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Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle

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Summary

1. Mortality caused by power lines is a conservation problem for many vulnerable bird species. Many large species are especially threatened by electrocution as they frequently perch on pylons leading to electrocution that typically causes death. Electrocution mitigation measures have been implemented to protect several species; however, a resulting decrease in mortality due to these measures has not previously been demonstrated at the population scale.

2. In this study, we used data from a long-term capture–recapture programme (combining resightings of live birds and recovery of dead birds) carried out on the French population of the Bonelli's eagle *Aquila fasciata* from 1990 to 2009 to estimate the impact of the insulation of power lines on key demographic rates.

3. We found that the survival probability of all age classes increased after the insulation of dangerous power lines, due to a decrease in mortality caused by electrocution. This decrease was partially compensated for by an increase in other causes of death.

4. Our findings show that insulation of power lines has a strong positive impact on juveniles and immature birds and a lesser impact on adults. The overall increase in survival due to power line insulation led to a sharp increase in predicted population growth rates (from 0·82 to 0·98), although our findings still suggest that the population is not self-sustaining. Elasticity values indicate that adult survival is the key parameter in the population dynamics of this species, and since adult mortality caused by electrocution seemed close to zero, our ability to act on this parameter is limited.

5. This study demonstrates that insulation of power lines is relevant for the conservation of large bird species at a population scale as it allows the survival rate of all age classes to increase and thus in turn has a strong positive impact on population growth rates.

6. *Synthesis and applications*. We demonstrated that mortality rates induced by electrocution are considerable and have major consequences for the population viability of birds. We also demonstrated that electrocution mitigation measures can lead to a sharp increase in survival through reducing mortality from electrocution leading to improved population viability. In the light of these results, there is an urgent need that conservationists contact power line stakeholders not only to urge them to generalize retrofitting actions but also, in planning new infrastructure development, to plan for less harmful power lines, since this will be far less costly than developing *a posteriori* mitigation actions.

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Introduction

Understanding the impact of human-induced mortality on animals is a key topic in conservation biology. Mortality due to power lines has been argued to be a major cause of the short-term decline of a large number of endangered avian species on both local and broad spatial scales (Leshem 1985; Ferrer, De La Riva & Castroviejo 1991; Real & Manosa 1997), as well as the cause of death of many bird species around the world (Bevanger & Brøseth, 2004; Bevanger 1998; Lehman, Kennedy & Savidge 2007). It has also been demonstrated as a threat for some bat species (Tidemann & Nelson 2011). In developing countries, where biodiversity is usually highest (Myers *et al.* 2000), the power grid is growing rapidly, and power lines are often installed in areas where the impact on the environment is unknown and mitigation measures are not typically imposed by legislation (Bevanger 1998). Thus, developing an effective electrocution mitigation strategy based on scientific evidence is becoming increasingly critical on a global scale.

Large- or medium-sized birds such as raptors and the white stork *Ciconia ciconia* (Schaub & Pradel 2004) are particularly threatened by electrocution from power lines (Bevanger 1998). This is because their wings easily span the distance between energized and grounded components of power poles, leading to an electric shock that can cause irreversible injury or death. Furthermore, these birds frequently use pylons to perch, hunt and nest (Janss & Ferrer 1999; Lehman, Kennedy & Savidge 2007). Most of these birds are naturally long-lived, with small populations whose dynamics are especially sensitive to adult mortality due to unnatural causes (Real & Manosa 1997; Saether & Bakke 2000). Mitigation of electrocution risk has thus been proposed as key to promote the conservation of several threatened species (Sergio *et al.* 2004; Schaub *et al.* 2010; Boshoff *et al.* 2011). Although the effectiveness of mitigation measures has been demonstrated for retrofitted pylons, even at larger scales (see, e.g., Tinto, Real & Manosa 2010), to our knowledge only one study has demonstrated in a methodologically sound way a decrease in bird mortality resulting from mitigation programmes (see Lopez-Lopez *et al.* 2011). This lack of evidence is primarily due to the inherent difficulties of monitoring and estimating the main vital rates of large-sized bird species, which usually have small populations. In addition, it is important to base such investigations on long-term studies that intensively monitor marked birds so their fates can be known, allowing the estimation of electrocution mortality rates and the associated consequences on the population (Lehman, Kennedy & Savidge 2007). Despite these difficulties, evidence-based conservation strategies (Sutherland *et al.* 2004) require the unambiguous demonstration that insulation of power lines is effective and eventually leads to increased survival, in turn improving the population growth rates of species at risk. In this study, we took advantage of an intensive capture–recapture programme conducted since 1990 on the French population of Bonelli's eagle *Aquila fasciata* to investigate the impact of insulation of power lines on population viability.

We first estimated the key demographic parameters of this population before and after the electrocution mitigation measures by using multistate capture–recapture analyses, which allow mortality by different causes to be estimated separately (Schaub & Pradel 2004). Then, we investigated the impact of insulation of power lines on overall population viability by building matrix models.

Materials and methods

THE STUDIED SPECIES

Bonelli's eagle is a medium-sized raptor species distributed from south-east Asia through the Middle East to the western Mediterranean (Del Hoyo, Elliott & Sargatal 1992). Its population in Europe is estimated at 920–1100 pairs (Birdlife International 2004) and has suffered a rapid decline in numbers and range in recent decades (Real 2004). As a consequence, the Bonelli's eagle is listed in numerous conventions that aim to protect biodiversity and it is currently considered as 'Endangered' at the European scale (Carrete *et al.* 2002; Birdlife International 2004). Although several factors, including habitat loss, competition with the golden eagle *Aquila chrysaetos* and disturbance at breeding sites from leisure activities, have a negative effect on its population, the main cause of its decline is high mortality (Real & Manosa 1997; Hernández-Matías *et al.* 2013). This is mainly due to shooting or trapping and, especially, electrocution by power lines (Real & Manosa 1997; Real *et al.* 2001; Carrete *et al.* 2002). In France, the species has declined sharply, from about 80 pairs in 1960 to 23 pairs in 2002, the population's lowest level to date. Its range has contracted and is now highly fragmented (CEN-LR 2013). To stop the decline of the population, a national conservation plan was adopted in 1984, leading to the implementation of several conservation actions, including power line insulation in the species' dispersal and breeding areas (CEN-LR 2013).

The Bonelli's eagle life cycle is characteristic of long-lived species with a fecundity around one fledging chick per pair per year, and an adult survival above 0·85 (Hernandez-Matias *et al.* 2010, 2011). Once they leave the nest, fledglings remain in the parents' territory for around 90 days (Balbontin 2005). Then, they undertake long-distance movement to areas where they are vagrants (Lopez-Lopez *et al.* 2004; Cadahia *et al.* 2010). At the age of three or four (Hernandez-Matias *et al.* 2010), individuals recruit into a territory, where they show strong site and pair bond tenacity (Bosch *et al.* 2010).

MONITORING PROGRAMME

Our study is based on capture–recapture data (hereafter CR) collected from 1990 to 2009. During this period, almost all the chicks born in the French population were individually ringed in the nest before fledging (450 chicks ringed out of 478 known to have fledged, i.e. 94%). They were double-banded with a plastic Darvic ring, carrying a code that can be read using a telescope at a distance of up to 200 m, and a standard metal ring. The recapture data consist of (i) resightings across the entire zone occupied by the species in France, which is intensively monitored by various NGOs (LPO, Salsepareille, CEN-LR, CEN-PACA, etc.), and (ii) occasional recoveries of dead birds. In the majority of cases, when a dead bird was recovered, the cause of death was determined by a veterinarian. Electrocutions were determined by the location of the dead bird as well as by the presence of burn marks or necrosis typical of electrocution. In some cases, the cause of death could not be identified.

INSULATION OF POWER LINES

Measures to retrofit power lines in the framework of the conservation of Bonelli's eagle began around 1990 in southern France, but concerned <20 poles. More significant insulation efforts were implemented from 1997 onwards, when specific contracts were signed between NGOs and some of the local electricity providers. To guide the mitigation measures, NGOs began to map the power lines in the vicinity of breeding pairs as well as in the area known to be used for dispersal. Based on available maps, some of the local energy providers began to insulate the lines considered as dangerous. Quantitative or spatial data regarding insulation works were gathered *a posteriori* for the National Action Plan report, but it is not complete (CEN-LR 2013). The insulation work began in 1997, and between 1999 and 2004, 500 dangerous poles were insulated in the home range of 15 breeding Bonelli's eagle pairs (i.e. about 75% of the population's breeding pairs). During these years, many dangerous power lines were also insulated in the Camargue delta, an important area for vagrants (mostly immature) in France. In addition, between 2005 and 2009 (the last year we considered in our analysis), fewer than 100 poles were insulated (CEN-LR 2013). From this information, we can conclude that most of the retrofitting measures were carried out between 1997 and 2004 and that they concerned a large proportion of both breeding and vagrant areas for this species.

STATISTICAL ANALYSES

Survival probability estimation

Survival probabilities were estimated based on the CR data using a 'special case' of the multistate approach (Arnason 1973; Schwarz, Schweigert & Arnason 1993) that combines data from the resightings of live birds and the recoveries of dead birds (Lebreton & Pradel 2002). This modelling approach has been shown to improve the accuracy of survival probability estimates (Kendall, Conn & Hines 2006). Recent developments in these models also enable the simultaneous modelling of survival and mortality probabilities associated with different causes, as well as the probability of tag loss (Schaub & Pradel 2004; Tavecchia *et al.* 2012).

By combining all the available data, an individual observed in a given year was assigned to one of the seven mutually exclusive states: (1) alive with a Darvic ring (state A+) or (2) without a Darvic ring (state A–); (3) dead by electrocution with a Darvic ring (state DE+) or (4) without a Darvic ring (state DE−); (5) dead by another cause with a Darvic ring (DO+) or (6) without a Darvic ring (DO−); and (7) 'long dead' (noted LD). The latter defines an unobservable and absorbing state corresponding to a bird previously recovered, in contrast to the observable states corresponding to recovery of a corpse (Lebreton, Almeras & Pradel 1999). This differentiation allowed us to estimate the reporting rate of dead animals and the probability of dying from different causes (Schaub & Pradel 2004). In any given year, a resighted individual might move from one state to another as recorded in a 7 × 7 transition matrix (see Table S1, Supporting Information). For instance, the transition from state A+ at time t to state A+ at time $t + 1$ represents the probability that the individual has not lost its Darvic ring and has survived from 1 year to the next. The transition from state A+ at time t to state DE+ at time $t + 1$ represents the probability that the individual has not lost its Darvic ring, but died by electrocution during the time interval. The probability of resighting may be influenced by the state of the individual (for instance, with or without a Darvic ring). Moreover, dead individuals are not systematically detected and different mortality causes can lead to different recovery rates. These probabilities are denoted as p for resightings of rings and r for report of recoveries.

We built several models with two different age-class structures for survival probability. One included four age classes (first year, second year, third year and survival after 3 years old), and the other also included four age classes (but with the second and third year having the same survival [following the best model from Hernandez-Matias *et al.* 2011]). Before the age of 3–4, when Bonelli's eagles recruit, individuals are usually vagrants. Consequently, individual detection probability could vary with age, so our models included two types of age-class structure for resighting probability. One included four age classes (first year, second year, third year, and the resighting of individuals 4 years old and older), the other included three age classes (first year, second year, and the resighting of individuals 3 years old and older). The resighting probabilities were considered different for birds with or without their Darvic ring. Regarding the tag loss, we tested whether they were constant or change with age by testing a constant, two or three age classes on this parameter.

To test the effect of power line insulation measures on survival probability, we divided the study period into two subperiods: 'before' (1990–1997) and 'after' (1998–2009) insulations of power lines and poles (mainly carried out since 1997). These two periods were used as a time constraint on transition probabilities within the same modelling framework.

In total, we fitted 48 different models that included all the combinations of the different effects on survival, detection probabilities and tag loss (see Table S2).

The software E-SURGE (Choquet, Rouan & Pradel 2009b) was used to obtain maximum likelihood estimates of parameters. Model selection was performed using QAICc, that is the AIC corrected for small sample size and potential over-dispersion (Burnham & Anderson 2002). No goodness-of-fit tests are available for models that include absorbing states (i.e. states corresponding to all dead individuals, D and LD), so we used the Cormack–Jolly–Seber (CJS) goodness-of-fit test on resighted birds only (ringed chicks were removed since they may generate artificial transience due to their low survival) using U-CARE 2.2.2 (Pradel, Gimenez & Lebreton 2005; Choquet *et al.* 2009a).

Fecundity estimation

The mean number of fledglings produced yearly by a breeding pair of Bonelli's eagles was modelled using a generalized linear mixed model (GLMM) assuming a Poisson distribution and using the breeding site and the year as random effects. We tested both whether fecundity showed a trend over time (year as a linear effect) and whether the period (before and after insulation of power lines) showed an effect on fecundity. Model comparison was performed using AIC values (Burnham & Anderson 2002).

Matrix projection

Estimated demographic parameters were integrated in a determinist population matrix model with three age classes, considering a pre-breeding census of females only. The age-class structure follows the structure we used in the CR modelling. The age classes of the matrix model were 'immature', 'subadult' and 'adult'. 'Immature' refers to 1-year-old individuals that survived from 1 year to the next with a probability noted as S_1 (second age class in CR modelling), becoming 'subadults' that themselves survived from 1 year to the next with a probability noted as S_2 (third age class in CR modelling) and then becoming 'adults' that survived with a probability noted as S_3 (fourth age class in CR modelling). Following Hernandez-Matias *et al.* (2010), the proportion of breeders was set at 0·16, 0·68 and 1·0 for immature (b1), subadult (b2) and adult (b3) birds, respectively, and the fecundity was assumed to be 0·45 for immature and subadult birds (f1). The fecundity for adults was the one we estimated in our fecundity analysis (see results). Fledging chicks survived with a rate S_0 to reach 'immature stage' (first age class in CR modelling). We considered the sex ratio to be at equilibrium. This cycle can be summarized as a transition matrix (Caswell 2001), which is shown in Table S3.

The matrix was used to calculate the asymptotic growth rate of the population (λ) with parameters estimated before and after power line insulation. The analysis of the matrix also provided the elasticity values of matrix components that quantify the contributions of each parameter of the life cycle to the population growth rate (Caswell 2001). All matrix population manipulations were conducted using ULM software (Legendre & Clobert 1995).

Results

The data set included 446 ringed birds, 585 resightings (of 116 different individuals) and 40 recoveries of dead birds over the study period (1990–2009). Among the recoveries, 23 deaths were attributed to electrocution and 17 to other causes.

SURVIVAL AND MORTALITY ESTIMATION

The CJS model fitted the data adequately (GOF test: $\chi^2_{53} = 32{\cdot}59$, $P = 0{\cdot}988$).

The 10 best models are shown in Table 1 (all fitted models are shown in Table S2). The best model has a QAICc of 1·99 points lower than the second best model. It also has a three-fold higher QAICc weight than the second best model. We can therefore conclude that this model is strongly supported by the data than all others tested. This model includes four age classes for survival probability, with classes 2 and 3 forced to equality, three age classes for resighting probability and a constant recovery probability between age classes. The model also includes a difference in survival probability for all age classes before and after power line insulation. Note that the five best models (deltaQAICc<4) included very close structures of survival and mortality rates (see

Table 1. The 10 best models and their respective QAICc obtained by the analysis of capture–recapture data on the French population of the Bonelli's eagle (c-hat = 1); 'np' is the number of parameters. In the 'Tag loss' column, the row 'Age classes' means that this parameter was estimated for two or three age classes or with all individuals together without age distinction. In the 'Survival' column, the row 'Age 2 = age 3' means that these two age class parameters were forced to be equal. A 'yes' in the column 'Recoveries' means that the recovery probabilities for birds killed by electrocution (E) and dead from another cause (O) were forced to be equal. All these models include the period effect on survival probability (i.e. before and after 1997)

						Transition			Event	
							Survival			
Rank	np	Deviance	QAICc	ΔQAICc	QAICc weight	Tag loss Age classes	Age 2 = age 3	Time effect	Age classes	Recoveries E = O
1	19	1374·06	1412·06		0·39	–	Yes	Two period	3	Yes
2	20	1374·05	1414·05	1·99	0·14	2	Yes	Two period	3	Yes
3	23	1369·31	1415·31	3·25	0·08	–	No	Two period	3	Yes
4	21	1373·40	1415·40	3·35	0·07	3	Yes	Two period	3	Yes
5	21	1373·43	1415·43	3·37	0·07	–	Yes	Two period	4	Yes
6	21	1373·93	1415·93	3·87	0·06	–	Yes	Two period	3	No
7	24	1369·30	1417·30	5·24	0·03	2	No	Two period	3	Yes
8	22	1373·39	1417·39	5·33	0·03	2	Yes	Two period	4	Yes
9	22	1373·92	1417·92	5·86	0·02	2	Yes	Two period	3	No
10	23	1372·31	1418·31	6·25	0·02	3	Yes	Two period	4	Yes

Table S4) and that the insulation effect has a QAICc weight of 1.

Resighting probability increased with age (Table 2), ranging from 0·19 for the youngest individuals to 0·57 for adult individuals still with their Darvic ring. The rate of tag loss was high, since individuals had a 12% probability of losing their Darvic ring every year (Table 2). The resighting of individuals that have lost their Darvic ring is, however, high (see Table 2), and this allows precise and unbiased estimates of survival probabilities despite high probability of tag loss. The recovery rate is estimated at around 0·11 for all birds; there is no difference between individuals that died from electrocution or other causes (Table 2).

The estimates of survival and mortality probabilities of the five best models are extremely similar (see Table S4). A detailed examination of survival probability estimated in the best model reveals a significant increase in survival after 1997 for all age classes (Fig. 1a). The largest increase was observed for the youngest age class and the smallest increase for adults. The probability of dying from electrocution decreased after 1997 for all age classes (Fig. 1b). The largest decrease was for juveniles (from 0·56 before power line insulation to 0·14 after). After 1997, no adults were found electrocuted. Note that even though overall survival increased with the decline in death from electrocution after 1997 for all age classes, the rate of death from other causes increased for non-adults and remained equal for adults (Fig. 1c).

Table 2. Estimates of the probabilities of survival, mortality, resighting and recovery provided by the best multistate model fitted on the capture–recapture data of the French population of the Bonelli's eagle

Parameters	Cause of death	Age class	Estimates	95% CI	SE
Tag loss		All	0·12	0·07; 0·18	0·03
Survival before power line insulation 1990–1997		1	0·30	0·19; 0·44	0·07
		2	0·49	0·31; 0·67	0·10
		3	0·49	0·31; 0·67	0·10
		4	0·77	0·42; 0·94	0·14
Survival after power line insulation 1998–2009		1	0·53	0·39; 0·66	0·07
		2	0·62	0·51; 0·72	0·06
		3	0·62	0·51; 0·72	0·06
		4	0·88	0·80; 0·93	0·03
Mortality before power line insulation 1990–1997	Electrocution	1	0·56	0·39; 0·72	0·09
		2	0·51	0·33; 0·69	0·10
		3	0·51	0·33; 0·69	0·10
		4	0·12	0·03; 0·32	0·08
	Other causes	1	0·14	0·05; 0·35	0·07
		2	0·00	–	0·00
		3	0·00	–	0·00
		4	0·11	0·04;0·28	0·06
Mortality after power line insulation 1998–2009	Electrocution	1	0·13	0·05; 0·30	0·06
		2	0·27	0·15; 0·44	0·08
		3	0·27	0·15; 0·44	0·08
		4	0·00	–	0·00
	Other causes	1	0·34	0·21; 0·50	0·08
		2	0·11	0·03; 0·32	0·07
		3	0·11	0·03; 0·32	0·07
		4	0·12	0·07; 0·20	0·03
Resighting probability		1	0·19	0·12; 0·27	0·04
		2	0·19	0·12; 0·31	0·05
		3	0·57	0·41; 0·71	0·08
Recovery probability		1	0·11	0·08; 0·14	0·02

FECUNDITY

The average fecundity estimated in this study was 0·91 fledglings per breeding pair per year. The analysis showed that there was no trend over time ($z = -0{\cdot}016$, d.f. = 1, $P = 0{\cdot}99$, AIC = 1260·7), nor differences before and after power line insulation ($z = -0{\cdot}89$, d.f. = 1, $P = 0{\cdot}37$, AIC = 1259·9) (see Tables S5 and S6 for model selection and the estimates of the constant model). Yearly estimates of fecundity are shown in Fig. S1.

MATRIX PROJECTION

The annual population growth rate sharply increased after power line insulation, from 0·82 to 0·98 (Table 3). This increase in growth rate translates into a significant delay in the time to extinction of the population (before power line insulation: 20 years to reach only one remaining individual; after insulation: 170 years). The elasticity values for the fecundity and survival probability of classes of young birds do not exceed 0·10, while that of adult survival is around 0·80 (Table 3), indicating that the key demographic parameter of the viability of this population is adult survival. Additionally, the ratio between the elasticity of adult survival and other demographic parameters decreases from 16 to 9 (before and after insulation), indicating a greater impact of the survival of juvenile and immature birds on population dynamics after mitigation measures against electrocution, although adult survival clearly remains the most important parameter for population dynamics. To stabilize the population, adult survival would have to increase by about 3% (to reach 0·91). In contrast, the survival rate of immature birds would have to increase by about 14% (to reach 0·71).

Discussion

Despite years of power line insulation around the world, studies that robustly analyse the real impact of these measures on population viability are extremely rare (Lehman, Kennedy & Savidge 2007). This study unambiguously demonstrates that electrocution mitigation measures led to an increase in survival by reducing mortality from electrocution, which in turn resulted in an increase in the population growth rate. The study found that electrocution was the main cause of mortality in the studied population and that mortality rates from electrocution were extremely high. Before mitigation measures, 56% of juveniles, 51% of immature individuals and 13% of adults

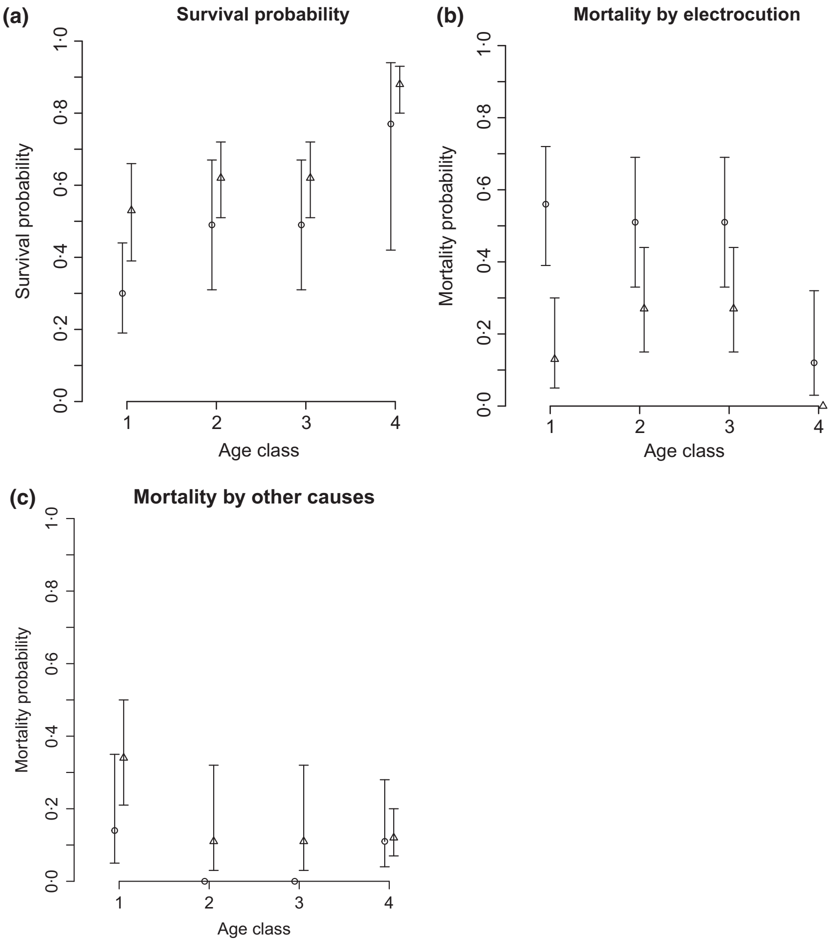

Fig. 1. Estimates (with 95% confidence interval) of survival probability (a); mortality probability by electrocution (b); and mortality probability by another cause (c), according to age class and period (circle: before power line insulation 1990–1997; triangle: after power line insulation 1998–2009) for the French population of Bonelli's eagle.

Table 3. Parameters provided by the analysis of Leslie matrix using the demographic parameters of the French population of Bonelli's eagle before (1990–1997) and after (1998–2009) power line insulation in their territories: population growth rate, time to extinction and elasticity of the demographic parameters

	Before insulation	After insulation
Growth rate	0·82	0·98
Time before extinction	20 years	170 years
Immature fecundity	<0·001	0·002
Subadult fecundity	0·002	0·005
Adult fecundity	0·055	0·086
Immature survival	0·057	0·091
Subadult survival	0·055	0·086
Adult survival	0·830	0·731

died annually from electrocution that can be compared to the full mortalities that are 0·70, 0·51 and 0·23, respectively. Such high mortality levels are not limited to the Bonelli's eagle. Schaub & Pradel (2004) have estimated the power line mortality rate in adult white storks as 0·06 (95% CI = 0·03–0·10) and in juveniles as 0·25 (95% CI = 0·14–0·36). In their study, Gonzalez *et al.* (2007) shown that 47·7% of recovered Spanish imperial eagles died by electrocution. For the eagle owl, Schaub *et al.* (2010) have estimated this rate as 24%, and Tidemann & Nelson (2011) have estimated it as 18·6% for the grey-headed flying fox. In all these cases, such high mortality rates have a serious consequence on population viability as the population growth rate of these large-sized species is especially sensitive to survival (Lebreton *et al.* 2012). Because mortality rates caused by electrocution are extremely difficult to estimate, they are rarely documented in the literature; however, these results are probably more the rule than the exception for large birds.

We found that following mitigation measures, the survival rate of Bonelli's eagles in their first year increased from 0·30 (SE = 0·07) to 0·53 (SE = 0·07), in their second and third year from 0·49 (SE = 0·1) to 0·62 (SE = 0·06) and in adults from 0·77 (SE = 0·14) to 0·88 (SE = 0·03). Our analysis of the causes of mortality confirmed that the observed increase in survival was due to a sharp decrease in mortality from electrocution (from 56% to 14% in juveniles, from 52% to 27% in immature individuals and from 13% to 0% in adults). The insulation of power lines, which was predicted to have a positive impact mainly on vagrant juveniles and immature birds (Balbontin 2005; Cadahia, Urios & Negro 2007), also had a positive effect on adult survival. This can be explained by the fact that mitigation measures were carried out not only in areas where vagrants disperse, but also in the home range of breeding pairs (CEN-LR 2013). This result is of high importance as it proves the relevance of investment in such programmes and their effectiveness as a conservation method.

However, our results also indicated that while mortality by electrocution decreased, mortality from other causes increased in non-adult birds. This may be due to a compensatory process, often demonstrated in hunting studies (Sedinger *et al.* 2010); that is, death by electrocution may 'compete' with other causes of mortality. For example, the number of recovered young birds killed in collisions with cars seems to have increased in recent years (one case before 2000, but four cases between 2000 and 2009). This finding seems relatively anecdotal, but it may suggest that some young birds that avoided electrocution due to power line insulation may have then been the victims of another cause of death (car collision, starvation, etc.). Although we cannot completely exclude that this finding is not the result of increased pressure from other causes of mortality, we believe this is the first study to show such compensation in the context of power lines since its demographic importance has been pointed out (Lehman, Kennedy & Savidge 2007). This phenomenon may mean that a decrease in mortality from electrocution may not fully translate into the ultimate survival of non-adult birds.

Fecundity, estimated at 0·91 fledglings per couple per year, did not exhibit any temporal trend over the studied period. Power line insulation did not seem to have a direct impact on eagle fecundity. This result is not surprising as electrocution mainly affects immature individuals. However, fecundity is related to a bird's age and is lower when new birds recruit in a pair (Martínez *et al.* 2008; Hernández-Matías, Real & Pradel 2011), so an increase in adult survival should induce fewer turnovers and then lead to a slight increase in mean fecundity at the population level. It may be that our data set was too small, and fecundity too variable annually, to allow the detection of such an effect. Our fecundity estimate is consistent with other estimates from Western Europe populations (Hernández-Matías *et al.* 2013). Thus, the French population does not seem to suffer a major problem in terms of fecundity.

In the first 3 years after electrocution mitigation measures, the survival estimates remain lower than those reported in a healthy population in southern Spain, whose survival rates are estimated at 0·69 (SE = 0·11) in an individual's first year and 0·72 (SE = 0·14) in its second year (Balbontin, Penteriani & Ferrer 2003). Furthermore, in the French population, the adult survival rate after mitigation, 0·88 (SE = 0·03), is one of the lowest known for all Western European populations (which range between 0·87 and 0·94, mean = 0·904, SE = 0·006, n = 12 populations; Hernández-Matías *et al.* 2013). It is also slightly lower than that of other long-lived birds of prey of similar size, such as the Spanish imperial eagle *Aquila adalberti* (0·92–0·99) (Ortega *et al.* 2009), the osprey *Pandion haliaetus* (0·87–0·97) (Wahl, Rolf & Barbraud 2005) and the red kite *Milvus milvus* (0·95) (Newton, Davis & Davis 1989). These results indicate that the survival rate of adult Bonelli's eagles in France is still comparatively low. As no electrocutions of adults were reported after 1998, other causes may be responsible for this. Several cases of shooting have been reported in recent years: the number of recovered shot individuals seems low in the raw data set (five immature birds between 2000 and 2009), but the recovery level is low (about 10%), so the true number of shot individuals may be up to 10 times the reported figure. The premature death of one adult immediately lowers survival probability by two points (since the number of pairs is about 25).

Our deterministic matrix models confirmed that electrocution mitigation measures can have a marked effect on overall population dynamics and as such can significantly improve the conservation status of endangered species. The estimated population growth rate was very low before the insulation of power lines (0·82), predicting a rapid extinction of the population (in around 20 years). Yet the increase in survival after retrofitting measures resulted in an estimated growth rate (0·98) that is about 20% higher than before, which would allow the survival of the population for almost 170 years (however, still currently not self-sustaining). Until 2002, the number of breeding pairs progressively declined to 23 pairs. Following work to insulate power lines, particularly from 1999 to 2004, the population decline slowed and then stopped, driven by reduced electrocution. In recent years, the population has increased to reach about 33 breeding pairs. Yet this observed increase does not match the predictions of our matrix model, which indicates further decline. This discrepancy could arise from random variation in the number of pairs caused by stochastic events or, more likely, from the arrival of immigrants from the Iberian Peninsula (Hernández-Matías *et al.* 2013). The apparent health of the population today may in fact be a result of immigration, as the local demographic parameters seem too low to allow population viability.

Our elasticity analyses confirm that the population dynamics of the Bonelli's eagle, as for most large species, are mainly influenced by adult survival (Saether 1989), which suggests that conservation efforts should aim at reinforcing this. Yet no adults have been reported as electrocuted since 1998, so further insulations are unlikely to lead to improvement in adult survival. Moreover, Chevallier *et al.* (2013) have demonstrated that there is little difference between survival rates in different territories, making it difficult to focus mitigation measures on specific breeding territories. Despite these considerations, our results demonstrate that a 14% increase in the survival rate of juvenile and immature birds can have a strong impact on population dynamics and therefore on the conservation of this endangered species. All young individuals in this population pass through a nomadic phase during which they aggregate in a few dispersal or vagrant areas (e.g. Cadahia *et al.* 2010). Insulating power lines in these dispersal areas may have a strong positive impact on the survival of these individuals and, as a result, on the whole population. These mitigation measures could be even more effective if carried out according to criteria that identified the most dangerous pylons (e.g. Tinto, Real & Manosa 2010). Even if the cost of mitigation actions is high, it will be far less expensive than habitat quality management for instance. For the Bonelli's eagle, the habitat management would involve mitigation for the loss of habitat through pasturage return.

To conclude, we demonstrate that mortality rates induced by electrocution are considerable and have major consequences on population viability of birds. This may hold true for other species suffering high mortality from power lines, such as large birds of prey or Ciconiiformes, Gruiformes and Pelecaniformes (Bevanger 1998), as the population growth rate of these species is highly sensitive to adult survival. We also demonstrated that electrocution mitigation measures can lead to a sharp increase in survival through reducing mortality from electrocution that eventually leads to improved population viability. In the light of these results, there is an urgent need that conservationists contact power line stakeholders to urge them to generalize retrofitting actions in areas where large-sized (and, especially, endangered) species are at risk but also to plan the set-up of harmful power lines in case of new infrastructure development since it will be far less costly than developing *a posteriori* mitigation actions.

Lastly, our study highlights the relevance of combining resightings and recoveries information to assess the impact of electrocution and the efficiency of mitigation actions. The multistate CR data modelling approach we adopted avoids many of the problems of standard electrocution-impact studies, such as inefficient sampling design, non-estimation of the detection probability of dead animals and even non-estimation of mortality probability (Lehman, Kennedy & Savidge 2007). We are aware that this method is limited to species for which large-scale CR monitoring is feasible. This may hold mostly for large and (relatively) easily tracked species that could really benefit from maximizing adult survival. We then recommend to develop CR monitoring programmes on a large panel of birds subjected to electrocution. Such programmes should also encourage the public to report dead individuals and to systematically identify the causes of death.

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Data accessibility

Chevallier C. Data from 'Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle'

- Fecundity data set:http://dx.doi.org/10.6084/m9.figshare.1431364 (Chevallier *et al.* 2015a).
- Capture–Mark–Recapture data set: http://dx.doi.org/10.6084/m9.figshare.1431363 (Chevallier *et al.* 2015b).

References

Arnason, A.N. (1973) The estimation of population size, migration rates, and survival in a stratified population. *Researches on Population Ecology*, **15**, 1–8.

Balbontin, J. (2005) Identifying suitable habitat for dispersal in Bonelli's eagle: an important issue in halting its decline in Europe. *Biological Conservation*, **126**, 74–83.

Balbontin, J., Penteriani, V. & Ferrer, M. (2003) Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's eagle in Andalusia. *Biological Conservation*, **109**, 417–423.

Bevanger, K. (1998) Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biological Conservation*, **86**, 67–76.

Bevanger, K. & Brøseth, H. (2004) Impact of power lines on bird mortality in a subalpine area. *Animal Biodiversity and Conservation*, **27**, 67–77.

Birdlife International (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge, UK.

Bosch, R., Real, J., Tinto, A., Zozaya, E.L. & Castell, C. (2010) Home-ranges and patterns of spatial use in territorial Bonelli's eagles *Aquila fasciata*. *Ibis*, **152**, 105–117.

Boshoff, A.F., Minnie, J.C., Tambling, C.J. & Michael, M.D. (2011) The impact of power line-related mortality on the Cape Vulture Gyps coprotheres in a part of its range, with an emphasis on electrocution. *Bird Conservation International*, **21**, 311–327.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference*, 2nd edn. Springer-Verlag, New York, NY.

Cadahia, L., Urios, V. & Negro, J.J. (2007) Bonelli's eagle *Hieraaetus fasciatus* juvenile dispersal: hourly and daily movements tracked by GPS. *Bird Study*, **54**, 271–274.

Cadahia, L., Lopez-Lopez, P., Urios, V. & Negro, J.J. (2010) Satellite telemetry reveals individual variation in juvenile Bonelli's eagle dispersal areas. *European Journal of Wildlife Research*, **56**, 923–990.

Carrete, M., Sanchez-Zapata, J.A., Martinez, J.E., Sanchez, M.A. & Calvo, J.F. (2002) Factors influencing the decline of Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: demography, habitat or competition? *Biodiversity and Conservation*, **11**, 975–985.

Caswell, H., ed. (2001) *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates Inc., Sunderland, MA.

CEN-LR (2013) *Plan National d'action en faveur de l'Aigle de Bonelli Aquila fasciata* (2013–2014), pp. 172. Ministère de l'environnement et du développement durable, Paris. http://www.languedoc-roussillon.developpement-durable.gouv.fr/IMG/pdf/pna_bonelli_vf_172p_bd_cle716819.pdf.

Chevallier, C., Crochet, P.-A., Vincent-Martin, N., Ravayrol, A. & Besnard, A. (2013) Use of mixture models to characterize site quality in philopatric animals: a case study with Bonelli's eagle. *Animal Conservation*, **16**, 198–206.

Chevallier, C., Hernández-Matías, A., Real, J., Vincent-Martin, N., Ravayrol, A. & Besnard, A. (2015a) Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle. figshare. http://dx.doi.org/10.6084/m9.figshare.1431364.

Chevallier, C., Hernández-Matías, A., Real, J., Vincent-Martin, N., Ravayrol, A. & Besnard, A. (2015b) Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle. figshare. http://dx.doi.org/10.6084/m9.figshare.1431363.

Choquet, R., Rouan, L. & Pradel, R. (2009b) Program E-Surge: a software application for fitting multievent models. *Environmental and Ecological Statistics*, **3**, 845–865.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M. & Pradel, R. (2009a) U-CARE: utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography*, **32**, 1071–1074.

Del Hoyo, J., Elliott, A. & Sargatal, J. (1992) *Handbook of the Birds of the World*. Lynx Edicions, Barcelona, Spain.

Ferrer, M., De La Riva, M. & Castroviejo, J. (1991) Electrocution of raptors on power lines on southwestern Spain. *Journal of Field Ornithology*, **62**, 181–190.

González, L.M., Margalida, A., Mañosa, S., Sánchez, R., Oria, J., Molina, J.I., Caldera, J., Aranda, A. & Prada, L. (2007) Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish imperial eagle *Aquila adalberti* during a recovery period. *Oryx*, **41**, 495–502.

Hernandez-Matias, A., Real, J., Pradel, R., Ravayrol, A., Vincent-Martin, N., Bosca, F. & Cheylan, G. (2010) Determinants of territorial recruitment in Bonelli's eagle (*Aquila fasciata*) populations. *The Auk*, **127**, 173–184.

Hernández-Matías, A., Real, J. & Pradel, R. (2011) Quick methods for evaluating survival of age-characterizable long-lived territorial birds. *The Journal of Wildlife Management*, **75**, 856–866.

Hernandez-Matias, A., Real, J., Pradel, R., Ravayrol, A. & Vincent-Martin, N. (2011) Effects of age, territoriality and breeding on survival of Bonelli's eagle *Aquila fasciata*. *Ibis*, **153**, 846–857.

Hernández-Matías, A., Real, J., Moleón, M., Palma, L., Sánchez-Zapata, J.A., Pradel, R. *et al.* (2013) From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in Western Europe. *Ecological Monographs*, **83**, 239–261.

Janss, G.F.E. & Ferrer, M. (eds.) (1999) *Avian Electrocution on Power Poles: European Experiences*. Birds and Power Lines, Quercus, Madrid, Spain.

Kendall, W.L., Conn, P.B. & Hines, J.E. (2006) Combining multi-strata capture–recapture data with tag recoveries to estimate demographic parameters. *Ecology*, **87**, 169–177.

Lebreton, J.-D., Almeras, T. & Pradel, R. (1999) Competing events, mixtures of information and multistrata recapture models. *Bird Study*, **46**, 39–46.

Lebreton, J.-D. & Pradel, R. (2002) Multistate recapture models: modelling incomplete individuals histories. *Journal of Applied Statistics*, **29**, 353–369.

Lebreton, J.-D., Devillard, S., Popy, S., Desprez, M., Besnard, A. & Gaillard, J.-M. (2012) Towards a vertebrate demographic data bank. *Journal of Ornithology*, **152**, 617–624.

Legendre, S. & Clobert, J. (1995) ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics*, **22**, 817–834.

Lehman, R.N., Kennedy, P.L. & Savidge, J.A. (2007) The state of the art in raptor electrocution research: a global review. *Biological Conservation*, **136**, 159–174.

Leshem, Y. (1985) Griffon Vultures in Israel: electrocution and other reasons for a declining population. *Vulture News*, **13**, 14–20.

Lopez-Lopez, P., Garcia-Ripolles, C., Garcia-Lopez, F., Aguilar, J.M. & Verdejo, M. (2004) Patron de distribucion del Aguila real *Aquila chrysaetos* y del aguila-azor perdicera *Hieraaetus fasciatus* en la provencia de Castellon. *Ardeola*, **51**, 275–283.

Lopez-Lopez, P., Ferrer, M.A., Madero, A., Casado, E. & McGrady, M. (2011) Solving man-induced large-scale conservation problems: the Spanish Imperial eagle and power lines. *PLoS ONE*, **6**, e17196.

Martínez, J.A., Calvo, J.F., Martínez, J.E., Zuberogoitia, I., Zabala, J. & Redpath, S.M. (2008) Breeding performance, age effects and territory occupancy in a Bonelli's eagle *Hieraaetus fasciatus* population. *Ibis*, **150**, 223–233.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Newton, I., Davis, P.E. & Davis, J.E. (1989) Age of first breeding, dispersal and survival of Red Kites Milvus milvus in Wales. *Ibis (Lond. 1859)*, **131**, 16–21.

Ortega, E., Mañosa, S., Margalida, A., Sánchez, R., Oria, J. & González, L.M. (2009) A demographic description of the recovery of the Vulnerable Spanish imperial eagle *Aquila adalberti*. *Oryx*, **43**, 113–121.

Pradel, R., Gimenez, O. & Lebreton, J.-D. (2005) Principles and interest of GOF testes for multistates capture–recapture models. *Animal Biodiversity and Conservation*, **28**, 189–204.

Real, J. (2004) Aguila azor-perdicera, *Hieraaetus fasciatus*. In *Libro Rojo de las Aves de Espana* (eds C.G.A. Madrono & J.C. Atienza), pp. 154–157. Direccion General para la Biodiversidad-SEO/Birdlife, Madrid, Spain.

Real, J. & Manosa, S. (1997) Demography and conservation of western European Bonelli's eagle *Hieraaetus fasciatus* populations. *Biological Conservation*, **79**, 59–66.

Real, J., Grande, J.M., Manosa, S. & Sanchez-Zapata, J.A. (2001) Causes of death in different areas for Bonelli's eagle *Hieraaetus fasciatus* in Spain. *Bird Study*, **48**, 221–228.

Saether, B.-E. (1989) Survival rates in relation to body weight in European birds. *Ornis Scandinavica*, **20**, 13–21.

Saether, B.-E. & Bakke, O. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.

Schaub, M. & Pradel, R. (2004) Assessing the relative importance of different sources of mortality from recoveries of marded animals.

Schaub, M., Aebischer, A., Gimenez, O., Berger, S. & Arlettaz, R. (2010) Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biological Conservation*, **143**, 1911–1918.

Schwarz, C.J., Schweigert, J.F. & Arnason, A.N. (1993) Estimating migration rates using tag-recovery data. *Biometrics*, **49**, 177–193.

Sedinger, J.S., White, G.C., Espinosa, S., Partee, E.T. & Braun, C.E. (2010) Assessing compensatory versus additive harvest mortality: an example using Greater Sage-Grouse. *Journal of Wildlife Management*, **74**, 326–332.

Sergio, F., Marchesi, L., Pedrini, P., Ferrer, M. & Penteriani, V. (2004) Electrocution alters the distribution and density of a top predator, the eagle owl *Bubo bubo*. *Journal of Applied Ecology*, **41**, 836–845.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305–308.

Tavecchia, G., Adrover, J., Navarro, A.M. & Pradel, R. (2012) Modelling mortality causes in longitudinal data in presence of tag loss: application to raptor poisoning and electrocution. *Journal of Applied Ecology*, **49**, 297–305.

Tidemann, C.R. & Nelson, J.E. (2011) Life expectancy, causes of death and movements of the Grey-Headed Flying-Fox (Pteropus poliocephalus) inferred from banding. *Acta Chiropterologica*, **13**, 419–429.

Tinto, A., Real, J. & Manosa, S. (2010) Predicting and correcting electrocution of birds in Mediterranean areas. *Journal of Wildlife Management*, **74**, 1852–1862.

Wahl, R., Rolf, C. & Barbraud, C. (2005) *Dynamique de population et conservation du balbuzard pêcheur Pandion haliaetus en région centre*. Société d'études ornithologiques, Dijon, France.

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Supporting Information

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

Fig. S1. Yearly fecundity estimates for the French population of Bonelli's eagle.

Table S1. State transition matrix used to fit models to the capture–recapture data on the French population of the Bonelli's eagle.

Table S2. List of the 48 models and their respective QAICc fitted for the analysis of the CR data on the French population of Bonelli's eagle.

Table S3. Leslie matrix for the French population of Bonelli's eagle.

Table S4. Estimates of the probabilities of survival, mortality, resighting and recovery provided by the 5 best multistate models fitted on the CR data of the French population of the Bonelli's eagle.

Table S5. Model selection procedure for the analysis of the fecundity of the French population of Bonelli's eagle.

Table S6. Estimates of the constant model used for the analysis of the fecundity of the French population of Bonelli's eagle.