

Electrocution alters the distribution and density of a top predator, the eagle owl *Bubo bubo*

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Summary

1. Electrocution has frequently been suggested as a cause of territory abandonment and eventual population decline of threatened species, but this has been rarely tested. We investigated the impact of electrocution in two eagle owl *Bubo bubo* populations located in the Italian Alps and Apennines and subject to different levels of electrocution risk (i.e. low and high risk). The eagle owl is one of the species most affected by electrocution, to the point of causing local conservation and economic concern. In a review of 25 studies, electrocution was frequently cited as the major cause of death and has progressively increased in the last three decades, independently from other causes of mortality.

2. The impact of electrocution was tested by (i) comparing estimates of electrocution risk between currently occupied owl territories and infrequently occupied or abandoned territories; (ii) collecting information on the spatiotemporal frequency of electrocution incidents; (iii) measuring density, breeding success and post-fledging survival for populations and territories subject to different electrocution risk.

3. In the low-risk population electrocution casualties varied spatiotemporally, peaking in the period of immature dispersal and at pylons that were good hunting perches. Furthermore, eagle owls over-selected low-altitude habitats, which forced them into close contact with power lines. However, nest-site selection was independent of electrocution risk, although territories that were not occupied every year were nearer to power lines than stable territories.

4. In contrast, in the high-risk population, territories near to power lines, most of them at low altitude, were progressively abandoned during a 10-year period, leading to a steeply declining, scattered, low-density and increasingly high-altitude population.

5. Although there was no effect on long-term breeding success, the presence of pylons within 200 m of the nest increased the likelihood of partial or complete brood loss in the post-fledging period. We estimated that 17% of the fledged young were lost to electrocution.

6. At the population level, density was negatively related to electrocution risk in eight Alpine study areas. However, comparison between the two regions suggested that electrocution impact may interact with other factors, such as resource availability.

7. *Synthesis and applications.* Our results show how subtle anthropogenic disturbance may affect population breeding performance and quickly alter the gradient of environmental quality for an endangered bird, leading to potential population limitation. Conservation guidelines should prioritize the insulation of those pylons most likely to cause casualties (e.g. in good hunting habitat and close to nests), ensuring that all new lines are raptor safe.

Key-words: anthropogenic disturbance, conservation guidelines, habitat selection, human-induced mortality, population effects, power lines, spatial effects

Introduction

Each year, power line electrocution causes the death of thousands of mostly large-bodied birds from endangered species (Ferrer & Janss 1999). Avian electrocution also involves high costs to the electric industry because of power outages and damage to the power lines. For example, the annual cost of bird-related damage to Canadian utilities was estimated in the early 1980s at \$374 600 (APLIC 1996). In Spain, where pole modifications for bird protection have been carried out extensively in the past decade, the estimated cost per pole is 500 euros, with a total investment of more than 7 000 000 euros (M. Ferrer, unpublished data). In the last two to three decades, growing attention to the economic and conservation impact of avian electrocution has resulted in the design and application of a number of mitigation measures, mostly modifications of pole design, widely applied in North America and Europe (APLIC 1996; Ferrer & Janss 1999). However, recent evidence suggests that such measures have brought few benefits and no certain solution to an increasing problem in both developed countries and biodiversity-rich developing countries (Bevanger 1994; Harness & Wilson 2001; Lehman 2001).

Most electrocution studies have involved lists of dead animals found under electricity poles (Harness & Wilson 2001; Rubolini *et al.* 2001), standardized counts of corpses per unit length of power line (Ferrer, de la Riva & Castroviejo 1991) and estimates of mortality rate caused by electrocution (Ferrer & Hiraldo 1992; Janss & Ferrer 2001). However, despite the magnitude of the problem for individuals, there has been little investigation of the population-level consequences of electrocution (Bevanger 1994, 1998; APLIC 1996; Lehman 2001). In particular, if mortality by electrocution is a distribution limiting factor, two predictions are testable. First, within a breeding population, territories or sites with a high electrocution risk should be abandoned or infrequently occupied, leading to spatial gaps in local distribution and eventual declines; this prediction has been suggested frequently but never tested (Bevanger & Overskaug 1998; Janss & Ferrer 2001). Secondly, populations differing in degree of electrocution risk should show different population densities and trends. To date, we are aware of only one study that found support for the first prediction (González, Bustamante & Hiraldo 1992) and none that have tested the second.

We reviewed the published literature and used a long-term data set from two eagle owl *Bubo bubo* Linnaeus populations to test the following predictions, that: (i) mortality by electrocution for this species is high and has been increasing in past decades; (ii) this mortality factor is unevenly distributed through time; (iii) pylons with certain characteristics and surrounded by specific landscapes are more likely than others to cause electrocution; (iv) within a population, electrocution risk affects spatial distribution, site occupation,

breeding performance and post-fledging survival; and (v) at the population level, population density and trend are negatively associated with electrocution risk.

The eagle owl, the largest owl in the world, is a generalist top predator with a vulnerable conservation status (Penteriani 1996). It is widely distributed throughout Europe, with highest densities recorded in low-altitude human-impacted landscapes (Marchesi, Sergio & Pedrini 2002), where the risk of electrocution is highest. As a result, electrocution has been widely identified as the major cause of mortality (see Results) and the species is thought to be one of the most affected by electrocution (Bevanger & Overskaug 1998; Penteriani 1998). In one telemetry study, 55% of 27 dispersing young were electrocuted within 1 year of their release from captivity (Larsen & Stensrud 1987), while electrocution rates of wild-born young are even higher (Bezzel & Schöpf 1986). The consequences carry economic concern and, for example, in Sweden a mitigation project was started to insulate transformers frequently damaged by eagle owl electrocution (Bevanger 1994).

Methods

STUDY AREAS

Eagle owls were monitored in two areas (hereafter referred to as main areas), from 1994 to 2003 in a 1330-km² plot located in the central-eastern Italian Alps (Trento region, 46°04'N, 11°08'E), and from 1980 to 1990 in a 3500-km² plot located in the central Apennines (Abruzzo region, central Italy, 41°49'N, 13°47'E). In the Trento plot, altitude ranged from 70 to 2400 m a.s.l. and the landscape was characterized by steep mountain slopes covered by woodland and intensively cultivated and urbanized valley floors. In the Abruzzo plot, altitude ranged from 400 to 2793 m a.s.l. and the landscape, often carved by deep rocky valleys, consisted predominantly of forested slopes with pastures and fallow farmland in the valley floors and high-altitude pastures above the tree line (Penteriani & Pinchera 1990; Marchesi, Sergio & Pedrini 2002). In addition, between 1996 and 2000, eagle owls were simultaneously censused in eight areas of the Alps: Lake Lugano, Iseo, Idro, Garda, Sarca Valley, Adige Valley, Non Valley and Brenta Valley (Sergio, Marchesi & Pedrini 2004).

STUDY DESIGN

In all study areas, eagle owls were systematically censused each year between October and January with a combination of direct and indirect methods: (i) listening to spontaneous territorial vocalizations (passive auditory surveys); (ii) eliciting territorial calls by broadcasting conspecific vocalizations (acoustic-lure surveys); (iii) observing potentially suitable cliffs during the day and at dusk for evidence of perching or departing individuals; (iv) visiting the area around potential nest or perch sites to look for recently moulted feathers, fresh

pellets and prey remains. In the Trento region, nest sites were checked when chicks were 60–70 days old to record the number of fledged young (chicks fledge at 50–60 days). Nests were checked at dusk and at night by locating fledged young from food begging calls and then observing the light reflected in the eyes of the young by using a torchlight taped to the binoculars (Marchesi, Sergio & Pedrini 2002). To assess post-fledging survival, breeding sites were checked again when chicks were 130–140 days old. To ensure the reliability of the detection method, each check (at 60–70 and at 130–140 days old) was repeated for three successive nights. In all cases the recorded number of young was consistent for all counts. The checks were very time consuming, hence, because of limited human resources, they were only carried out in 1999–2002 at a sample of 37 nests, each one from a different territory. Because telemetry data on eagle owl juveniles indicated that the earliest dispersal occurs when the young are older than 150 days (V. Penteriani & M. Delgado, unpublished data), we were confident that disappearance of ≥ 1 fledged young between the two checks was probably caused by mortality.

No productivity data were collected in the Abruzzo region because of the exceptionally time-consuming search of occupied territories and extreme inaccessibility of the nest sites. In both study areas, we collected all available information on deceased individuals reported to local authorities ($n = 28$ in Trento and $n = 10$ in Abruzzo). Dead owls were classified as electrocuted when they had burn marks or from the results of necropsies. In 11 cases (all in the Trento region) we could identify the pylon that had caused the death of the individual.

Review of published estimates of mortality by electrocution

To assess the geographical and temporal distribution of electrocution events, we reviewed all studies that reported the cause of death of at least 10 individuals. We classified the causes of death as electrocution, collision with a vehicle, persecution (e.g. shooting, trapping) or 'other'. To minimize biases, studies that only focused on electrocution were discounted from analyses. Data were available for 25 studies from eight European countries (Choussy 1971; Herrlinger 1973; Gömer 1977; Haller 1978; Rockenbauch 1978; Olsson 1979; Saurola 1979; Wickl 1979; Förstel 1983; Piechocki 1984; Bezzel & Schöpf 1986; Larsen & Stensrud 1987; Radler & Bergerhausen 1988; Hernández 1989; Penteriani & Pinchera 1990; Bayle 1992; Martínez *et al.* 1992; Rigacci 1993; Tormen & Cibien 1993; Beneyto & Borau 1996; Sascor & Maistri 1996; Marchesi, Sergio & Pedrini 2002). The time period of each study was classified as: before 1980, 1981–90 and after 1990, in order to allow for the temporal pattern of causes of death to be investigated using non-parametric correlations (Sokal & Rohlf 1981).

Identifying dangerous pylons

We used logistic regression (Tabachnick & Fidell 1996) to compare the pole design (see below) and surrounding habitat quality of 11 pylons that had caused eagle owl deaths in the Trento area, and 11 randomly selected pylons in the Trento region. Based on previous work on the species, habitat quality was measured as the distance of the pylon to the nearest freshwater body, and as the length of shorelines and the percentage of open habitats within 100 m of the pylon. Open habitats, freshwater bodies and their shores are rich in the local main prey species (Marchesi, Sergio & Pedrini 2002; see also Penteriani *et al.* 2001; Penteriani, Gallardo & Roche 2002) and their availability positively affects eagle owl productivity (Sergio, Marchesi & Pedrini 2004).

Nest site selection and territory abandonment

In the Trento region, we have previously shown that, compared with availability, eagle owls select breeding sites at lower altitude, with a more complex topography and a higher availability of open habitats and wetland shorelines within 1.5 km of the nest (Sergio, Marchesi & Pedrini 2004). We used a stepwise logistic regression discriminating between 38 owl territories and 38 random locations, which yielded the following equation: $y = -0.15(\sqrt{\text{altitude}}) + 2.87(\log_e \text{ ruggedness index}) + 0.04(\sqrt{\text{shoreline length}}) + 4.40(\arcsin \sqrt{\text{proportion of open areas}}) - 12.33$, where y is the probability of site occupancy. To test whether electrocution risk affected nest site selection, we re-ran the same stepwise model by adding the following explanatory variables to it: the distance of the nest to the nearest medium tension pylon (15–30 kV), the length of medium tension power lines and number of medium tension pylons within 1.5 km of the nest, and the number of medium tension pylons within 200 m of the nest. To weigh the mortality threat posed by each pylon further, we grouped pylons into four categories of declining danger, on the basis of previous electrocution studies: (1) pylons with transformers, cross-arms and pin-type insulators, exposed jumper wires, exposed circuit breakers, or angle pylons that allow changes in direction of the power line; (2) all other pylons with at least one conductor wire positioned on top of the cross-arms; (3) pylons with strained (horizontal) insulators; (4) pylons with suspended insulators, or which cannot cause electrocution (e.g. elicord or insulated wires) (photos available on request from the authors; for graphical representations see Harness & Wilson 2001; Mañosa 2001). We entered into the stepwise logistic model as additional explanatory variables the number of pylons within 200 m and 1.5 km of the nest and included in the threat category 1, 1 + 2, 1 + 2 + 3, and 1 + 2 + 3 + 4. All the above electrocution variables were recorded in the field and then digitized into a GIS database; hereafter, they will be referred to as estimates of electrocution risk.

To test further whether eagle owl spatial distribution was limited by electrocution risk within suitable habitat, we (i) applied the above logistic equation to the whole Trento region (6200 km²) by means of a GIS (Sergio, Marchesi & Pedrini 2004); (ii) randomly selected 38 locations within the habitat patches defined as suitable for the owl by the GIS model; (iii) collected estimates of electrocution risk in the field for the additional 38 locations; and (iv) compared them with the 38 owl territories by means of logistic regression. The explanatory variables fitted to this model were the same as those used for the previous one, with the addition of nearest neighbour distance (NND), because we have previously shown that territoriality may limit distribution within suitable habitat (Sergio, Marchesi & Pedrini 2004).

In the Abruzzo region, detailed GIS land-use maps were not available and it was impossible to collect as detailed estimates of electrocution risk as in the Trento region because of human resource limitations and inaccessibility of many breeding and random sites. Therefore, nest site selection was investigated by means of a stepwise logistic regression discriminating between 10 owl territories and 25 random locations on the basis of the following potential explanatory variables: (i) altitude, (ii) distance to the nearest medium tension pylon and (iii) length of power lines within 1.5 km of the nest. Within both the Trento and Abruzzo regions, random locations were always located on cliffs (eagle owls only nest on cliffs in both areas) and in the same range of altitude as the owl nests.

The same set of explanatory variables was used to discriminate, by means of logistic regression, between territories that were always occupied and territories that were abandoned (i.e. not reoccupied for at least 7 consecutive years) during the study period. In contrast to the Abruzzo area, in the Trento region too few territories were abandoned for a meaningful comparison but some were not occupied every year, suggesting death of their occupants or breeding dispersal (Sergio & Newton 2003). Thus, we compared the infrequently occupied (unstable) territories with the always occupied (stable) ones.

Breeding performance and post-fledging survival

We used multiple regression (Sokal & Rohlf 1981) to test the effect of habitat and electrocution variables on long-term breeding performance (number of fledged young per territorial pair averaged through the years). We employed logistic regression to compare broods with and without mortality events (i.e. ≥ 1 fledged young disappeared between the first and second check) during the post-fledging period. We used the estimates of habitat quality and electrocution risk cited above as explanatory variables.

Population-level effects: a 'natural' experiment

To establish which of the two study areas was subject to the higher electrocution risk, we used a *t*-test (Sokal &

Rohlf 1981) to compare the estimates of electrocution risk for the 38 random locations in the Trento region with those for 25 random locations in the Abruzzo region. To ensure data comparability, the latter 25 locations were chosen in the same altitude range used for the Trento region (0–800 m). On the basis of this, we classified the two populations as high-electrocution and low-electrocution risk treatments and then compared their density, NND, territory abandonment rate and long-term population trend by means of *t*-tests and χ^2 tests (Sokal & Rohlf 1981). We predicted that the population with the higher electrocution risk would show lower densities and a steeper decline. In addition, we fitted the length of power lines around the nest, the study area (as a factor variable) and their interaction to a generalized linear model (GLM) logistic regression, with the stability or abandonment of each territory ($n = 38$ Trento territories and 25 Abruzzo territories) as the dependent variable. We tested the following predictions: (i) if only the area main effect is significant, the pattern of differential territory extinction (which determined the population trend in the Abruzzo area) is caused by local factors independent of electrocution (e.g. differential resource availability); (ii) if only the electrocution risk main effect is significant, electrocution is the most likely cause of decline; (iii) if only the interaction term is significant, the effect of electrocution is dependent on local context (e.g. resource availability). Finally, because a comparison between two areas may not yield conclusive evidence of the effect of a single variable (Hurlbert 2004), we further related population density to electrocution risk in eight Alpine study areas. Electrocution risk was assessed by: (i) plotting 10 random locations in each area and measuring estimates of electrocution risk within 1.5 km of each location, and (ii) calculating the mean values of electrocution risk for each area. Because we have previously shown that owl density is related to the availability of open areas, we calculated owl density as the number of territories per unit area of open habitat.

Throughout the analyses, when data distribution allowed it, all multivariate models were run through a standard and GLM procedure (software $\overline{\text{M}}\overline{\text{N}}\overline{\text{N}}\overline{\text{V}} 4.0$). We then retained the model with the highest predictive power (R^2). GLM modelling procedures followed Crawley (1993). To reduce collinearity and the number of variables presented to logistic models, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (Sergio & Bogliani 2000 and references therein). In this method, pairs of intercorrelated variables ($r > 0.6$) are considered as estimates of a single underlying factor. Only the variable judged of greatest importance to the study organism is retained for analysis. Of the remaining variables, only those for which high univariate differences ($P < 0.1$) were detected between nest sites and random locations were included in multivariate analyses.

Prior to parametric tests, variables were logarithmically, square root- or arcsin square root-transformed, if

necessary, to achieve a normal distribution. For all analyses means are given ± 1 SE; tests were two-tailed and the statistical significance was set at $\alpha \leq 0.05$. When multiple tests were performed on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989). Throughout the paper, the term pylon and power lines refer exclusively to medium tension pylons and power lines.

Results

Electrocution was the greatest cause of mortality in 68% of the 25 published studies and accounted, on average, for $38.2 \pm 3.8\%$ of the reported deaths (range 9.7–75.0%). The reported percentage mortality by electrocution had increased over the past three decades ($r_s = 0.465$, $n = 25$, $P = 0.045$) but there was no significant trend for either persecution ($r_s = 0.07$, $n = 25$, $P = 0.735$) or collision with a vehicle ($r_s = -0.27$, $n = 25$, $P = 0.322$). Therefore, the increasing incidence of electrocution was not an artefact of a decline in the other main causes of mortality.

In the Trento region, electrocution was only recorded between June and October, with a peak between August and October. This corresponded with the period of dispersal of the young (Fig. 1).

The percentage of open areas within 100 m of the pylon was the only variable to differ between pylons that caused owl mortality and random pylons in univariate comparisons (Table 1). It was also the only variable to enter the stepwise logistic model that discriminated between dangerous and random pylons ($B = -3.02 \pm 1.39$, Wald

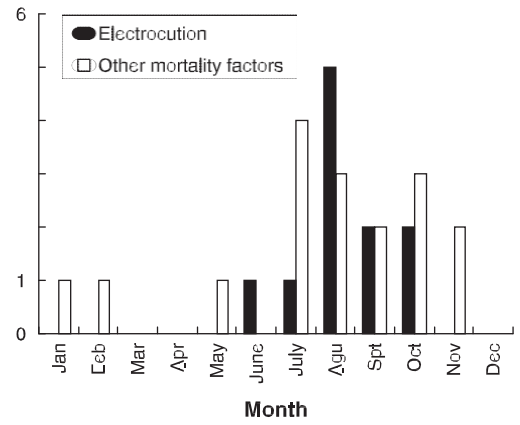


Fig. 1. The monthly variation in the number of eagle owls reported to local authorities and killed by electrocution or other causes showed that mortality peaked between August and October, the period of juvenile dispersal (Trento region, Italian Alps, 1994–2003).

$= 4.68$, $P = 0.049$; B for constant = 2.87 ± 1.42 , percentage correctly reclassified cases = 77.3%).

In univariate comparisons for the Trento region, eagle owl territories were at a higher risk of electrocution than random locations (Table 2). However, this was probably caused by a preference for low-altitude prey-rich sites (Marchesi, Sergio & Pedrini 2002; Sergio, Marchesi & Pedrini 2004) coupled with an increase in electrocution risk with declining altitude (for all estimates of electrocution risk: $r \geq |0.26|$, $n = 76$, $P \leq 0.022$). In fact, once the effects of altitude and habitat quality were accounted for, none of the estimates of electrocution risk entered the stepwise logistic model discriminating between the 38 owl territories and the 38 random locations. Therefore, the equation of the logistic model remained unchanged (see Methods; Sergio, Marchesi & Pedrini 2004).

Table 1. Mean (± 1 SE) estimates of habitat variables and pole design for 11 pylons that caused eagle owl electrocution accidents and 11 random pylons (Trento region, 1993–2002). Univariate differences between the two samples were tested by means of t -tests: $*P < 0.05$

Variable	Dangerous pylons	Random pylons
Altitude (m a.s.l.)	479.5 \pm 81.9	533.2 \pm 96.0
% open areas ^{††*}	78.42 \pm 7.44	45.15 \pm 9.54
Length of wetland shoreline (m) [§]	275.4 \pm 85.3	269.4 \pm 79.1
Distance to the nearest water body (m) [¶]	201.6 \pm 54.5	275.9 \pm 117.4
% pylons in threat category 1 ^{††††}	54.5	36.4

[†]Within 100 m of the pylon.

^{††} t -test performed on the variable converted to its proportion and arcsin $\sqrt{}$ transformed.

[§] t -test performed on the variable $\sqrt{}$ transformed.

[¶] t -test performed on the variable \log_e transformed.

^{†††}Includes pylons with transformers, cross-arms and pin-type insulators, exposed jumper wires, exposed circuit breakers or angle-pylons that allow changes in direction of the power line (see the Methods).

^{††††}Tested by means of a χ^2 on frequency counts.

Table 2. Mean (± 1 SE) estimates of habitat quality and electrocution risk for 38 eagle owl territories and 38 random locations (Trento region, 1993–2002). The habitat quality variables were chosen on the basis of previous work on the species (Marchesi, Sergio & Pedrini 2002; Sergio, Marchesi & Pedrini 2004). Altitude and all distance variables are expressed in metres. Univariate differences between the two samples were tested by means of *t*-tests: ** $P < 0.01$, *** $P < 0.001$

Variable	Eagle owl territories	Random locations
Altitude†***	530.4 \pm 57.8	790.0 \pm 28.9
Ruggedness index‡***	54.2 \pm 3.0	36.1 \pm 2.2
Length of wetland shoreline‡§***	10 252.3 \pm 729.2	6516.8 \pm 500.0
% open areas¶***	40.0 \pm 3.5	12.3 \pm 1.9
Length of power lines†§**	3863.0 \pm 384.6	2192.2 \pm 283.8
No. of pylons of threat category 1†§***	11.8 \pm 1.5	5.7 \pm 0.9
No. of pylons of threat category 1 + 2§***	26.7 \pm 3.2	10.9 \pm 1.9
No. of pylons of threat category 1 + 2 + 3§***	28.6 \pm 3.3	13.1 \pm 2.1
No. of pylons of threat category 1 + 2 + 3 + 4†§***	31.8 \pm 3.2	15.8 \pm 2.0
No. of pylons of threat category 1 (200 m)††	0.26 \pm 0.13	0.08 \pm 0.06
No. of pylons of threat category 1 + 2 (200 m)††	0.42 \pm 0.17	0.08 \pm 0.06
No. of pylons of threat category 1 + 2 + 3 (200 m)††	0.53 \pm 0.19	0.18 \pm 0.09
No. of pylons of threat category 1 + 2 + 3 + 4 (200 m)††	0.58 \pm 0.21	0.24 \pm 0.11
Distance to nearest pylon of category 1‡§***	558.0 \pm 59.4	1053.5 \pm 94.6
Distance to nearest pylon of category 1 + 2***	511.7 \pm 60.4	1029.1 \pm 91.2
Distance to nearest pylon of category 1 + 2 + 3**	504.2 \pm 61.3	994.3 \pm 96.8
Distance to nearest pylon of category 1 + 2 + 3 + 4†§***	492.2 \pm 64.5	880.5 \pm 108.9

†*t*-test performed on the variable $\sqrt{\quad}$ transformed.

‡*t*-test performed on the variable \log_e transformed.

§Measured within 1.5 km of the nest or random location.

¶*t*-test performed on the variable converted to its proportion and arcsin $\sqrt{\quad}$ transformed.

††Measured within 200 m of the nest or random location.

Four variables entered a GLM logistic regression discriminating between 38 owl territories and 38 random locations chosen within habitat patches defined as suitable by the GIS model: ruggedness index (\log_e transformed, $B = 4.13 \pm 1.09$, $F = 33.5$, $P < 0.0001$), NND (\log_e transformed, $B = 3.21 \pm 0.68$, $F = 48.9$, $P < 0.0001$), shoreline length ($\sqrt{\quad}$ transformed, $B = 0.06 \pm 0.01$, $F = 7.5$, $P < 0.02$) and percentage of open areas within 1.5 km of the nest (arcsin $\sqrt{\quad}$ transformed, $B = 3.4 \pm 1.22$, $F = 13.2$, $P < 0.002$; B for constant = -49.74 ± 9.71 , percentage correctly reclassified cases = 86.2%). No estimate of electrocution risk entered the model. Therefore, within suitable habitat, eagle owls maximized their distance to conspecifics and the availability of suitable foraging habitats in the nest surroundings.

In the Abruzzo region, estimates of electrocution risk also increased with declining altitude ($r \geq |0.53|$, $n = 35$, $P \leq 0.002$). The distance to the nearest pylon was the only variable to enter a logistic regression discriminating between 10 currently occupied owl territories and 25 random locations (\log_e transformed, $B = -1.80 \pm 0.72$, Wald = 6.27, $P = 0.012$, B for constant = 14.14 ± 5.37). Altitude and the other estimates of electrocution risk did not enter the model, which correctly reclassified 80% of the cases. The mean distance to the nearest pylon was 2695 \pm 562 m for owl territories and less than half, 1312 \pm 205 m, for random locations.

In the Trento region, unstable territories had consistently higher levels of electrocution risk than stable territories for all variables (binomial test, $P = 0.0002$; Table 3) but none of the individual comparisons was significant and none of the electrocution or habitat variables entered the logistic model. In the Abruzzo

region, abandoned territories were at lower altitude and had higher levels of electrocution risk than stable territories (Table 3). The distance to the nearest pylon was the only variable to enter the stepwise logistic regression discriminating between stable and abandoned territories (\log_e transformed, $B = -3.20 \pm 1.26$, Wald = 6.49, $P < 0.011$; B for constant = 23.23 ± 9.01 , percentage correctly reclassified cases = 80.0%).

Shoreline length was the only variable to enter a stepwise multiple regression with the mean number of fledged young as the dependent variable ($B = 0.43 \pm 0.15$, $t = 2.86$, $P = 0.008$, $R^2 = 0.21$). The presence/absence of pylons within 200 m of the nest was the only variable to enter a stepwise logistic regression discriminating between broods with and without mortality events in the post-fledging period ($B = 3.95 \pm 1.18$, Wald = 11.09, $P = 0.001$; B for constant = -0.81 ± 0.60 , percentage correctly reclassified cases = 86.5%). Nine of 10 broods with partial or complete brood mortality had at least one pylon within 200 m of the nest (Fig. 2). In five cases missing young were found dead by electrocution under the pylon nearest to the nest.

Random locations in the Abruzzo region were nearer to the nearest pylon and had a higher length of power lines within 1.5 km than those in the Trento region

Table 3. Mean (± 1 SE) estimates of habitat quality and electrocution risk for eagle owl territories occupied throughout the study (stable) and owl territories abandoned or occupied only in some of the year of study (unstable) (in the Trento region, $n = 31$ stable and 7 unstable territories, in the Abruzzo region, $n = 10$ stable and 15 abandoned territories). Univariate differences between the two samples were tested by means of t -tests: ** $P < 0.01$, *** $P < 0.001$

Variable	Stable territories	Unstable or abandoned territories
Trento region		
Altitude [†]	549.8 \pm 68.4	444.3 \pm 69.5
Ruggedness index [‡]	55.7 \pm 3.3	47.6 \pm 7.3
Length of wetland shoreline ^{†§}	10534.6 \pm 844.1	9002.2 \pm 1305.0
% open areas [¶]	25.9 \pm 3.1	53.4 \pm 10.1
Length of power lines ^{†§}	3860.9 \pm 354.7	4115.8 \pm 1620.4
No. of pylons of threat category 1 ^{‡§}	10.9 \pm 1.1	15.9 \pm 6.5
No. of pylons of threat category 1 + 2 [§]	25.3 \pm 2.9	32.9 \pm 12.6
No. of pylons of threat category 1 + 2 + 3 [§]	27.4 \pm 2.8	34.0 \pm 13.7
No. of pylons of threat category 1 + 2 + 3 + 4 ^{†§}	30.9 \pm 2.9	35.6 \pm 13.1
No. of pylons of threat category 1 (200 m) ^{†††}	0.13 \pm 0.01	0.86 \pm 0.59
No. of pylons of threat category 1 + 2 (200 m) ^{††}	0.26 \pm 0.11	1.14 \pm 0.74
No. of pylons of threat category 1 + 2 + 3 (200 m) ^{††}	0.35 \pm 0.13	1.29 \pm 0.84
No. of pylons of threat category 1 + 2 + 3 + 4 (200 m) ^{††}	0.42 \pm 0.17	1.29 \pm 0.84
Distance to nearest pylon of category 1 [‡]	586.3 \pm 68.1	432.9 \pm 109.7
Distance to nearest pylon of category 1 + 2	530.1 \pm 70.2	430.0 \pm 107.6
Distance to nearest pylon of category 1 + 2 + 3	523.2 \pm 71.0	420.0 \pm 112.5
Distance to nearest pylon of category 1 + 2 + 3 + 4 [‡]	508.5 \pm 75.3	420.0 \pm 112.5
Abruzzo region		
Altitude ^{**}	1217.0 \pm 26.4	939.3 \pm 69.1
Length of power lines ^{†§**}	560.0 \pm 260.0	2810.0 \pm 492.8
Distance to nearest pylon ^{†***}	2695.0 \pm 562.1	850.0 \pm 139.1

[†] t -test performed on the variable $\sqrt{\quad}$ transformed.

[‡] t -test performed on the variable \log_e transformed.

[§]Measured within 1.5 km of the nest or random location.

[¶] t -test performed on the variable converted to its proportion and arcsin $\sqrt{\quad}$ transformed.

^{††}Measured within 200 m of the nest or random location.

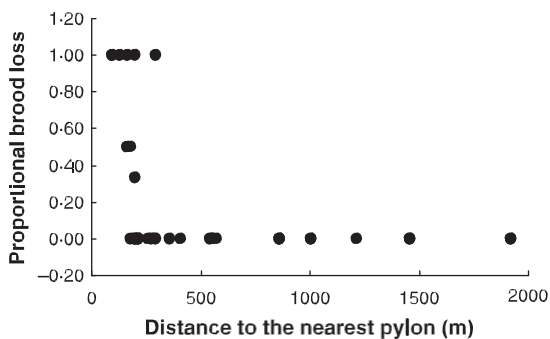


Fig. 2. Partial or complete brood loss (proportion of fledged young missing at the second check) in the post-fledging dependence period related to proximity to the nearest pylon in an eagle owl population in the Trento region (Italian Alps, 1999–2002).

(Table 4). Therefore, we classified the Abruzzo region as a high electrocution-risk treatment. The high electrocution-risk population had a lower density, a higher mean NND, a higher rate of territory abandonment and a higher incidence of mortality by electrocution than the lower electrocution risk population (Table 4). Furthermore, in the 10 years of study, the Abruzzo population was in steep decline while the Trento one was stable (Table 4). However, in a GLM logistic regression with territory stability or abandonment as the dependent variable, only the interaction term of

study area and electrocution risk was significant (area main effect: $B = -0.69 \pm 1.12$, $t = 0.62$, $P = \text{NS}$; electrocution main effect: $B = 0.001 \pm 0.001$, $t = 0.72$, $P = \text{NS}$; $B = 0.01 \pm 0.001$, $t = 2.11$, $P < 0.05$). Finally, population density was negatively related to electrocution risk [number of pylons of threat category 1 per unit area] in the eight Alpine study areas ($r_s = -0.86$, $P = 0.007$).

Discussion

Electrocution had diffuse effects on most tested variables, the effects being more severe in the population subject to the higher electrocution risk. Furthermore, the data available for the Trento region showed that the impact of electrocution varied both in time and space. Spatially, pairs of owls with a pylon in the immediate proximity of the nest had a high probability of partial or complete brood loss in the post-fledging period. We estimated that 17% of the chicks fledged by the population were lost to electrocution at pylons near the nests. Similarly, pylons surrounded by open areas, i.e. good hunting perches (Penteriani 1996), were more likely to cause electrocution than random pylons. Such 'attractive' pylons may function as ecological traps (Gates & Gysel 1978), as previously reported for other species (Benson 1982). Temporally, electrocution casualties peaked in the period of juvenile dispersal,

Table 4. Mean (± 1 SE) amount of electrocution risk, population trend and abundance for two eagle owl populations subject to differential levels of electrocution risk (Abruzzo and Trento region of central and northern Italy). Univariate differences between the two samples were tested by means of *t*-tests: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Variable	Abruzzo region	Trento region
Distance to the nearest pylon (m) ^{†*}	570.4 \pm 75.8 (25)	880.5 \pm 108.9 (38)
Length of power lines within 1.5 km (m) ^{†**}	2714.0 \pm 336.8 (25)	2192.2 \pm 283.8 (38)
Density (territories/100 km ²) [‡]	0.28	1.82
Nearest neighbour distance (m) ^{***}	18 000 \pm 1542 (10 §)	3684.9 \pm 192.6 (38§)
Territory abandonment rate ^{¶**}	60.0 (25)	18.4 (38)
% population trend [#]	-60.0	0.0
% mortality by electrocution ^{§§}	70.0 (10)	47.1 (34)

[†]Measured in the altitude range 0–800 m a.s.l. at 25 and 38 random locations in the Abruzzo and Trento region, respectively.

[‡]Averaged across the last 5 years (1986–90) and the first 5 years (1994–98) of study for the Abruzzo and Trento region, respectively, to make the periods coincide as much as possible.

[§]Number of territories in the population.

[¶]Percentage of territories abandoned during the study period.

^{††}Tested by means of a χ^2 test on frequency counts.

[#]Measured as: (density in the last year of study – density in first year)/density in first year.

^{§§}Tested by Fisher's exact test (Sokal & Rohlf 1981).

probably because of their higher mobility and because the population was highest in this period (Benson 1982; Harness & Wilson 2001). The fact that mortality by electrocution targeted recently fledged and dispersing young does not discount the possibility of a population effect, because (i) adult individuals also regularly feature among electrocution victims (Hernández 1989) and (ii) erosion of the floater sector of a population may result in sudden population crashes in the long term (Delibes, Gaona & Ferreras 2001).

Even if the preference for low-altitude areas in the Alps (Marchesi, Sergio & Pedrini 2002) exposed them to high electrocution risk, eagle owls did not seem to actively avoid sites rich in power lines, suggesting that they were either incapable of recognizing them as hazardous or were not systematically killed to the point of permanent territory abandonment. However, unstable territories were subject to a consistently higher electrocution risk than stable ones, suggesting that they may have a higher turnover of individuals (Newton 1991). The temporal evolution of territory distribution was even more extreme in the higher electrocution risk Abruzzo area. There, territories were originally distributed across the entire spectrum of altitude between 400 and 1350 m a.s.l. Subsequently, territories in the proximity of power lines, most of which were at lower altitude, were progressively abandoned, so that the original portion of the population below 1000 m completely disappeared. Such a trend was unlikely to be caused by other factors, such as prey abundance and persecution. Brown rats *Rattus norvegicus*, hedgehogs *Erinaceus europaeus* and edible dormice *Glis glis*, the main prey species in the Alps (Marchesi, Sergio & Pedrini 2002), are extremely abundant in low-altitude areas of the Apennines (Spagnesi & De Marinis 2002) and human persecution was present in the Apennines during the study period, not only at low altitude (Ragni, Magrini & Armentano 1986). In contrast, the abandonment of low-altitude territories and of a few

high-altitude ones, all of which were in close proximity to power lines, was consistent with abandonment due to electrocution of owls without subsequent replacement. This was confirmed by three cases in which the installation of new power lines near three owl nests was shortly followed by the electrocution of both the adults, with consequent territory abandonment.

Finally, the high electrocution-related abandonment rate of territories in the Abruzzo area resulted in a steeply declining, low-density population in the higher electrocution risk area and a stable, high-density population in the lower electrocution risk area, confirming our predictions. However, the effect of electrocution on territory abandonment interacted with an area effect, suggesting that the impact of electrocution may be context-dependent: in both areas, electrocution risk was higher at abandoned than at stable territories, but territory abandonment seemed to require a higher level of electrocution risk in the Trento region (Table 3). We suspect that the Trento population had higher food availability, as suggested by its higher density even before the progressive decline of the Abruzzo population. This could lead to higher productivity and abundance of floaters, young itinerant owls, ready to replace any territory holders eliminated by electrocution. Such a scenario would be compatible with the higher frequency of unstable but not abandoned territories in Trento. Finally, when we limited our analysis to eight study areas within the same region (i.e. with similar resource availability), density was negatively related to electrocution risk. Overall, such results were suggestive of a locally tailored threshold of landscape 'power line load' (Bevanger 1994) beyond which there may be a population effect on local distribution, nest dispersion and population trend. Unfortunately, this implies the absence of an absolute threshold value applicable to all areas.

In conclusion, our results showed how a subtle anthropogenic disturbance may alter the gradient of environmental quality for a conservation-sensitive

species in a short time frame, leading to potential population limitation through erosion of available habitat. Similar consequences may be caused by other human-induced sources of mortality (Barrios & Rodríguez

2004). In our case, the hazardous landscape features peaked at low altitude, which may potentially result in fragmented populations progressively isolated on mountain tops, with the eventual risk of local extinction being especially likely for low dispersal species (Hanski 1999). As a result, we may expect the highest impacts on low-altitude, low-density and low-dispersal species. Furthermore, in mountain environments biodiversity often peaks at low altitude (e.g. in the Alps; Sergio, Marchesi & Pedrini 2004), leading to conflict between human development and commitments to biodiversity preservation.

Pylon design, on which most mitigation measures are based (APLIC 1996), did not enter any of our models, not even the one discriminating between pylons with and without mortality events. This is probably because most pylons in our area were hazardous. For example, of the 1817 poles measured in the Trento area, only 13% were safe and 79% were in the two most hazardous threat categories. Therefore, any pylon that an owl landed on was likely to represent an electrocution hazard. In this scenario, the strategic location of a pylon (in good hunting habitat or near a nest) was probably more important than its design. Furthermore, given the enormous spread of dangerous pylons, it is unrealistic to propose they should all be insulated but the type of pylons to be insulated should be prioritized urgently. Based on our data, we suggest the following guidelines: (i) insulate all pylons within 200–300 m of known nests; (ii) because the (cliff) nests of this species are often difficult to locate, insulate all pylons within 300 m of all cliffs, especially those below 800 m altitude; (iii) insulate all pylons with more than 40–50% open habitat in a 100-m radius; (iv) for already depleted populations, such as the Abruzzo population, insulate all pylons within 2 km of stable and abandoned nest sites; (v) insist that local electricity companies (a) build new lines that are not dangerous (which is cheaper than retrofitting existing ones, e.g. in the USA retrofitting an average pole costs \$400 while building a new raptor-safe three-phase tangent pole adds \$25 to its construction cost; R. Harness, personal communication), (b) digitize in GIS the location and design details of all pylons and (c) initiate systematic, GIS-based recording of bird casualties [both types of information (b and c) are currently non-existent or largely incomplete in several countries]; (vi) ensure adequate population monitoring after the application of mitigation measures; and (vii) evaluate the characteristics of the landscape crossed by power lines to curtail their presence in large patches of open areas with scarce availability of alternative perch sites.

Finally, even though a complete demographic study would be needed to assess fully the population impact of electrocution, collecting detailed data on survival and immigration rates may be a daunting task for long-lived, low-density species such as the eagle owl, especially for already depleted populations. Therefore, when hypotheses of population impact need to be tested urgently, the approach we have used may be a potential substitute or a useful complementary and preliminary investigation. Given the steeply growing number of habitat selection studies, the growing availability of GIS land-use maps, and the increasing use of GIS by electricity companies (APLIC 1996), it is surprising that only two studies to date have incorporated electrocution risk in a habitat selection model (González, Bustamante & Hiraldo 1992; Ferrer & Harte 1997). Furthermore, our data demonstrate how the failure to include electrocution risk in habitat models of electrocution-sensitive species may result in misleading results. For example, a standard nest site selection model ignoring electrocution risk for the Abruzzo region would have led us to conclude that eagle owls avoided low-altitude areas, i.e. the opposite of the situation found throughout Europe (reviewed in Marchesi, Sergio & Pedrini 2002). Therefore, there is an urgent need for more investigation of the habitat-mediated population effects of electrocution, especially for other species subject to a high risk of electrocution.

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References

- APLIC (Avian Power Line Interaction Committee) (1996) *Suggested Practices for Raptor Protection on Power Lines: The State of the Art in 1996 Edison*. Electric Institute / Raptor Research Foundation, Washington, DC.
- Barrios, L. & Rodríguez, A. (2004) Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *Journal of Applied Ecology*, **41**, 72–81.
- Bayle, P. (1992) *Le Hibou Grand-duc, Bubo bubo, dans le Parc National du Mercantour et ses environs*. Parc National du Mercantour, Nice, France.
- Beneyto, A. & Borau, J.A. (1996) El Buho real (*Bubo bubo*) en Cataluña (NE de España). *Biología y Conservación de las Rapaces Mediterráneas, 1994* (eds J. Muntaner & J. Mayol), pp. 477–483. SEO, Madrid, Spain.
- Benson, P.C. (1982) *Prevention of Golden Eagle Electrocution*. Electric Power Research Institute, Palo Alto, CA.
- Bevanger, K. (1994) Bird interactions with utility structures: collision, electrocution, causes and mitigation measures. *Ibis*, **136**, 412–425.

- Bevanger, K. (1998) Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biological Conservation*, **86**, 67–76.
- Bevanger, K. & Overskaug, K. (1998) Utility structures as a mortality rate for raptors and owls in Norway. *Holarctic Birds of Prey* (eds R.D. Chancellor, B.U. Meyburg & J.J. Ferrero), pp. 381–392. ADENEX-WWGBP, Calamonte, Spain.
- Bezzel, E. & Schöpf, H. (1986) Anmerkungen zur Bestandentwicklung des Uhus (*Bubo bubo*) in Bayern. *Journal für Ornithologie*, **127**, 217–228.
- Choussy, D. (1971) Etude d'une population de Grand-ducs *Bubo bubo* dans le Massif Central. *Nos Oiseaux*, **31**, 37–56.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Science, Oxford, UK.
- Delibes, M., Gaona, P. & Ferreras, P. (2001) Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist*, **158**, 277–285.
- Ferrer, M. & Harte, M. (1997) Habitat selection by immature Spanish imperial eagles during the dispersal period. *Journal of Applied Ecology*, **34**, 1359–1364.
- Ferrer, M. & Hiraldo, F. (1992) Man-induced sex-biased mortality in the Spanish imperial eagle. *Biological Conservation*, **60**, 57–60.
- Ferrer, M. & Janss, G.F.E. (1999) *Birds and Power Lines: Collision, Electrocutation and Breeding*. Servicios Informativos Ambientales/Quercus, Madrid, Spain.
- Ferrer, M., de la Riva, M. & Castroviejo, J. (1991) Electrocutation of raptors on power lines in southwestern Spain. *Journal of Field Ornithology*, **62**, 181–190.
- Förstel, A. (1983) Bestandsaufstockung des Uhus *Bubo bubo* in Bayern. *Anzeiger der Ornithologischen Gesellschaft in Bayern*, **22**, 145–167.
- Gates, J.E. & Gysel, L.W. (1978) Avian nest dispersion and nesting success in field–forest ecotones. *Ecology*, **59**, 871–883.
- González, L.M., Bustamante, J. & Hiraldo, F. (1992) Factors influencing the present distribution of the Spanish imperial eagle *Aquila adalberti*. *Biological Conservation*, **51**, 311–319.
- Görner, M. (1977) Der Uhu und sein Schutz in Thüringen. *Landschaftspflege und Naturschutz in Thüringen*, **14**, 1–16.
- Green, R.H. (1979) *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley & Sons, NY.
- Haller, H. (1978) Zur populationsökologie des Uhus *Bubo bubo* im Hochgebirge: Bestand, bestandesentwicklung und Lebensraum in den Rätischen Alpen. *Ornithologische Beobachter*, **75**, 237–265.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Harness, R.E. & Wilson, K.R. (2001) Electric-utility structures associated with raptor electrocutions in rural areas. *Wildlife Society Bulletin*, **29**, 612–623.
- Hernández, M. (1989) Mortalidad del buho real en España. *Quercus*, **40**, 24–25.
- Herrlinger, E. (1973) *Die Wiedereinbürgerung des Uhus, Bubo bubo, in der Bundesrepublik Deutschland*. Monographien No. 4. Bonner Zoologische Beiträge, Bonn, Germany.
- Hurlbert, S.T. (2004) On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. *Oikos*, **104**, 591–597.
- Janss, G.F.E. & Ferrer, M. (2001) Avian electrocution mortality in relation to pole design and adjacent habitat in Spain. *Bird Conservation International*, **11**, 3–12.
- Larsen, R.S. & Stensrud, O.H. (1987) Dispersal and mortality of juvenile eagle owls released from captivity in southeast Norway as revealed by radio telemetry. *US Forest Service General Technical Report*, **142**, 215–219.
- Lehman, R.N. (2001) Raptor electrocution on power lines: current issues and outlook. *Wildlife Society Bulletin*, **29**, 804–813.
- Mañosa, S. (2001) Strategies to identify dangerous electricity pylons for birds. *Biodiversity and Conservation*, **10**, 1997–2012.
- Marchesi, L., Sergio, F. & Pedrini, P. (2002) Costs and benefits of breeding in human-altered landscapes for the eagle owl *Bubo bubo*. *Ibis*, **144**, 164–177.
- Martinez, J.E., Sanchez, M.A., Carmona, D., Sanchez, J.A., Ortuño, A. & Martinez, R. (1992) The ecology and conservation of the eagle owl *Bubo bubo* in Murcia, south-east Spain. *The Ecology and Conservation of European Owls* (eds C. A. Galbraith, I. R. Taylor & S. Percival), pp. 84–88. Joint Nature Conservation Committee, Peterborough, UK.
- Newton, I. (1991) Habitat variation and population regulation in sparrowhawks. *Ibis*, **133** (Supplement 1), 76–88.
- Olsson, V. (1979) Studies on a population of eagle owls, *Bubo bubo* (L.), in southeast Sweden. *Viltrevy*, **11**, 3–99.
- Penteriani, V. (1996) *The Eagle Owl*. Edagricole, Bologna, Italy.
- Penteriani, V. (1998) *The Impact of Power Lines on Bird Fauna*. WWF, Firenze, Italy.
- Penteriani, V. & Pinchera, F. (1990) Censimento del Gufo reale, *Bubo bubo*, in un'area dell'Appennino abruzzese. *Rivista Italiana di Ornithologia*, **60**, 119–128.
- Penteriani, V., Gallardo, M. & Roche, P. (2002) Landscape structure and food supply affect eagle owl (*Bubo bubo*) density and breeding performance. A case of intra-population heterogeneity. *Journal of Zoology, London*, **257**, 365–372.
- Penteriani, V., Gallardo, M., Roche, P. & Cazassus, H. (2001) Effects of spatial structure and composition on the settlement of the eagle owl *Bubo bubo* in a Mediterranean habitat. *Ardea*, **89**, 331–340.
- Piechocki, R. (1984) Todesursachen, Gewichte und Maße vom Uhu (*Bubo b. bubo*). *Hercynia*, **21**, 52–66.
- Radler, K. & Bergerhausen, W. (1988) On the life history of a reintroduced population of eagle owls (*Bubo bubo*). *Proceedings of the International Symposium on Raptor Reintroductions* (eds D.K. Garcelon & G.W. Roemer), pp. 83–94. Institute of Wildlife Studies, Arcata, CA, USA.
- Ragni, B., Magrini, M. & Armentano, L. (1986) Aspetti della biologia dell'Aquila Reale *Aquila chrysaetos* nell'Appennino umbro-marchigiano. *Avocetta*, **10**, 71–85.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Rigacci, L. (1993) *Il Gufo reale in Toscana: studio per la reintroduzione*. WWF, Firenze, Italy.
- Rockenbach, D. (1978) Untergang und Wiederkehr des Uhus, *Bubo bubo*, in Baden-Württemberg. *Anzeiger der Ornithologischen Gesellschaft in Bayern*, **17**, 293–328.
- Rubolini, D., Bassi, E., Bogliani, G., Galeotti, P. & Garavaglia, R. (2001) Eagle owl *Bubo bubo* and power line interactions in the Alps. *Bird Conservation International*, **11**, 319–324.
- Sascor, R. & Maistri, R. (1996) *Il Gufo reale: ecologia, status e dinamica di popolazione in Alto Adige*. WWF and Centro di Ecologia Alpina, Trento, Italy.
- Saurola, P. (1979) Rengastettujen petolintujemme löytymistavat. *Lintumies*, **14**, 15–21.
- Sergio, F. & Bogliani, G. (2000) Hobby *Falco subbuteo* nest-site selection and productivity in relation to intensive agriculture and forestry. *Journal of Wildlife Management*, **64**, 637–646.
- Sergio, F. & Newton, I. (2003) Occupancy as a measure of territory quality. *Journal of Animal Ecology*, **72**, 857–865.
- Sergio, F., Marchesi, L. & Pedrini, P. (2004) Integrating individual habitat choices and regional distribution of a biodiversity indicator and top predator. *Journal of Biogeography*, **31**, 619–628.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W.H. Freeman, NY.
- Spagnesi, M. & De Marinis, A.M. (2002) *Mammiferi d'Italia*. Istituto Nazionale per la Fauna Selvatica and Ministero dell'Ambiente e della Tutela del Territorio, Savignano, Italy.
- Tabachnick, B.G. & Fidell, L.S. (1996) *Using Multivariate Statistics*. HarperCollins, New York, NY.
- Tormen, G. & Cibien, A. (1993) Il Gufo reale *Bubo bubo* in provincia di Belluno. Dati preliminari. *Atti 1o Convegno Faunisti Veneti*, **1**, 53–59.
- Wickl, K.H. (1979) Der Uhu (*Bubo bubo*) in Bayern. *Garmischer Vogelkundliche Berichte*, **6**, 1–47.