

1 **Factors affecting survival in Mediterranean populations of the**
2 **Eurasian eagle owl**

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18 **Abstract**

19 The survival rate is a key parameter for population management and the monitoring of
20 populations. Thus, an analysis of survival rate variations and the factors influencing the
21 same is essential for understanding population dynamics. Here, we study the factors
22 determining the survival and the causes of mortality of the Eurasian eagle owl (*Bubo*
23 *bubo*) in two Spanish Mediterranean populations (Murcia and Seville) where the species
24 has a high population density and breeding success; yet its survival rates and the factors
25 that affect them are unknown. Between 2003 and 2010, 63 breeding owls were captured
26 and radio-tracked. Three-monthly (quarterly) survival rates were estimated using
27 known-fate models in the program MARK. The mean overall annual survival rate was
28 0.776 (95% CI = 0.773-0.779). We observed survival differences between sexes, and
29 between the breeding and non-breeding periods, although no overwhelming support was
30 found for any particular model. We concluded that: (i) females have a lower survival
31 rate than males, probably due to their larger home ranges, which increase the risk of
32 mortality; (ii) the survival rates of both sexes were lower during the non-breeding
33 period; and (iii) the causes of mortality differed significantly between the two
34 populations, gunshot being the main cause in Seville and electrocution in Murcia.

35

36 **Keywords**

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

38 **Introduction**

39 The study of demographic parameters in wildlife populations is essential for
40 understanding the trends and changes of wild populations (Moyes et al. 2006; Schaub et
41 al. 2010; Smith et al. 2010; Tenan et al. 2012). Within the different demographic
42 parameters, survival is considered the most important for population dynamics, since
43 this parameter is the greatest contributor to the population growth rate in *K*-selected
44 organisms (Sibly and Hone 2002; Grande et al. 2009; Margalida et al. 2014). The
45 survival rate is also a key parameter for population management and for monitoring
46 populations of conservation concern, especially in the case of long-lived species
47 (Wisdom et al. 2000; Hernández-Matías et al. 2011). Thus, understanding the patterns of
48 variation in survival is necessary for interpreting both life-history variations and the
49 mechanisms of population change and dynamics (Robinson et al. 2010; Smith et al.
50 2014).

51 To our knowledge, not a single work on owl survival in Mediterranean European
52 regions has been yet published, whereas in boreal and temperate regions of Europe and
53 North America this information is available for several species. These studies revealed
54 that owl survival: (i) shows temporal patterns of variation related to cyclic food
55 abundance and climatic factors (Seamans et al. 2002; Francis and Saurola 2004;
56 Lehtikoinen et al. 2011; Pavón-Jordán et al. 2013); (ii) is influenced by habitat structure
57 (Hakkarainen et al. 2008); (iii) decreases with the presence of human infrastructures
58 (Grilo et al. 2012; Thorup et al. 2013; Borda de Água et al. 2014); and (iv) is reduced by
59 the predation of young individuals (Sunde 2005). In addition to age, other individual-
60 related variables, such as sex or physical condition, are expected to be important factors
61 affecting survival. For example, age- and sex-biased mortality has been observed in
62 some wild bird populations (Tavecchia et al. 2001; Martín et al. 2007; Rymešová et al.
63 2012), and other studies have documented higher survival rates for individuals with

64 better body condition or health status (Dinsmore and Collazo 2003; Hylton et al. 2006).
65 Differences in survival rates between males and females are usually associated to
66 differences in behaviour and energetic investment during the reproduction period (Liker
67 and Székely 2005; Rymešová et al. 2012), but also to differences in habitat use or
68 foraging activities (Lambertucci et al. 2012).

69 For the Eurasian eagle owl *Bubo bubo* (Linnaeus, 1758), a socially monogamous
70 and long-lived species (> 15 years in the field and > 60 years in captivity; Penteriani et
71 al. 2010), which has a sedentary and territorial behaviour, a high adult survival is
72 probably attributable to the acquisition of a territory and increased foraging experience
73 (Newton 1989; Martin 1995). Although some studies on the causes of death of Eurasian
74 eagle owls showed high mortality by electrocution and direct persecution (Marchesi et
75 al. 2002; Sergio et al. 2004; Martínez et al. 2006), little information exists about
76 determining the factors that affect their survival, with only two studies showing that
77 survival rates increases with age (Olsson 1997; Schaub et al. 2010), although other
78 possible factors such as sex were not taken into account. The above studies used ring-
79 recoveries of birds that had been ringed in the nest (Olsson 1997) and data on dead owls
80 reported from bird rescue centres and museums of natural history (Schaub et al. 2010).
81 Hence, a possible bias in the estimation of adult survival could be possible.

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

90 2013, Newton et al. 2016).

91 In this paper we aim to assess the factors determining survival and attempt to
92 identify the causes of death in two Spanish populations of the Eurasian eagle owl, using
93 radio-tracking methods and known-fate survival models. The two populations studied
94 are located in areas characterized by the high availability of rabbits *Oryctolagus*
95 *cuniculus* (the main prey of the Eurasian eagle owl; Penteriani et al. 2010) and different
96 degrees of humanization (so that habitat management and land uses may be determining
97 differences in the survival rates). The high density that this species reaches in our study
98 areas allowed us to capture a high number of territorial individuals with relative ease by
99 trapping (Campioni et al. 2013), and therefore, the populations studied provide an
100 excellent opportunity to study survival in a long-lived species using radio-tracking
101 techniques. Our objectives were: (1) to examine the effects of sex and age on the
102 survival rates of Eurasian eagle owls, (2) to compare survival rates between the two
103 populations, which are characterised by different human pressures and environmental
104 characteristics, (3) to determine temporal patterns of survival and (4) to document the
105 causes of mortality and analyse the factors influencing it.

106

107 **Methods**

108 **Study areas**

109 The study was carried out from January 2003 to December 2010 in two populations in
110 southern Spain: (i) the Sierras of Columbares, Altaona and Escalona, a hilly area
111 ranging from 40 to 646 m a.s.l. in the province of Murcia (south-eastern Spain 37°45' N,
112 0°57' W; hereafter Murcia), which includes a Special Protection Area (SPA) “Monte El
113 Valle y Sierras de Altaona y Escalona” (ES0000269; León-Ortega et al. 2014); and (ii)
114 the Sierra Norte of Seville (Sierra Morena massif, south-western Spain; 37°30' N,
115 06°03' W; hereafter Seville), a hilly area 60-200 m a.s.l. (Penteriani et al. 2005).

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

126

127 Trapping and radio-tracking

128 Owls were trapped using two methods: (i) simulating a territorial intrusion with a
129 combination of a taxidermy mount of an Eurasian eagle owl and a mist-net (Penteriani
130 et al. 2007); (ii) using a bow-net placed in the nest when nestlings were 20-35 days old
131 (i.e., when they were already able to thermoregulate; Campioni et al. 2013). Each
132 trapped bird was fitted with a 30 g radio-transmitter (Biotrack Ltd, Wareham, Dorset,
133 UK) attached as a back-pack harness made from Teflon ribbon, which contained a
134 mercury posture sensor that allowed us to discriminate whether the owls were alive or
135 dead. During eight years of continuous radio-tracking, we recorded no adverse effect of
136 back-packs on birds or breeding performance. The backpacks were not removed after
137 the study due to the difficulty of recapturing the same individual (Penteriani et al. 2011).
138 To locate the owls, the surveys were made from four-wheel drive vehicles, using three-
139 element hand-held Yagi antennas (Biotrack; Wareham, Dorset, UK;
140 <http://www.biotrack.co.uk>) with either Stabo (XR-100) portable ICOM receivers (IC-
141 R20) or SIKA radio tracking receivers. At least two attempts of re-sighting were made

142 during each three month interval throughout the study. When an owl was detected, we
143 proceeded to determine its status (alive, dead); when the bird was not detected in several
144 successive occasions, it was considered censored (i.e., end of monitoring).

145

146 Survival analysis

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

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

165 To examine inter- and intra-annual variations in survival we considered two
166 time-specific group covariables: year and period. Inter-annual variations were studied
167 using eight years (2003-2010), and the annual cycle was divided into breeding and non-

168 breeding periods, each related with different breeding stress, home range activity and
169 food availability. The breeding season includes nine months (three quarterly intervals),
170 from December to August, and the non-breeding season includes only three months (one
171 quarterly interval), from September to November (Campioni et al. 2013).

172 Model selection was performed using Akaike's information criterion corrected
173 for small sample size (AIC_c) and models differing by $\leq 2 \Delta AIC_c$ were considered as
174 potential alternatives (Burnham and Anderson 2002). Akaike weights (w_i) were used to
175 evaluate the strength of evidence among competing models. Because there is no
176 goodness-of-fit for classical known-fate data, the variance inflation factor (i.e. the
177 overdispersion term, \hat{c}) cannot be estimated adequately. Therefore, model robustness
178 was investigated following the approach described in Smith et al. (2014), i.e., artificially
179 inflating the overdispersion term from 1 to 3 (i.e. no dispersion to extreme dispersion)
180 to simulate various levels of dispersion reflected in Quasi- AIC_c ($QAIC_c$).

181

182 Causes of mortality

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

185 (i) *Human-induced causes*. (1) Gunshot: pellets observed through radiography, or
186 when the holes were clearly visible in the body or wings. (2) Electrocution: the
187 carcass was found below power lines, usually with burns in both plumage and
188 claws caused by electrocution. (3) Collision with fences: attributed to carcasses
189 found close to fences and with broken bones or neck.

190 (ii) *Natural causes*. (1) Killing by other Eurasian eagle owls: the carcass was found
191 partly eaten under roots, perches or in the nests of other territorial owls. (2)
192 Disease: the carcass was found shortly after death and was complete, with no
193 sign of injury through predation, starvation or human manipulation, but the

194 necropsy showed abnormalities in internal organs.

195 (iii) *Unknown*: the carcass was found without any external evidence and a high
196 degree of decomposition that did not permit us to determinate the cause of death.

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

203 Multinomial regression is a simple extension of binary logistic regression that allows
204 for more than two categories of the dependent variable, and is considered suitable for
205 analysing multiway contingency tables. The analyses were performed using the “nnet”
206 (Venables and Ripley 2002) and “car” (Fox and Weisberg 2011) packages in R version
207 3.1.1 (R Core Team 2014).

208

209 **Results**

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

213 Of the 24 candidate models selected to examine the influence of the variables
214 considered on survival, the additive model including sex and period (breeding vs non-
215 breeding season) was the most parsimonious (Table 2), although the model including
216 only sex, and the model including the interaction term between sex and period, were
217 suitable alternatives. The remaining models were $> 2.00 \Delta AIC_c$, which suggests no
218 effect of age or population on survival rates or inter-annual variation. The best model
219 showed a higher survival rate for males and a higher survival rate in the breeding season

220 (Fig. 1). These differences were not very large (less than 0.1), although they appear
221 more important when expressed as annual rates: e.g. 0.852 (95% CI = 0.845- 0.859) for
222 males vs. 0.648 (95% CI = 0.625- 0.670) for females. Nevertheless, the low Akaike
223 weights of the two best alternative models indicate no overwhelming support for any
224 particular model. Furthermore, when we set $\hat{c} = 2$, the constant (null) model was a
225 plausible alternative model ($\Delta\text{QAIC}_c = 0.93$), and when $\hat{c} = 3$, the constant model was
226 the best model, which points to no substantial variation in survival attributable to the
227 factors analysed. The quarterly estimate of survival of the constant model was 0.939
228 (95% CI = 0.910-0.959), which yields a mean overall annual survival rate of 0.776
229 (95% CI = 0.773-0.779).

230 A total of 24 deaths (38.1%) were recorded during the study among the radio-
231 tracked individuals. The main causes were human-induced (Table 3). Gunshot and
232 electrocution represented 37.5% and 29.2% of the deaths, respectively. Death by disease
233 also showed a high percentage (16.7%) of deaths. The multinomial analysis did not
234 show any difference in the cause of mortality between sexes ($\chi^2 = 2.35$, $df = 3$, $P =$
235 0.503), or between breeding and non-breeding seasons ($\chi^2 = 0.99$, $df = 3$, $P = 0.804$).
236 However, differences were observed among populations ($\chi^2 = 11.88$, $df = 3$, $P = 0.008$),
237 with gunshot being the first cause for Seville and electrocution for Murcia.

238

239 **Discussion**

240 Our results obtained using known-fate analysis with radio-tracked breeders identified a
241 sex-biased survival rate in favour of males, and differences between the breeding and
242 non-breeding periods of the annual cycle. While sex-biased survival has commonly
243 been reported in demographic studies (Donald 2007), there are few studies
244 demonstrating survival differences between different phases of the biological cycle
245 (e.g., Robinson et al. 2010; Leyrer et al. 2013; Varmer et al. 2014). However, the results

246 of our model selection procedure should be taken with caution given the low Akaike
247 weights of the best models and that the constant model was among the higher-ranked
248 models when considering overdispersion in the data.

249 This work provides evidence of different survival rates between genders, the
250 annual survival rate being 1.31 times higher for males. Some studies have suggested
251 that differences in male and female mortality are positively correlated with size
252 dimorphism (Tavecchia et al. 2001) or asymmetric habitat use by the two sexes
253 (Lambertucci et al. 2012). These differences in sex survival are sometimes associated
254 with anthropogenic causes in large birds of prey (Ferrer and Hiraldo 1992), which
255 affects the adult sex ratio of wild populations and causes males to outnumber females,
256 even when the offspring sex ratio is 1:1 (as in the Eurasian eagle owl case; Mora et al.
257 2010). In fact, higher female mortality, rather than a skewed offspring sex ratio, is the
258 main driver of male-skewed adult sex ratios in bird populations (Donald 2007; Székely
259 et al. 2014), a circumstance which may influence multiple aspects of pair-bond and
260 mating behaviour (Liker et al. 2014), and may have important consequences for the
261 viability of populations of long-lived organisms that appear numerically stable (Grayson
262 et al. 2014).

263 Given that we identified electrocution and shooting as the main causes of
264 mortality in the populations studied, human-induced mortality might be expected to
265 affect male owls less. However, no differences in the causes of mortality between sexes
266 were observed, so the higher mortality of females is probably associated with
267 differences in behaviour, habitat use or energetic investment during the reproduction
268 period. More specifically, we hypothesize that the higher mortality of female Eurasian
269 eagle owls is associated with differences in habitat use by the two sexes, with females
270 foraging in larger home ranges (Campioni et al. 2013), which increase the interaction
271 with human infrastructures such as power lines, fences, roads and hunting enclosures. In

272 addition, survival may be associated to the different home range behaviour (e.g., space
273 use, movement patterns and rhythms of activity) of males and females during the
274 different phases of the biological cycle (Campioni et al. 2013). Our results point to
275 survival differences between the breeding and non-breeding periods, but, interestingly,
276 the weight of evidence supporting the additive model $S_{sex+period}$ was 2.0 times greater
277 than the model including the interaction term ($S_{sex*period}$), which indicates an indirect
278 relationship between these factors (or independence). Moreover, we observed lower
279 quarterly survival rates during the non-breeding period, whereas, given the reproductive
280 effort and the degree of stress of individuals during the breeding season, the opposite
281 pattern might be expected (Severinghaus and Rothery 2001; Thorup et al. 2013). During
282 the breeding season, Eurasian eagle owl pairs spend most time in or near the nest, a
283 behaviour characteristic that could reduce the exposure time in the most humanized
284 areas of their home ranges, thereby minimizing the risk of being shot or electrocuted. In
285 addition, with respect to food availability in these two periods, the marked intra-annual
286 variations in the density of rabbits could affect survival rates at a particular time.
287 Rabbits are less abundant in late summer and autumn (the nonbreeding season for the
288 owls), due to a hunting pressure, the higher frequency of disease and limited food
289 availability because of summer droughts (Beltrán 1991). Hence, the intra-annual density
290 variations of prey could explain the intra-annual pattern of survival in the Eurasian
291 eagle owl. In contrast, survival variation in most owl species in northern latitudes is
292 year-dependent (Altwegg et al. 2003; Francis and Saurola 2004; Le Gouar et al. 2011;
293 Pavón-Jordán et al. 2013) and associated to the cyclic food abundance of the main prey
294 (Korpimäki 1992; Rutz and Bijlsma 2006; Karell et al. 2009; Lehikoinen et al. 2011).
295 However, in Mediterranean ecosystems predator communities are mostly made up of
296 generalists, and therefore predator-prey systems are more complex than those of
297 northern latitudes (Fargallo et al. 2009; Moleón et al. 2012). Rabbit, a keystone species

298 in southern Europe (Delibes-Mateos et al. 2007), does not suffer regular cyclic
299 oscillations, and, while this prey forms the bulk of the Eurasian eagle owl diet
300 (Penteriani et al. 2002; Lourenço 2006), the species has a high capacity to switch to
301 alternative prey if the basic prey does become scarce (Martínez and Calvo 2001). This
302 could explain why we found no inter-annual variations in Eurasian Eagle Owl survival.

303 The survival of Eurasian eagle owls in Alpine and northern latitudes has
304 previously been estimated from the recovery of owls marked as nestlings (Olsson 1997)
305 and using a Bayesian integrated population model combining different data sets (Schaub
306 et al. 2010). In contrast to our results (models including age were not well supported),
307 these studies pointed to a variation in survival that depended on age-class (first, second
308 and the subsequent years), and similar results have been found in other long-lived
309 species (e.g., Daunt et al. 2007; Angelier et al. 2007; Grande et al. 2009; Hernández-
310 Matías et al. 2011). However, it must be noted that, unlike the above mentioned studies,
311 our study has been conducted on breeding individuals, which may explain the absence
312 of an age effect on survival. In our study areas, a substantial proportion of first-time
313 breeders were being recruited each year, resulting in a high number of immature
314 breeders being captured. This circumstance denotes the existence of a high turn-over
315 rate in territorial individuals, mainly females, and, although no evidence of lower
316 survival in immature breeders was found, the differences in breeding success between
317 immature and adult individuals might be worth investigating. However, assessing the
318 effects of the cost of first reproduction requires a long-term data set with a large number
319 of individuals (Tavecchia et al. 2001). It should be noted that the overall survival rate
320 observed in our populations was intermediate between those reported in the studies of
321 Olsson (1997) and Schaub et al. (2010).

322 Of note was the fact that our know-fate survival analyses showed no differences
323 between the two populations studied (Murcia and Seville), but that the multinomial

324 analysis of the causes of mortality showed significant differences between them.
325 Previous studies have identified the source of variations in mortality in several owl
326 species in Europe (Martínez et al. 2006; Thorup et al. 2013). In Spain, the main known
327 cause of death in Eurasian eagle owl is interaction with power lines, followed by
328 persecution and collisions with game fences and cars (Martínez et al. 2006). These
329 authors found that some human-induced causes of mortality depended on the
330 geographical region. The Seville population showed a higher frequency of deaths by
331 shooting, whereas in Murcia the most common anthropogenic cause of death was
332 electrocution. These differences appear to be directly related to range management and
333 land uses in these separate study areas. The Murcia population inhabits more humanized
334 landscapes than the Seville population. In Murcia the area dedicated to irrigated crops
335 and urbanizations has grown continuously in the last 15 years, accompanied by an
336 increase in other man-made structures, including roads, railways and new power
337 generation facilities. This would explain the significant differences found in the causes
338 of mortality between both populations. Our results demonstrate that human-induced
339 mortality is a pending problem for Eurasian eagle owl conservation in Spain (Martínez
340 et al. 2006), despite the considerable effort put into the creation of protected areas
341 during the last 10 years, the identification of dangerous pylons and the application of
342 appropriate insulation techniques on power lines (Moleón et al. 2007; López-López et
343 al. 2011; Barrientos et al. 2012). Thus, the combination of public awareness and
344 education programmes and an increase in mitigation measures implemented in power
345 lines, should contribute positively to the conservation of the Eurasian eagle owl and
346 may underpin survival and population growth, with positive side effects on other
347 endangered birds of prey (López-López et al. 2011; Pérez-García et al. 2011).

348

349

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581 **Tables**

582

583 **Table 1** Summary of the radio-tracking data of Eurasian eagle owls in Murcia and
584 Seville, 2003-2010.

585

586 **Table 2** Summary of known-fate survival model selection results for Eurasian eagle
587 owls in Murcia and Seville, 2003-2013 when the overdispersion term was 1.0.
588 Models are ranked according to Akaike's information criterion (AIC_c). Headers
589 for columns are: number of parameters (K), change in AIC_c relative to the
590 highest ranked model (ΔAIC_c), and Akaike weight (w_i).

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

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607 **Figure legends**

608 **Fig. 1.** Three-monthly (quarterly) survival probabilities of Eurasian eagle owls
609 estimated from the best approximating model in known-fate analyses, Table 2.
610 Vertical lines represent 95% confidence intervals.