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European Journal of Wildlife Research

ISSN 1612-4642

Volume 62

Number 6

Eur J Wildl Res (2016) 62:643-651

DOI 10.1007/s10344-016-1036-7



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Factors affecting survival in Mediterranean populations of the Eurasian eagle owl

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Received: 21 March 2016 / Revised: 6 July 2016 / Accepted: 27 July 2016 / Published online: 12 August 2016
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Abstract The survival rate is a key parameter for population management and the monitoring of populations. Thus, an analysis of survival rate variations and the factors influencing the same is essential for understanding population dynamics. Here, we study the factors determining the survival and the causes of mortality of the Eurasian eagle owl (*Bubo bubo*) in two Spanish Mediterranean populations (Murcia and Seville) where the species has a high population density and breeding success; yet its survival rates and the factors that affect them are unknown. Between 2003 and 2010, 63 breeding owls were captured and radio-tracked. Three monthly (quarterly) survival rates were estimated using known-fate models in the program MARK. The mean overall annual survival rate was 0.776 (95 % CI: 0.677, 0.875). We observed survival differences between sexes, and between the breeding and non-breeding periods, although no overwhelming support was found for any particular model. We concluded that (i) females have a lower survival rate than males, probably due to their larger home ranges, which increase the risk of mortality; (ii) the survival rates of both sexes were lower during the non-breeding period; and (iii) the causes of mortality differed

significantly between the two populations, gunshot being the main cause in Seville and electrocution in Murcia.

Keywords Home range · Human-induced mortality · Known-fate model · Sex-biased mortality

Introduction

The study of demographic parameters is essential for understanding the trends and changes of wild populations (Moyes et al. 2006; Schaub et al. 2010; Smith et al. 2010; Tenan et al. 2012). Among various vital rates that affect population change (i.e. survival, productivity, immigration/emigration), survival is usually considered the most important driver of population dynamics, because this parameter is usually the greatest contributor to the population growth rate in *K*-selected organisms (Sibly and Hone 2002; Grande et al. 2009; Margalida et al. 2014). Thus, annual survival can be a key parameter for monitoring and managing populations of conservation concern, especially in the case of long-lived species (Wisdom et al. 2000; Hernández-Matías et al. 2011). Thus, understanding patterns of variation in survival is necessary to interpret both life history variation and the mechanisms driving population change (Robinson et al. 2010; Smith et al. 2014).

To our knowledge, although few estimates on owl survival in Mediterranean European regions have been published (e.g. Boano and Silvano 2015), owl survival estimates are available for several species in boreal and temperate regions of Europe and North America (Newton et al. 2016). These studies revealed that owl survival (i) shows temporal patterns of variation related to cyclic food abundance and climatic factors (Seamans et al. 2002; Francis and Saurola 2004; Lehtikoinen et al. 2011; Pavón-Jordán et al. 2013; Dugger et al. 2016); (ii) is influenced by habitat structure (Franklin et al. 2000;

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Hakkarainen et al. 2008; Dugger et al. 2005); (iii) decreases with the presence of human infrastructures (Grilo et al. 2012; Thorup et al. 2013; Borda de Água et al. 2014); and (iv) is reduced by the predation of young individuals (Sunde 2005). In addition to age, other individual-related variables, such as sex or physical condition, are expected to be important factors affecting survival. For example, age- and sex-biased mortality has been observed in many wild bird populations (Tavecchia et al. 2001; Martín et al. 2007; Rymešová et al. 2012), and other studies have documented higher survival rates for individuals with better body condition or health status (Dinsmore and Collazo 2003; Hylton et al. 2006). Differences in survival rates between males and females are usually associated to differences in behaviour and energetic investment during the reproduction period (Liker and Székely 2005; Rymešová et al. 2012), but also to differences in habitat use or foraging activities (Lambertucci et al. 2012).

The Eurasian eagle owl *Bubo bubo* (Linnaeus, 1758) is socially monogamous, long-lived (>15 years in the field and >60 years in captivity; Penteriani et al. 2010), non-migratory and territorial, life history traits that would predict high adult survival rates. Previous research suggests that Eurasian eagle owls may experience high mortality by electrocution and direct persecution from humans (Marchesi et al. 2002; Sergio et al. 2004; Martínez et al. 2006; Rubolini et al. 2001), and two studies suggest that survival rates increase with age (Olsson 1997; Schaub et al. 2010), although other possible factors such as sex were not taken into account.

Survival is frequently estimated using capture-mark-recapture techniques based on recaptures and/or recoveries of birds ringed with metal or coloured rings, or a combination of both (Lebreton et al. 1992), or by radio-tracking (Kenward 2001). These methods have been widely used in population monitoring studies, which determine general demographic parameters in wildlife, such as immigration, emigration, survival and population size (Altwegg et al. 2003, Newton et al. 2016). In particular, the use of radio telemetry represents an ideal method for survival studies, as it provides unbiased results for relatively long periods of an individual's life (Smith et al. 2010; Thorup et al. 2013, Newton et al. 2016).

In this paper, we aim to assess the factors associated with variation in survival and attempt to identify the causes of death in two Spanish populations of the Eurasian eagle owl, using radio-tracking methods and known-fate survival models. The two populations studied are located in areas characterised by the high availability of rabbits *Oryctolagus cuniculus* (the main prey of the Eurasian eagle owl; Penteriani et al. 2010) and different degrees of humanization (so that habitat management and land uses may be determining differences in the survival rates). This species reaches high densities in our study areas which allowed us to capture a large number of territorial individuals with relative ease by trapping (Campioni et al.

2013). The objectives of this study were (1) to determine temporal patterns of survival, (2) to examine the effects of sex and age on the survival rates of Eurasian eagle owls, (3) to compare survival rates between the two populations, living in areas characterised by different human pressures and environmental characteristics and (4) to document the causes of mortality and analyse the factors influencing it.

Methods

Study areas

The study was carried out from January 2003 to December 2010 in two populations in southern Spain: (i) the Sierras de Columbares, Altaona and Escalona, a hilly area ranging from 40 to 646 m a.s.l. in the province of Murcia (south-eastern Spain 37°45' N, 0°57' W; hereafter Murcia), which includes a special protection area (SPA) 'Monte El Valle y Sierras de Altaona y Escalona' (ES0000269; León-Ortega et al. 2014); and (ii) the Sierra Norte of Seville (Sierra Morena massif, south-western Spain; 37°30' N, 06°03' W; hereafter Seville), a hilly area 60–200 m a.s.l. (Penteriani et al. 2005).

Both study areas share a Mediterranean climate and have high densities of rabbits and Eurasian eagle owl pairs (ca. 40 territories per 100 km² over the whole study area; Penteriani et al. 2010; León-Ortega et al. 2014). The landscape in Murcia is a mosaic of forest of Aleppo Pines *Pinus halepensis*, scrublands, irrigated and rainfed crops, hunting enclosures and urbanised areas. In contrast, the Seville landscape is dominated by sparse woodlands composed of Holm Oaks *Quercus ilex*, Gall Oaks *Quercus faginea*, Stone Pine *Pinus pinea*, Olive Trees *Olea europaea*, Mastic Tree *Pistacea lentiscus* and small plantations of *Eucalyptus sideroxylon*. In many areas, scrubland has replaced woodland. Most of the area is managed for game species (mainly partridges and rabbits).

Trapping and radio-tracking

Owls were trapped using two methods: (i) simulation of a territorial intrusion using a combination of a taxidermy mount of an Eurasian eagle owl and a mist-net to capture the territorial bird when it responds to the simulated intruder (Penteriani et al. 2007); (ii) placement of a bow-net in the nest when nestlings were 20–35 days old (i.e. when they were already able to thermoregulate; Campioni et al. 2013) so that adults could be captured when they returned to care for chicks at the nest. Each captured bird was fitted with a 30 g radio-transmitter (Biotrack Ltd, Wareham, Dorset, UK) attached as a backpack harness made from Teflon ribbon, which contained a mercury posture sensor that allowed us to discriminate whether the owls were alive or dead. Battery life was almost more than 1 year for each individual, so between 2003

and 2010, we monitored radioed individuals until they died or stopped transmitting. We recorded no adverse effect of backpacks on birds or breeding performance. The backpacks were not removed after the study due to the difficulty of recapturing the same individual (Penteriani et al. 2011). To locate the owls, the surveys were made from four-wheel drive vehicles, using three-element hand-held Yagi antennas (Biotrack; Wareham, Dorset, UK; <http://www.biotrack.co.uk>) with either Stabo (XR-100) portable ICOM receivers (IC-R20) or SIKA radio tracking receivers. We did at least two attempts per month to locate each of the radio-tagged individual. When an owl was detected, we proceeded to determine its status (alive, dead). Birds not detected in successive occasions were considered censored (i.e. end of monitoring).

Survival analysis

To estimate survival and determine factors affecting owl survival, we used the know-fate model with the logit-link function in the program MARK (Pollock et al. 1989, White and Burnham 1999). Know-fate modelling is an appropriate method for estimating survival parameters in radio-tracking studies, in which the status (dead or alive) of all tagged animals is known at each sampling occasion. We estimated survival rates for 32 3-month (quarterly) intervals, using the 63 encounter histories obtained by relocating the radio-tracked individuals. The individual covariables included sex, age, population (Murcia, Seville) and two time-specific factors (year and period). To test which variables were most likely to influence owl survival, a set of candidate models was specified, including a number of additive and interaction models representing plausible biological hypotheses.

Birds were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998) or using discriminant functions based on body measurements that classified 98.4 % of the birds correctly (Delgado and Penteriani 2004). Eurasian eagle owls can begin to breed in the second calendar year, and the bird age can be assessed by plumage characteristics until the fifth year (Martínez et al. 2002). Therefore, we classified the individuals into two age-class groups: juvenile (owls from 1 to 5 years old) and adult (owls older than 5 years).

To examine inter- and intra-annual variations in survival, we considered two time-specific group covariables: year and period. Inter-annual variations were studied using 8 years (2003–2010), and the annual cycle was divided into breeding and non-breeding periods, each related with different breeding stress, home range activity and food availability. The breeding season includes 9 months (three quarterly intervals), from December to August, and the non-breeding season includes only 3 months (one quarterly interval), from September to November (Campioni et al. 2013).

Model selection was performed using Akaike's information criterion corrected for small sample size (AIC_c) and models

differing by $\leq 2 \Delta AIC_c$ were considered as potential alternatives (Burnham and Anderson 2002). Akaike weights (w_i) were used to evaluate the strength of evidence among competing models. The degree to which 95 % confidence intervals for covariate coefficients (β_i) overlapped zero was also used to evaluate the strength of evidence for competing models.

Because there is no goodness-of-fit for classical known-fate data, the variance inflation factor (i.e. the overdispersion term \hat{c}) cannot be estimated adequately. Therefore, model robustness was investigated following the approach described in Smith et al. (2014), i.e. artificially inflating the overdispersion term from 1 to 3 (i.e. no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in Quasi- AIC_c ($QAIC_c$).

We used the model-averaging procedure in program MARK to estimate survival rates. The 95 % confidence intervals (CI) for annual rates were calculated using the deltha method (Cooch and White 2016).

Causes of mortality

The cause of mortality was determined through necropsy, although it could be identified visually in most cases. We classified the causes of mortality into the following classes:

- (i) *Human-induced causes*. (1) Gunshot: pellets observed through radiography, or when the holes were clearly visible in the body or wings. (2) Electrocutation: the carcass was found below power lines, usually with burns in both plumage and claws caused by electrocutation. (3) Collision with fences: attributed to carcasses found close to fences and with broken bones or neck.
- (ii) *Natural causes*. (1) Killing by other Eurasian eagle owls: the carcass was found partly eaten under roots, perches or in the nests of other territorial owls. (2) Disease: the carcass was found shortly after death and was complete, with no sign of injury through predation, starvation or human manipulation, but the necropsy showed abnormalities in internal organs.
- (iii) *Unknown*: the carcass was found without any external evidence and a high degree of decomposition that did not permit us to determinate the cause of death.

In order to investigate the factors influencing the causes of mortality, and given the low number of dead owls found, the cause of mortality was modelled as a nominal response variable with only four classes: gunshot, electrocutation, disease and other. We then performed a multinomial regression analysis (Venables and Ripley 2002) and type II likelihood-ratio tests (Fox and Weisberg 2011) to examine the significance of three potential explanatory variables: sex, population and period.

Multinomial regression is a simple extension of binary logistic regression that allows for more than two categories of the dependent variable and is considered suitable for analysing multiway contingency tables. The analyses were performed using the ‘nnet’ (Venables and Ripley 2002) and ‘car’ (Fox and Weisberg 2011) packages in R version 3.1.1 (R Core Team 2014).

Results

Between 2003 and 2010, we captured radio-tagged and tracked 63 breeding individuals (Table 1), of which 27 were females and 36 males. Most of them (51) were aged as juvenile (≤ 5 years old) and 12 were aged as adults.

Of the 24 candidate models selected to examine the influence of the variables considered on survival, the additive model including sex and period (breeding vs. non-breeding season) was the most parsimonious (Table 2), although the model including only sex, and the interaction term between sex and period, was competitive. The remaining models were $>2.00 \Delta AIC_c$, providing little support for the effects of age, population or year on survival rates. The best model provided support for higher survival rates for males and the breeding season compared to females and the non-breeding season (Fig. 1). These differences were not very large (less than 0.1), although they appear more important when expressed as annual rates 0.842 (95 % CI 0.738, 0.947) for males vs. 0.667 (95 % CI 0.492, 0.842) for females. Nevertheless, the low Akaike weights of the best alternative models indicate no overwhelming support for any particular model, although the slope coefficients for period and the sex \times period interaction had 95 % confidence intervals that included zero (Table 2), suggesting weak differences between periods in survival rates. Furthermore, when we set $\hat{c} = 2$, the constant (null) model was a plausible alternative model ($\Delta QAIC_c = 0.93$), and when $\hat{c} = 3$, the constant model was the best model, which points to no substantial variation in survival attributable to the factors analysed. The quarterly estimate of survival of the constant model was 0.939 (95 % CI 0.910, 0.959), which yields a mean overall annual survival rate of 0.776 (95 % CI 0.677, 0.875).

A total of 24 deaths (38.1 %) were recorded during the study among the radio-tracked individuals. The main causes were human-induced (Table 3). Gunshot and electrocution represented 37.5 and 29.2 % of the deaths, respectively. Death by disease also showed a high percentage (16.7 %) of deaths. The multinomial analysis did not show any difference in the cause of mortality between sexes ($\chi^2 = 2.35$, $df = 3$, $P = 0.503$), or between breeding and non-breeding seasons ($\chi^2 = 0.99$, $df = 3$, $P = 0.804$). However, differences were observed among populations ($\chi^2 = 11.88$, $df = 3$, $P = 0.008$), with gunshot being the first cause for Seville and electrocution for Murcia.

Table 1 Summary of the radio-tracking data of Eurasian eagle owls in Murcia and Seville, 2003–2010

	Murcia	Seville	Overall
Females	15	12	27
Adult	4	0	4
Immature	11	12	23
Males	15	21	36
Adult	7	0	7
Immature	8	21	29
Total adult	12	0	12
Total immature	18	33	51
Total individuals tracked	30	33	63
Death	12	12	24
Censored	5	21	26
Alive at the end of the study	13	0	13
Average tracking time (months)	16.5	20.5	18.6

Adult owls are individuals aged >5 years old

Discussion

Our results obtained using known-fate analysis with radio-tracked breeders identified a sex-biased survival rate in favour of males, and differences between the breeding and non-breeding periods of the annual cycle. Sex-biased survival has commonly been reported in demographic studies of bird populations (Donald 2007), and some studies demonstrate survival differences between different phases of the biological cycle (e.g. Robinson et al. 2010; Leyrer et al. 2013; Varmer et al. 2014).

This work provides evidence of different survival rates between genders, the annual survival rate being 1.26 times higher for males. Some studies have suggested that differences in male and female mortality are positively correlated with size dimorphism (Tavecchia et al. 2001) or asymmetric habitat use by the two sexes (Lambertucci et al. 2012). These differences in sex survival are sometimes associated with anthropogenic causes in large birds of prey (Ferrer and Hiraldo 1992), which affects the adult sex ratio of wild populations and causes males to outnumber females, even when the offspring sex ratio is 1:1 (as in the Eurasian eagle owl case; Mora et al. 2010). In fact, higher female mortality, rather than a skewed offspring sex ratio, is the main driver of male-skewed adult sex ratios in bird populations (Donald 2007; Székely et al. 2014), a circumstance which may influence multiple aspects of pair-bond and mating behaviour (Liker et al. 2014), and may have important consequences for the viability of populations of long-lived organisms that appear numerically stable (Grayson et al. 2014).

Because no differences in the proportion of mortalities attributed to each cause by sex were observed, the higher

Table 2 Summary of known-fate survival model selection results for Eurasian eagle owls in Murcia and Seville, 2003–2013 when the overdispersion term was 1.0. Models are ranked according to Akaike's information criterion (AIC_c)

Model	K	AIC_c	ΔAIC_c	w_i	Coefficients (95 % CI)
$S_{sex+period}$	3	178.18	0.00	0.28	$\beta_{sex} = 1.048 (0.204, 1.892)$ $\beta_{period} = 0.713 (-0.158, 1.584)$
S_{sex}	2	178.57	0.39	0.23	$\beta_{sex} = 1.034 (0.194, 1.874)$
$S_{sex*period}$	4	179.60	1.41	0.14	$\beta_{sex} = 1.513 (0.052, 2.973)$ $\beta_{period} = 1.016 (-0.125, 2.162)$ $\beta_{sex \times period} = -0.718 (-2.513, 1.078)$
$S_{sex+population}$	3	180.46	2.28	0.09	
$S_{sex+age}$	3	180.58	2.40	0.08	
S_{period}	2	182.17	3.99	0.04	
$S_{constant}$	1	182.46	4.27	0.03	
$S_{sex*age}$	4	182.56	4.38	0.03	
$S_{population+period}$	3	183.69	5.51	0.02	
$S_{population}$	2	183.85	5.66	0.02	
$S_{age*period}$	4	183.87	5.69	0.02	
$S_{age+period}$	3	184.11	5.93	0.01	
S_{age}	2	184.42	6.24	0.01	
$S_{age+population}$	3	185.31	7.12	0.01	
$S_{sex+year}$	9	189.49	11.30	0.00	
S_{year}	8	192.33	14.15	0.00	
$S_{population+year}$	9	194.10	15.92	0.00	
$S_{age+year}$	9	194.28	16.10	0.00	

The symbol '+' denotes an additive model, while '*' is used for interaction models. Headers for columns are number of parameters (K), change in AIC_c relative to the highest ranked model (ΔAIC_c) and Akaike weight (w_i). Covariate coefficients and 95 % confidence intervals (CI) are given only for the best ($\Delta AIC_c < 2.0$) models

mortality of females is probably associated with differences in behaviour, habitat use or energetic investment during the reproduction period. More specifically, we hypothesise that the higher mortality of female Eurasian eagle owls is associated with differences in habitat use by the two sexes, with females foraging in larger home ranges (Campioni et al. 2013), which increase the interaction with human infrastructures such as

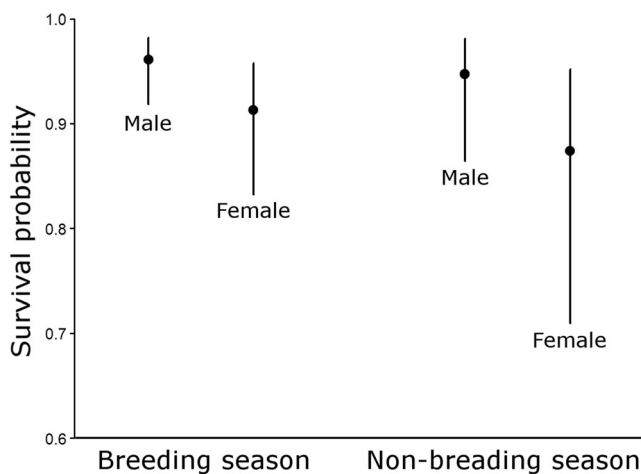


Fig. 1 Three monthly (quarterly) survival probabilities of Eurasian eagle owls estimated using model-averaging in known-fate analyses, Table 2. Vertical lines represent 95 % confidence intervals

power lines, fences, roads and hunting enclosures. In addition, survival may be associated to the different home range behaviour (e.g. space use, movement patterns and rhythms of activity) of males and females during the different phases of the biological cycle (Campioni et al. 2013). Our results point to survival differences between the breeding and non-breeding periods, but we observed lower quarterly survival rates during the non-breeding period, whereas, given the reproductive effort and the degree of stress of individuals during the breeding season, the opposite pattern might be expected (Severinghaus and Rothery 2001; Thorup et al. 2013). During the breeding season, Eurasian eagle owl pairs spend most time in or near the nest, a behaviour characteristic that could reduce the exposure time in the most humanised areas of their home ranges, thereby minimising the risk of being shot or electrocuted. In addition, with respect to food availability in these two periods, the marked intra-annual variations in the density of rabbits could affect survival rates between seasons. Rabbits are less abundant in late summer and autumn (the non-breeding season for the owls), due to a hunting pressure, the higher frequency of disease and limited food availability because of summer droughts (Beltrán 1991). Hence, the intra-annual variation in the density of prey could be associated with the intra-annual pattern of survival in the Eurasian eagle owl. Variation in annual survival rates in many owl species in northern latitudes has been shown

Table 3 Causes of death of Eurasian eagle-owls in the study areas, 2003–2010

Cause	Murcia		Seville		Overall		
	Male	Female	Male	Female	Male	Female	Total
Human-induced							
Gunshot	0	1	5	3	5	4	9
Electrocution	2	4	0	1	2	5	7
Collision with fences	1	0	0	0	1	0	1
Natural							
Killing	0	0	1	0	1	0	1
Disease	1	3	0	0	1	3	4
Unknown	0	0	0	2	0	2	2
Total dead	4	8	6	6	10	14	24

to vary annually (Altwegg et al. 2003; Francis and Saurola 2004; Le Gouar et al. 2011; Pavón-Jordán et al. 2013) and in association to the cyclic food abundance of the main prey (Korpimäki 1992; Rutz and Bijlsma 2006; Karell et al. 2009; Lehikoinen et al. 2011). However, in Mediterranean ecosystems, predator communities are mostly made up of generalists, and therefore, predator-prey systems are more complex than those of northern latitudes (Fargallo et al. 2009; Moleón et al. 2012). The rabbit is a keystone species in southern Europe (Delibes-Mateos et al. 2007) that does not suffer regular cyclic oscillations, and, while this prey forms the bulk of the Eurasian eagle owl diet (Penteriani et al. 2002; Lourenço 2006), the species has a high capacity to switch to alternative prey if the basic prey does become scarce (Martínez and Calvo 2001). This could explain why we found no inter-annual variations in Eurasian eagle owl survival.

The survival of Eurasian eagle owls in Alpine and northern latitudes has previously been estimated from the recovery of owls marked as nestlings (Olsson 1997) and using a Bayesian-integrated population model combining different data sets (Schaub et al. 2010). In contrast to our results (models including age were not well supported), these studies pointed to a variation in survival that depended on age-class, and similar results have been found in other long-lived species (e.g. Daunt et al. 2007; Angelier et al. 2007; Grande et al. 2009; Hernández-Matías et al. 2011). However, it must be noted that, unlike the above-mentioned studies, our study has been conducted on breeding individuals, which may explain the absence of an age effect on survival. In our study areas, a substantial proportion of first-time breeders was being recruited each year, resulting in a high number of juvenile breeders being captured. This circumstance denotes the existence of a high turn-over rate in territorial individuals, mainly females, and, although no evidence of lower survival in juvenile breeders was found, the differences in breeding success between juvenile and adult individuals might be worth investigating.

However, assessing the effects of the cost of first reproduction requires a long-term data set with a large number of individuals (Tavecchia et al. 2001). It should be noted that the overall survival rate observed in our populations was intermediate between those reported in the studies of Olsson (1997) and Schaub et al. (2010).

Of note was the fact that we observed no differences in survival rates between the two populations studied (Murcia and Seville), but the primary causes of mortality were different, but both associated with anthropogenic affects. In Northern Europe, electrocution and traffic have been identified as the main sources of Eurasian eagle owl mortality (Valkama et al. 2015). In Spain, the primary cause of death in this species is electrocution, followed by persecution and collisions with game fences and cars (Martínez et al. 2006). This noted that some human-induced causes of mortality varied by geographic region. In our study, the Seville population showed a higher frequency of deaths by shooting, whereas in Murcia, the most common anthropogenic cause of death was electrocution. These differences appear to be directly related to range management and land uses in these separate study areas. The Murcia population inhabits more humanised landscapes than the Seville population. In Murcia, the area dedicated to irrigated crops and urbanizations has grown continuously in the last decades (Martínez-Fernández et al. 2000, 2013), accompanied by an increase in other man-made structures, including roads, railways and new power generation facilities. This could explain the significant differences found in the causes of mortality between both populations. Our results suggest that human-induced mortality may be a pending problem for Eurasian eagle owl conservation in Spain (Martínez et al. 2006), despite the considerable effort put into the creation of protected areas during the last 10 years, the identification of dangerous pylons and the application of appropriate insulation techniques on power lines (Moleón et al. 2007; López-López et al. 2011; Barrientos et al. 2012).

Acknowledgments We are very grateful to Eloy Peréz, José Alfonso Lacalle, Letizia Campioni, Chiara Bettega, Rui Lourenço and other collaborators for their help on the field work. We thank Encarni Montoya, María Victoria Jiménez-Franco and Silvia Villaverde for their unconditional support and comments. The suggestions and comments of Jari Valkama and two anonymous reviewers considerably helped to improve the manuscript. The Asociación de Naturalistas del Sureste (ANSE) is also acknowledged for partial financial support in the Murcia area. The Spanish Ministry of Economy and Competitiveness (CGL2012–33240; FEDER co-financing) funded this study in the Seville area. The research adheres to the legal requirements of the country where it has been carried out.

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