al., 2013), Asia (Goroshko, 2011; Harness et al., 2013) and Oceania (Fox and Wynn, 2010). Nonetheless, the extent to which electrocution drives population dynamics has only been precisely calculated for a few species over small ranges (Schaub et al., 2010). This task requires, firstly, a calculation of how electrocution reduces survival corrected by the probability of encounter (e.g. capture–recapture) and, secondly, the implementation of realistic demographic models to assess whether or not electrocution is shaping population dynamics. Nevertheless, rare species in which both marking and resighting are complex represent a challenge when applying available quantitative methods and thus procedures that can tackle uncertainty in data sets must be developed (Doak et al., 2005).

The main aim of this paper is to provide a framework based on population modeling that will be useful both for estimating the demographic effects of electrocution and for furnishing conservation managers with information regarding the mitigation effort required to restore threatened populations, even when marked uncertainty regarding parameter estimates exists. To do so, we used, as a case study the north-east Iberian population of Bonelli's eagle (*Aquila fasciata*), an endangered species in Europe (2009/147/EC). First, we estimated survival by applying modern multievent capture–recapture methods whose flexibility allowed us to parameterize the underlying model of survival estimation and, for example, to use information on both live and dead reencounters of individual birds and to handle uncertainty when assigning states to individual birds (Pradel, 2005). Furthermore, we developed a new statistical method to estimate parameters such as the probability of electrocution that are not separately estimable from the models, which is the most common case when the detection of marked individuals killed by different causes is imperfect. Additionally, we employed detailed demographic models to analyze to what extent electrocution shapes population dynamics. Finally, we propose a procedure for handling uncertainty in estimates of electrocution probability, which will permit the quantification of the mitigation effort required to ensure that a population is self-sustainable, a reasonable conservation goal for populations at risk.

2. Materials and methods

2.1. Study species and target population

Bonelli's eagle is a territorial raptor that is patchily distributed from SE Asia through the Middle East to the western Mediterranean (del Hoyo et al., 1992). The European Bonelli's eagle population is estimated at 920–1100 pairs, most of which are found in the Iberian Peninsula (BirdLife International, 2004). This species has undergone a dramatic decline in recent decades and is now listed as endangered in Europe (2009/147/EC; BirdLife International, 2004). Previous analyses have highlighted high levels of adult and pre-adult mortalities (Real and Mañosa, 1997; Soutullo et al., 2008; Hernández-Matías et al., 2013), mainly caused by electrocution and direct persecution (Real et al., 2001).

Bonelli's Eagle populations are composed of two fractions – non-territorial and territorial birds – that have markedly different life styles. After post-fledging dependence but before recruitment, eagles pass through a transient nomadic phase in which they perform long-distance movements to dispersal areas and show no territorial behavior (Real and Mañosa, 2001; Cadahía et al., 2010). By contrast, territorial Bonelli's eagles (mostly three-year olds or older, Hernández-Matías et al., 2010) are sedentary and have strong site fidelity.

We studied a Bonelli's eagle population in Catalonia (NE Spain) in an area ranging from the French border in the northeast (3°10'26", 42°26'7") to south of the Ebro Delta in the southwest (0°28'42", 40°33'22"), characterized by habitats containing Mediterranean landscape features, an average annual rainfall of 425–664 mm, and nesting areas situated at 30–776 m asl. The study population had 85–90 pairs during the 1970s

but decreased in number until it stabilized at 63 pairs in 2000; nevertheless, in recent years, numbers have timidly increased up to 70 pairs (Real et al., 2004; DARPAMN, 2015). However, this increase is not a response to any improvement in main vital rates, which have actually worsened recently (see below), and seems, rather, to be the consequence of the net entry of immigrant eagles from neighboring populations (Hernández-Matías et al., 2013).

2.2. Long-term monitoring and ringing schemes

Constant and consistent monitoring of the population via repeated surveys during the breeding season (January–July) of a representative sample of territories (ca. 70%) was carried out in 1990–2014. We recorded occupation rates of territories, identity (if marked), the plumage-age and sex of territorial birds, and the number of fledged chicks. We used information from 2005 to 2014 to estimate breeding productivity and its environmental variance (Morris and Doak, 2002), as well as adult survival (S_{TORC} method in Hernández-Matías et al., 2011a). These vital rate estimations were used for population models (see below) and so, in order to provide more realistic predictions given current scenarios, we focused on this decade (2005–2014) because of the worsening of vital rates during this period in comparison with the previous decade.

Additionally, we gathered information on both marked and unmarked individuals that were found dead or injured (period 1990–2014). In most cases the cause of death or injury was established through necropsy or veterinary analysis conducted in animal recovery centers, or was assigned because of clear evidence (e.g. burns on birds found under a dangerous pylon). We used information from birds found in our study area, as well as from individuals from outside the area that we had ringed during the study period. For all the analyses, dead and injured individuals were pooled together and classified according to the cause of the accident and – if known – the eagle's territorial stage. A chi-squared test was used to compare the distribution of the causes of mortality in non-territorial and territorial birds. For this analysis, birds were classified as killed by electrocution, by persecution or by other causes. Additionally, we used Generalized Linear Models (GENLIN function of the program SPSS for Windows, Version 15.0, Chicago, SPSS Inc.) to analyze whether there was any temporal trend in the probability that a bird found dead was killed by electrocution during the study period. In this case, statistical observations corresponded to birds found dead, the dependent variable was whether the bird was killed by electrocution or by other causes, and the independent variable was time (years since 1990).

Since 2008 we have ringed annually a representative sample of chicks ($n = 251$). Once nestlings are 35–45-days old, with the aid of experienced climbers, we fit chicks with an alphanumerically coded colored metal ring that permits individual identification from a distance. Since 2010 we have gathered data from both non-territorial and territorial ringed birds (September–December), and long-term monitoring schemes carried out in neighboring populations have also provided information on marked individuals (France, Aragón and Castelló; see Acknowledgments section).

2.3. Implementation of multievent models

Multievent capture–recapture models (Pradel, 2005) were run to estimate survival and encounter probabilities of both live and dead/injured birds (resighted and retrieved eagles, respectively). Multievent models represent a generalization of multistate models (Lebreton and Pradel, 2002) in which the estimation of transitions between states explicitly accounts for uncertainty in state assignment and thus allow us to obtain unbiased estimates of these parameters. In our models, we used data for both resighted live individuals and retrieved individuals to obtain more precise survival estimates (Lebreton et al., 1999). The observations of individuals, whether territorial or otherwise, form the set of observable events used to estimate the proportion of individuals killed by electrocution (Tavecchia et al., 2012). We used a probabilistic

model that considered several alternative states (Fig. 1). The three main states, alive ('A'), killed by electrocution ('DE') or killed by other causes ('DO'), were split into two additional states each corresponding to non-territorial or territorial individuals ('ANT' and 'AT', 'DENTE' and 'DET', and 'DONT' and 'DOT', respectively) given that territorial behavior determines eagles' life styles and may affect survival and resighting probabilities (Hernández-Matías et al., 2011b). We also considered a non-observable state for dead individuals ('†') to account for the fact that 'recently' dead individuals (either 'DE' or 'DO') will not remain observable in the future (Lebreton et al., 1999).

The overall transition matrix, Φ , from state in t (rows) to state in $t + 1$ (columns) can be expressed as

$$\Phi = \begin{pmatrix} & \text{ANT} & \text{AT} & \text{DNTE} & \text{DNTO} & \text{DTE} & \text{DTO} & \dagger \\ \text{ANT} & S(1-\eta) & S\eta & (1-S)(1-\eta)\alpha & (1-S)(1-\eta)(1-\alpha) & (1-S)\eta\alpha & (1-S)\eta(1-\alpha) & 0 \\ \text{AT} & 0 & S & 0 & 0 & (1-S)\eta\alpha & (1-S)\eta(1-\alpha) & 0 \\ \text{DNTE} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \text{DNTO} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \text{DTE} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \text{DTO} & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ \dagger & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

where S corresponds to survival, η is the probability that a non-territorial individual in t becomes territorial in $t + 1$, and α is the probability that an eagle is electrocuted conditional on it being dead.

The matrix can be decomposed into three successive steps that describe the processes of recruitment, survival and cause of death. At any given occasion seven different events are observable (see Fig. 1 and Supplementary material). The first event, coded '0', indicates that the individual has not been observed. On the other hand, the following six events, coded 1–6, correspond to observations of the individual, which allow for its state – ANT, AT, DNTE, DNTO, DTE or DTO – to be unambiguously established. Between consecutive occasions, individuals may move between states as indicated by the transition matrix. To construct encounter histories, we used six-month intervals (February–July and August–January) (Hargrove and Borland, 1994; Hernández-Matías

et al., 2011b) and the estimated survival rates correspond to these six-month periods. In the Results section, we provide yearly survival rates estimated as the square of the six-month survivals, as well as the corresponding 95% confidence intervals estimated using the delta method (see Supplementary material).

We considered the following encounter probabilities: p the probability of encounter of a live non-territorial individual, c the probability of encounter of a live territorial individual, λ_1 the probability of encounter of an eagle killed by electrocution and, λ_2 the probability of encounter of an eagle killed by other causes. The model was built and fitted to the data using the software program E-SURGE (Choquet et al., 2009a). We used the goodness-of-fit test of the JMV model for resighted birds using U-CARE 2.2.2 (Pradel et al., 2003; Choquet et al., 2009b).

2.4. Modeling survival

Our first aim was to estimate survival according to the age and the territorial stage of individuals. Then, we fitted models that did not take into account the cause of death. The initial model considered that: η was dependent on age (4 classes: first-, second-, third- and fourth-year and older birds); S was dependent on age (4 classes) and the territorial stage; α was independent of both age and territorial state. The probability of encounter depended on whether the individual was alive and, if so, its territorial state (p and c for non-territorial and territorial eagles, respectively) or dead, in which case we assumed that the probability of encounter of individuals killed by different causes was the same ($\lambda_1 = \lambda_2$). Although we expected that λ_1 and λ_2 would not be equal, we assumed that they were equal in this section to simplify calculations (see next section) and because this assumption did not affect the survival estimation. We generated seven models, each with different structures for survival probability (see Table 1 and Supplementary material). Model selection was conducted using the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). We also estimated the Akaike weights (w_i) of each model as a measurement of the plausibility of the model.

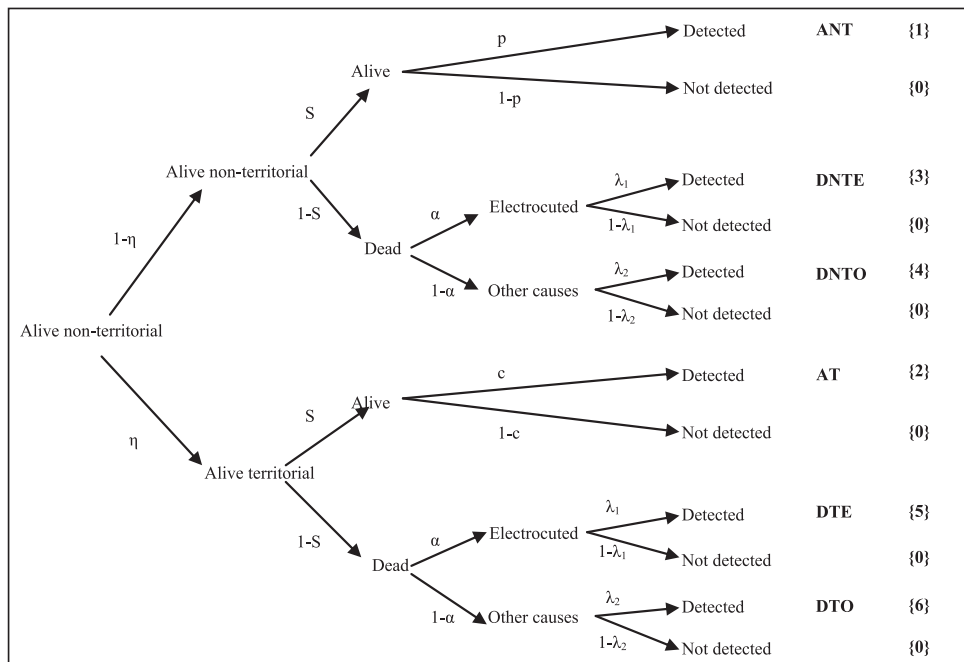


Fig. 1. Graphical representation of possible events and corresponding probabilities in encounter histories. The initial event (alive non-territorial) occurs in t , while events in the next step ($t + 1$) are described by the events in bold on the right-hand side of the figure. Names in bold correspond to the codes used to describe the states that an individual may reach: alive non-territorial (ANT), alive territorial (AT), dead non-territorial electrocuted (DNTE), dead non-territorial killed by other causes (DNTO), dead territorial electrocuted (DTE) and dead territorial killed by other causes (DTO). Numbers in brackets are the codes used for different events (possible events correspond to the states, as well as to the event 'not detected'). For example, 00000011300 would correspond to the encounter history of an individual tagged in spring 2011 (periods last for 6 months), detected alive and non-territorial in autumn 2011 and found dead by electrocution in spring 2012.

Table 1

Modeling survival (S) as a function of age and territorial stage. A maximum of four age classes were considered (first, second, third and fourth or more years of life). Two territorial states are considered: non-territorial (no terr) and territorial (terr), which account for the states VNT and VT, respectively shown in Fig. 1. The symbol “/” was used to define different age classes or territorial states affecting survival. For example, the model defined as “Age (1/2/3/4)” considers different survival parameters for birds in their first, second and third, or more years of life. The number of estimable parameters (K), AICc, the AICc increment and Akaike weights (w) are given.

Model	Survival dependent on	K	AICc	Delta AICc	w
Model 1	Age (1 2/3 4)	9	772.9	0	0.418
Model 2	Age (1/2/3 4)	10	774.7	1.17	0.233
Model 3	Age (1/2/3/4)	11	775.5	1.84	0.167
Model 4	Territorial state (no terr/terr)	9	776.5	3.04	0.091
Model 5	Age (1/2 3 4)	9	777.4	3.97	0.057
Model 6	Age (1/2 3/4)	10	778.8	5.28	0.030
Model 7	i	8	782.9	9.55	0.003

2.5. Modeling electrocution probability

Once the best model for estimating survival had been selected, we fitted a similar model in which λ_1 was not equal to λ_2 , thereby aiming to obtain a realistic estimate of α . Based on previous knowledge, we assumed that λ_1 and λ_2 did not differ between territorial and non-territorial birds, but that α could be different for territorial and non-territorial eagles (Real et al., 2001). However, the estimation of λ_1 and α cannot be derived straightforwardly from our capture-recapture approach since these parameters cannot be estimated separately (Schaub and Pradel, 2004). To obtain them, we first estimated the products $P_1 = \alpha_{nt} * \lambda_1$ and $P_2 = (1 - \alpha_{nt}) * \lambda_2$, which are directly estimable, and then combined them with independent monitoring information. Specifically, we assumed that $P'_1 = \alpha_t * \lambda_1 = N_{fe} / N_{td}$ and $P'_2 = (1 - \alpha_t) * \lambda_2 = N_{fo} / N_{td}$, where N_{fe} is the number of territorial individuals found and known to be killed by electrocution, N_{fo} the number of territorial individuals found and known to be killed by other causes, and N_{td} the total number of territorial individuals assumed to be dead, which in our case was the number of individuals known to be replaced in their territories in 1990–2014. These expressions gave $\lambda_1 = [(P_1 * P'_2) - (P'_1 * P_2)] / (P'_2 - P_2)$ and $\lambda_2 = [(P'_1 * P_2) - (P_1 * P'_2)] / (P'_1 - P_1)$. Once λ_1 and λ_2 were estimated, the estimation of α_{nt} and α_t was straightforward. Finally, 95% confidence intervals were estimated using variance estimates based on the delta method (see Supplementary material).

2.6. Quantifying the demographic consequences of the mitigation of electrocution

Survival after mitigation was estimated as $S_m = S_i^{1 - (\alpha * \varepsilon)}$, where S_m is survival after mitigation, S_i survival before mitigation, α the probability of electrocution and ε the mitigation effort required to increase values from 0 (no mitigation) to 1 (complete mitigation) (Supplementary material). Mortality caused by electrocution was thus assumed to be additive.

We implemented a Population Viability Analysis (PVA) to evaluate the effect of several levels of electrocution mitigation on population dynamics. The demographic model assumed that the population was structured in six age-classes and a post-breeding census. The main vital rates, i.e. survival, recruitment probability and fertility, were dependent on the age of individuals (Hernández-Matías et al., 2010, 2011b, 2013). We used survival and fertilities estimated here from multievent models and long-term monitoring. Our model was based on one of the models used by Hernández-Matías et al. (2013) that assumes closed local populations. Local populations in Western Europe are connected by dispersal (Hernández-Matías et al., 2013) and so our assumption that the population is closed was not realistic. Nevertheless, by assuming that our study population was isolated we

were able to simplify the interpretation of the results, since our focus was on estimating the electrocution mitigation effort required to achieve self-sustainability, a reasonable conservation goal in populations at risk. Our projections also considered the uncertainty caused by demographic (all vital rates) and environmental stochasticity (adult survival and fertility). Additionally, to account for uncertainty in α_{nt} and α_t , we ran simulations assuming the estimated 95% confidence interval range. Therefore, for each assumed value of α_{nt} and α_t , we estimated the probability of population self-sustainability as the proportion of simulated trajectories (out of 1000), which gave population growth rates that were greater than or equal to one.

3. Results

3.1. Long-term monitoring and records of dead individuals

A total of 150 Bonelli's eagles were found dead or injured in the period 1990–2014. The identified causes of death or injury were as follows: electrocution (61.2%), shot (17.2%), collision with power lines (5.2%), drowning in artificial water bodies (5.2%), natural causes (starvation, predation, etc.) (3.7%), collision with fences (2.2%) and collision with cars (0.7%); sixteen cases of death by unknown causes were not taken into consideration. Non-territorial birds were more often electrocuted than territorial birds (69.4% vs. 50.0%) and death by persecution was similar in territorial and non-territorial birds (18.1% vs. 21.2%) ($\chi^2 = 6.181$, $df = 2$, $p = 0.045$, $n = 124$). There was no temporal trend in the probability that a bird found dead was killed by electrocution during the study period (null model: $AIC_c = 86.3$; model with time effect: $AIC_c = 88.5$; coefficient of time effect = -0.006 , $SE = 0.022$, $p = 0.782$).

Based on the 1990–2014 monitoring of territorial eagles ($n = 2243$ individual-years of observations), 41 of the 219 eagles known to have been replaced on their territories were found dead. Of these, 13 individuals were found due to their radio-transmitters and were not considered in the analyses. The raw probability of encountering a dead territorial eagle was 0.135 if we assume that replaced individuals had died. Based on the 2005–2014 period, the survival of adult territorial eagles was estimated at 0.888 (95 CI = 0.863–0.910; temporal variance = 0.0003) by the S_{TORC} method ($n = 10$ years and 810 individual-years of observations) and productivity at 0.952 (95 CI = 0.784–1.120; temporal variance = 0.023; $n = 10$ years and 451 territory-years).

3.2. Ringing scheme and survival estimation using multievent models

In 2008–2014, we tagged 251 chicks from 43 territories. Of these, we subsequently re-contacted 71 individuals (28.3%) on 186 occasions: 31 were recruited as territorial birds (three were found dead) and 40 as non-territorial birds (31 found dead or injured). In all, 28 out of the 34 individuals found dead or injured were electrocuted.

The JMV model fitted the data adequately (GOF test: $\chi^2 = 13.41$; $df = 14$; $p = 0.495$). Survival increased with age, being lower during the first and second years of life (0.536; 95 CI = 0.442–0.627) and higher in two-year-old or older eagles (0.831; 95 CI = 0.702–0.911) (model 1 in Table 1). The model considering differences in survival during the first and second years of life (model 2) and the model also considering differences in survival during the third and fourth years of life (model 3) were partially supported by our results (see Table 1 and Supplementary material).

3.3. Estimates of mortality by electrocution

In the most plausible model in the previous section, the probability that a bird was electrocuted given that it was dead (α) was estimated at 0.823 (95 CI = 0.658–0.918) assuming that the probability of recovering a dead individual was independent of the cause of death ($\lambda_1 = \lambda_2 = 0.198$, 95 CI = 0.143–0.268). However, assuming that λ_1 and λ_2 differed and by combining the monitoring information,

we estimated that $\lambda_1 = 0.264$ (95 CI = 0.101–0.534) and $\lambda_2 = 0.091$ (95 CI = 0.044–0.181), which gives $\alpha_{nt} = 0.618$ (95 CI = 0.186–0.920) and $\alpha_t = 0.258$ (95 CI = 0.078–0.588).

3.4. Effect of electrocution mitigation on the population viability

Based on the estimated vital rates, demographic models indicate that the study population is not self-sustainable (self-sustainability probability of 0.07). For non-territorial eagles (Fig. 2a) and assuming $\alpha_{nt} = 0.62$, a mitigation effort of 13% will ensure self-sustainability probability values of 0.5, which correspond approximately to stability in population numbers. If we account for uncertainty, the scenario with the lowest values of α_{nt} (0.19) will need to mitigate 44% of electrocutions if it is to achieve self-sustainability, while in a scenario assuming $\alpha_{nt} = 0.92$, a 10% mitigation effort will raise the probability of self-sustainability to 0.60. For territorial eagles (Fig. 2b) and assuming

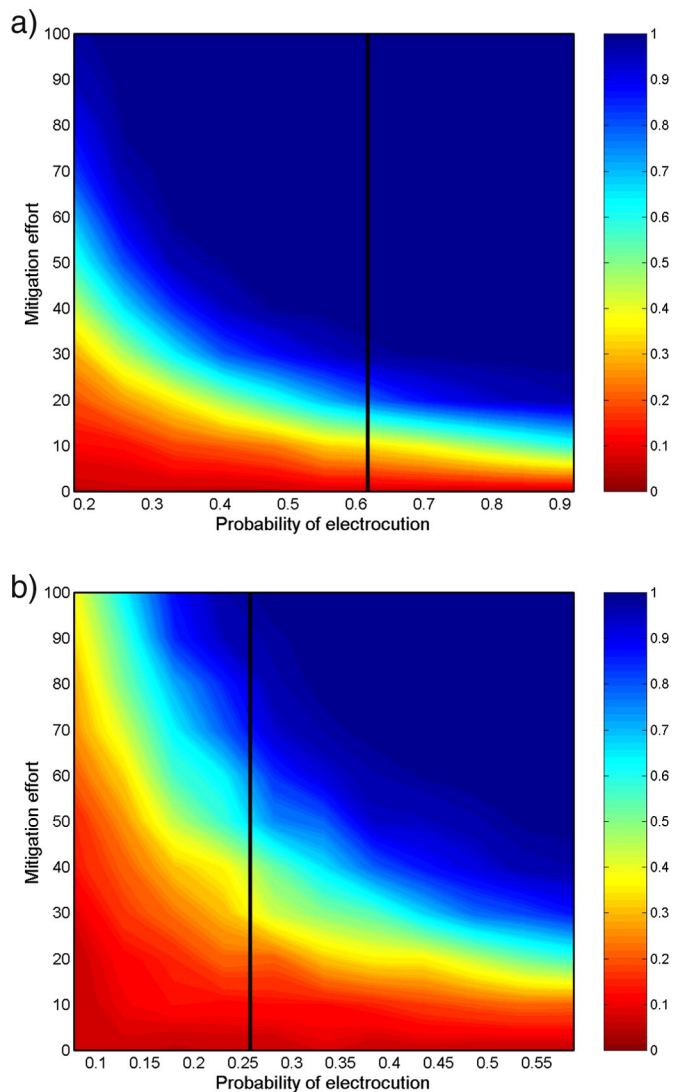


Fig. 2. Probability of population self-sustainability (graded color) in terms of the probability of electrocution (α) (x axis) and the mitigation effort of electrocution ($\epsilon \cdot 100$) (y axis) in both non-territorial (a) and territorial eagles (b). The probability of self-sustainability was calculated as the proportion of trajectories (out of 1000) that provide population growth rates of 1 or higher over a time horizon of 50 years on the basis of the current population size (see text for details). The mitigation effort is defined as the percentage of mortality caused by electrocution that will be eradicated. The probability of electrocution was estimated at 0.618 and 0.258 for non-territorial and territorial eagles, respectively (represented with a black line); the range of values represented corresponds to the 95% confidence intervals.

$\alpha_t = 0.26$, self-sustainability can be achieved by mitigating 40% of electrocutions. If we account for uncertainty, the scenario with the lowest values of α_t (0.08) will not ensure population growth even with a mitigation effort of 100% (self-sustainability probability = 0.38), while for the highest considered values ($\alpha_t = 0.59$) a mitigation effort of just over 17% will ensure population stability.

4. Discussion

Understanding how human-induced environmental changes are driving declines in endangered populations is mandatory if appropriate priorities are to be awarded to conservation actions. Electrocution is a worrying threat to birds, many of which are species of conservation concern. Nevertheless, despite the assumption that it is important, the overall effect of electrocution on population dynamics is still unknown for most species (Bevanger, 1994, 1998; Lehman et al., 2007; but see Schaub et al., 2010; López-López et al., 2011). Up-to-date multievent capture–recapture methods allow us to obtain robust estimates of the contribution of multiple sources of mortality – even in cases of imperfect detection (Schaub and Pradel, 2004; Tavecchia et al., 2012). Based on these methods, we provide here a framework for estimating the magnitude of mortality caused by electrocution when the identifiability of parameters is constrained. Likewise, we provide a method for assessing the mitigation effort required to ensure the viability of populations threatened by electrocution, even when uncertainty in parameter estimates – a common limitation in endangered species – is present.

In our approach, the fraction of individuals killed by a given cause and encountered depended on the probability of death by this cause and the probability of encounter. Consequently, if we assume that the probability of encounter differs for different causes of death, the probability of electrocution (α) was not separately estimable. Thus, to estimate α we used a combination of information from multievent models and basic monitoring (see Materials and methods section), data that can be gathered for many raptor species (Newton, 1979). We estimated that the probability of encounter of individuals killed by electrocution was over three times higher than that of individuals killed by other causes and that electrocution accounted for 62 and 26% of deaths in non-territorial and territorial Bonelli's eagles, respectively. Therefore, our results illustrate that the raw proportions of the causes of mortality derived from the number of individuals found dead may be biased.

Nevertheless, the uncertainty in our estimates of mortality by electrocution was high, a constraint that is common when studying endangered species, particularly when the long-term data-gathering required to refine parameter estimates is not feasible because conservation actions are urgently required. To tackle this constraint we developed a method based on population viability analysis that accounts for both uncertainties caused by demographic and environmental stochasticity and uncertainty in parameter estimates. Thus, our approach permits the calculation of the probability of self-sustainability in a population for any given amount of mitigation effort in the range of possible values of the mortality caused by electrocution. Importantly, our results reveal that even very low levels of electrocution may drive a local population to extinction.

Therefore, the message is clear: our study shows that mitigating electrocution will restore the conservation status of the study population, a scenario that may be applicable to many other species of conservation concern that are currently threatened by electrocution. Raw percentages of mortality caused by electrocution were estimated at 47.7% for Spanish imperial eagles in Spain (González et al., 2008), 47% for New Zealand falcons (*Falco novaeseelandiae*) in New Zealand (Fox and Wynn, 2010) and 25% and 12%, respectively, for golden (*Aquila chrysaetos*) and bald eagles (*Haliaeetus leucocephalus*) in the United States (Franson et al., 1995). Other species known to be severely affected by electrocution include Cape vulture *Gyps coprotheres* in South Africa (Boshoff et al., 2011), Egyptian vulture *Neophron percnopterus* in East Africa (Angelov et al., 2013) and Eagle owl *Bubo bubo* in Central Europe (Rubolini et al.,

2001), which suggest that electrocution may be an important cause of population decline in a wide variety of species distributed worldwide (Bevanger, 1998; Lehman et al., 2007).

In order to mitigate electrocution, however, knowledge of how to prioritize corrections is mandatory given that power lines are ubiquitous in modern landscapes. A first step is to decide whether to focus on the adult or non-adult fraction of the population, which in many territorial species use spatially separate areas. In Bonelli's eagle, while population growth rates are less sensitive to non-adult than to adult survival (Hernández-Matías et al., 2013), a crude interpretation of our results suggests that a focus on non-territorial birds (mostly non-adults) is preferable (Fig. 2). Nevertheless, we assumed that mortality by electrocution is additive, which may in fact not be true (Schaub and Pradel, 2004; Péron, 2013), particularly in non-territorial birds (Koons et al., 2014). The mechanisms by which compensatory mortality operates are complex, but in general they are closely linked to density dependence in vital rates. Non-territorial eagles use extensive areas with high prey abundances (Real and Mañosa, 2001) that are unstable over time, and exhibit important temporal variation in recruitment rates (Hernández-Matías et al., 2010), thereby indirectly suggesting that compensatory mortality may be operating. By contrast, territories are quite stable spatially, even if environmental changes occur over time, and adult individuals usually hold the same territory until they die (Hernández-Matías et al., 2011a). Accordingly, the temporal variance in adult survival was very low in 12 studied populations in Western Europe (Hernández-Matías et al., 2013). Additionally, populations that suffer the highest levels of human-induced mortality are also those that have the lowest survival rates (Hernández-Matías et al., 2013), thereby suggesting that human-induced mortality is additive in territorial eagles. In light of these considerations, we believe that the optimum strategy in Bonelli's eagle is to focus initially on mitigating the electrocution of territorial birds, although the most effective procedure may differ according to the demographic and biological characteristics of the target species.

A second step is to assess the required mitigation effort to restore a threatened species or population. We provide a useful method for estimating this effort that accounts for the uncertainty caused by the estimates of α and environmental and demographic stochasticity (Fig. 2). Uncertainty in estimates of α could be reduced by increasing the effort devoted to tracing marked individuals and by extending the duration of the study (a problem if conservation actions are urgent). In addition, λ_1 can be estimated using birds tagged with transmitters and monitored after transmitter decay, and then by applying suitable statistical methods (Tavecchia et al., 2012). The main constraint for applying this method is the cost of long-term radio-tagging programs for large numbers of birds, particularly given the relatively short lifespan of these devices in relation to lifespan of long-lived species.

Finally, a third step should be to identify the specific areas or electric pylons to be corrected in the target population range. Criteria exist that can define priorities such as the need to correct pylons in the areas most intensively used by eagles (Rollan et al., 2010) and/or to modify the most dangerous pylons (Tintó et al., 2010; Dwyer et al., 2014) but still need to be applied in a truly concerted and rigorous fashion. Additionally, continuous monitoring of vital rates such as survival should be conducted prior, during and after corrections in order to gauge their effectiveness and to reorientate mitigation tasks wherever necessary (Wilhere, 2002).

5. Conclusions

Our study highlights the fact that even low levels of electrocution may threaten the overall population viability of a long-lived species. We provide a framework based on population modeling that will be useful both for estimating the effect of electrocution on survival and for providing conservation managers with up-to-date information on the mitigation effort required to restore threatened populations, even when marked uncertainty is present. Overall, our study provides evidence of the importance of combining long-term monitoring and modern

quantitative methods when estimating key vital rates, identifying the main threats to a population and assessing the suitability and effectiveness of conservation actions.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.06.028>.

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