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ORIGINAL ARTICLE

Rainfall and landscape features affect productivity in an alpine population of Eagle Owl *Bubo bubo*

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Abstract We investigated the effects of habitat structure and composition, rainfall and nest spacing on the productivity of an Eagle Owl *Bubo bubo* population in Piedmont, northern Italy, at 10 sites from 1996 to 2007. We modeled the effects of the above factors on the productivity of 85 breeding attempts through a mixed model procedure. The number of fledged young per pair was affected positively by wetland interspersion index (a potential estimate of prey abundance) and negatively by rainfall during chick-rearing and by cover of urbanized land in the nest surroundings. Our results demonstrated that productivity can be affected by a variety of factors of different kinds, which should be considered together in studies on habitat quality.

Keywords Cliff · Competition · Nesting habitat · Productivity · Rainfall · Raptors

Zusammenfassung Wir haben die Effekte von Habitatstruktur und -zusammensetzung, Niederschlag und Nestabstand auf die Produktivität einer Population des Uhus *Bubo bubo* in Piedmont, Norditalien, an zehn Standorten zwischen 1996 und 2007 untersucht. Wir haben die Effekte der obengenannten Faktoren auf die Produktivität von 85 Brutversuchen mit Hilfe einer gemischten Modell-Prozedur modelliert. Die Anzahl ausgeflogener Jungvögel pro Paar wurde positiv vom Feuchtgebiets-Interspersion-Index (einem potenziellen Maß der Beuteabundanz) und negativ vom Niederschlag während der Kükenaufzucht sowie von der Bedeckung mit urbanisiertem Land in der Nestumgebung beeinflusst. Unsere Ergebnisse zeigten, dass die Produktivität von einer Vielfalt unterschiedlicher Faktoren beeinflusst werden kann, die in Studien über Habitatqualität berücksichtigt werden sollten.

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Introduction

Population dynamics can be affected by a variety of different factors, including intra- and interspecific relationships, population size, age and individual quality of breeders, mortality and immigration/dispersal rates, and habitat quality (McPeek et al. 2001; Penteriani et al. 2004; Aebischer et al. 2010; Schaub et al. 2010). Habitat quality is shaped by environmental factors and affects fitness of a species (Newton 1998), and is commonly measured through the breeding outputs (e.g., Förschler et al. 2005). Population dynamics of territorial and solitary breeding species are affected by the quality of habitats included in the breeding territories and consequently by the distribution of resources and constraints within the landscape (Krüger and Lindström 2001; Penteriani et al. 2003, 2004). Variation in territory suitability exists to some degrees in most of animal populations (Delibes et al. 2001), and can be very strong (e.g., Ferrer and Bisson 2003; Penteriani et al. 2004).

Habitat quality studies have either analysed the effect of several factors together (e.g., Krüger 2004) or have focused on some specific elements: climatic variables (e.g., Lehikoinen et al. 2009), habitat structure (e.g., Sergio et al. 2004), land-use cover and specific pattern of resource distribution (e.g., Penteriani et al. 2004), intra- and inter-specific interactions (e.g., Brambilla et al. 2006), impact of human activity (Marchesi et al. 2002; Brambilla et al. 2010), and food availability (e.g., Lehikoinen et al. 2009) are among the ones which can affect habitat quality for animal species.

We aim at modeling how both environmental factors (such as climatic variables, habitat type and structure) and competition may influence the quality of breeding sites. Our model species, the Eagle Owl *Bubo bubo*, has been the subject of different studies on habitat quality, which focused almost exclusively on the effect of habitat traits (Sergio et al. 2004; Ortego 2007; Brambilla et al. 2010), or on spatially varying habitat traits coupled with density (Penteriani et al. 2004). Recently, interspecific competition effects and coarse measures of climatic traits have also been considered, but on a limited dataset (Brambilla et al. 2010). Moreover, some females abandon their nest after prolonged rainfall (V. Penteriani, personal communications), and the species has been recently reported to avoid high-rainfall sectors within otherwise rather uniform areas (Brambilla et al. 2010), but no study has investigated in detail the effect of rainfall on the owl breeding performance. Therefore, we explore: (1) the effect of rainfall during different phases of the breeding period; (2) the effect of competitive (intraspecific) interactions at the local scale; and (3) the effects of habitat variables, such as land-use and landscape indices known to affect habitat selection or quality in other areas.

Methods

The study area (2,255 km^2, elevation 192–4,634 m. a.s.l., 64% of territory above 1,000 m) was located in the central-western Italian Alps (Province of Verbano-Cusio-Ossola, Piedmont, 8°19′N, 46°06′E; Fig. 1). Annual precipitation averages 1,594 mm (Biancotti and Bovo 1998). The study area includes woodlands (52% of the surface), alpine meadows (11%), shrublands (9%), rocky outcrops and cliffs (8%), grasslands and cultivations (7%), wetlands (4%) and urbanized areas (3%) (CORINE Land Use; C.E.C. 1993).

From 1996 to 2007, ten Eagle Owl breeding sites (each including from one to three alternative nest-sites) were checked during November–February to assess occupancy and in late May–July to estimate reproductive success. Not all sites were occupied all years and data were available for 85 breeding attempts.

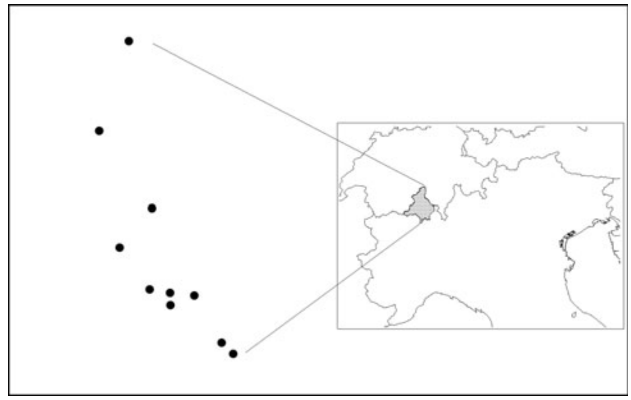

Fig. 1 Geographical location of the study province and distribution of breeding sites of Eagle Owl *Bubo bubo* in the study area; the boundaries of the study area are not shown to prevent divulging the exact location of breeding sites

Hatching dates were obtained by backdating from feather development of nestlings (Penteriani et al. 2005), while laying date was obtained by subtracting 35 days, the average incubation period, from the hatching date (Cramp 1985; Penteriani 1996).

For each breeding attempt, we recorded monthly rainfall value (in mm). Given the breeding phenology, the pre-laying period could be identified with February, the brooding period with March and chick-rearing period with April. Timing was delayed of 1 month for the territory located in the alpine area (see below). Rainfall values were obtained from two meteorological stations (ARPA Piemonte: Domodossola for nine territories in valley floors, Alpe Devero for the territory in the alpine area). The nearest neighbor distance (NND, 5.5 km ± 1.43, min 1.76, max 13.42), used as a proxy for the potential effect of intraspecific interactions, was measured through GIS software (ESRI ArcView 3.2). Interspecific interactions were not considered, as the only species known to affect habitat quality for Eagle Owl, the Peregrine Falcon *Falco peregrinus*, is a rare breeder in the area, and the two species do not share occupied cliffs.

We estimated the proportional cover of relevant land-use variables, woodland, open habitats and urbanized areas, within a 1.7-km radius, set on the basis of pair distribution (approximately half the NND) and telemetry data, which showed how radio-tagged Eagle Owls mainly forage within 1.5–2 km of the nest during breeding (Leditzing 1996; Penteriani 1996; Penteriani et al. 2008). We calculated a wetland interspersion index (WII; Sergio et al. 2004) and the length of shoreline (SHL), two factors potentially affecting prey abundance and hunting opportunities (Sergio et al. 2004). We also measured cliff length (an important factor affecting habitat selection by the species in Italian pre-Alps; Brambilla et al. 2010) for each breeding attempt (some pairs used alternative nest cliffs within their breeding site). For details of variables, see Table 1.

We calculated productivity as the average number of young fledged per pair (thus including both successful and unsuccessful breeding attempts), fledging rate as the average number of young fledged per successful pair (thus excluding failed breeding attempts), and the proportion of successful breeding attempts over the yearly total of breeding attempts. We built Poisson mixed models and binomial logistic models in which the dependent variable was the number of fledged young and the breeding success (successful attempts: at least one young fledged; or failed attempts: no young fledged), respectively, and the predictors were habitat variables (land-use cover, WII, SHL, cliff length), NND and rainfall values. Cliff length was log-transformed, while land-use cover variables were square root-arcsine transformed. To control for non-independence of breeding data, we entered year, breeding site, and area (valley floors vs. alpine, corresponding to the two meteorological stations) as random factors. The analyses were performed by means of the R software (R 2.11.1, package lme4). We sequentially removed non-significant terms from the model, so as to get a minimum adequate model (Crawley 1993). Simultaneously, we carried out an information-theoretic approach, through an AIC-based model selection (Burnham and Anderson 2002). Values and parameter estimates are reported with their standard errors.

Results

Median hatching date of pairs in valley floors was 28 March ($n = 5$), but was delayed by 1 month (1 May, $n = 2$) in the alpine area. Annual productivity averaged 0.88 ± 0.14 fledged juveniles per pair/year (min 0.29, max 1.83). Fledging rate averaged 1.89 ± 0.17 fledged juveniles per pair/year (range 1–3), and the overall proportion of successful breeding attempts was 0.46 ± 0.07 (range 0.17–1).

Two pairs of variables were highly intercorrelated ($r > |0.6|$): WII and SHL ($r = 0.69$, $P < 0.001$), cover of woodland and urbanized areas ($r = -0.69$, $P < 0.001$). We considered five alternative variable sets: one including all variables, and four excluding correlated ones (see Table 2).

In the Poisson analysis, both backward and AIC-based selection led to the same model (Table 2), which included (intercept: -3.41 ± 0.92) rainfall during rearing ($\beta = -4.93 \times 10^{-3} \pm 1.52^{-3}$, $z = -3.25$, $P = 0.001$), WII ($\beta = 0.24 \pm 0.05$, $z = 5.06$, $P < 0.001$) and cover of urbanized areas ($\beta = -2.00 \pm 0.87$, $z = -2.29$, $P = 0.022$). For that model, the ratio between the explained and the total deviance was equal to 0.40 and residuals approached a normal distribution.

The binomial logistic analysis led to a similar model: both backward and AIC-based selection led to a model similarly including (intercept: -4.41 ± 2.04) rainfall during rearing ($\beta = -8.0 \times 10^{-3} \pm 3.0^{-3}$, $z = -2.63$, $P = 0.009$), WII

Table 1 Detailed description of variables considered in the analysis

Variable	Description	Statistical notes
PRE	Rainfall during pre-laying period (mm; rainfall in February for valley floors, rainfall in March for alpine area)	
BROOD	Rainfall during brooding period (mm; rainfall in March for valley floors, rainfall in April for alpine area)	
REAR	Rainfall during chick-rearing period (mm; rainfall in April for valley floors, rainfall in May for alpine area)	
WOOD	Proportional cover of woodland in the 1.7-km radius centred on the nest (calculated once)	Square root-arcsine transformed
OPEN	Proportional cover of open habitats (grassland, cultivated areas and shrubland) in the 1.7-km radius centred on the nest (calculated once)	Square root-arcsine transformed
URB	Proportional cover of urban areas in the 1.7-km radius centred on the nest (calculated once)	Square root-arcsine transformed
WII	Wetland interspersion index, calculated once for each territory following Sergio et al. (2004), as the number of shoreline crossed by four transects (1.7 km-long) N–S, NE–SW, E–W and SE–NW	
SHL	Shoreline length, calculated once for each territory following Sergio et al. (2004)	
NND	Nearest neighbor distance, recorded each year for each nest on a GIS software	
CL	Cliff length, recorded each year for each breeding cliff	Log-transformed
AREA	Random factor included to control for non-independence of data collected within the same areas (valley floors, alpine area)	Random factor (1,2)
SITE	Random factor included to control for non-independence of data collected within the same breeding site	Random factor (1–10)
YEAR	Random factor included to control for non-independence of data collected in the same year	Random factor (1996–2007)

Table 2 Results of Poisson AIC-based model selection (all breeding attempts considered) procedures carried out starting with all variables (first two lines) and excluding correlated variables

Variables tested	Model summary	Deviance	AIC	ΔAIC
All variables	**WII–URB–REAR**	75.30	89.30	–
All variables	All other models			>2
PRE, BROOD, REAR, WOOD, OPEN, SHL, NND, CL	**SHL–REAR**	86.33	98.33	9.33
PRE, BROOD, REAR, OPEN, URB, SHL, NND, CL	SHL–REAR–URB	84.11	98.11	8.81
PRE, BROOD, REAR, WOOD, OPEN, WII, NND, CL	**WII–REAR**	79.69	91.69	2.39
PRE, BROOD, REAR, OPEN, URB, WII, NND, CL	**WII–URB–REAR**	75.30	89.30	–

Model summaries in bold represent the combinations also selected by the backward procedures

($\beta = 0.39 \pm 0.10$, $z = 3.70$, $P < 0.001$) and cover of urbanized areas ($\beta = -5.04 \pm 2.17$, $z = -2.32$, $P = 0.020$). Two alternative models with AIC comparable to the above one obtained using the full variable set were discarded because of clear collinearity problems: together with the same variables of the above one, both these two models also included cover of woodland (highly correlated with urban cover) and coefficients of the habitat cover variables in the models were clearly inflated (details not shown).

Discussion

One of the most important factors affecting population dynamics of animal species is habitat quality (McPeek et al. 2001; Penteriani et al. 2004). This is a complex concept summarizing into one term the effects of many different factors, including habitat structure, land-use cover, intra- and interspecific interactions, climate, and pattern of resource distribution.

In our model species, three different environmental factors, belonging to climate, habitat structure and land-use cover, were involved in determining habitat quality via an effect on both the number of fledged juveniles and the probability of breeding success rather than failure: the amount of rainfall during chick rearing, the wetland interspersion index and the cover of urbanized areas. Climatic factors are important determinants of reproductive success in a large number of animal species, and studies suggest that many raptor species suffer heavy rain during brood rearing (e.g., Mearns and Newton 1988; Kostrzewa and Kostrzewa 1990; Penteriani 1997; Selås 2001; Rodríguez and Bustamante 2003; Krüger 2004), likely because rain (1) increases the risk of hypothermia for young, and (2) degrades the hunting conditions of adults (Lehikoinen et al. 2009). Therefore, the effect of rainfall on owl breeding performance is perhaps not surprising, but our study is the first one to analyze in detail rainfall effects on owl productivity. The results highlight the importance of rainfall during chick-rearing, while before rearing, rainfall has no detectable effect on reproduction. As in our study area Eagle Owls nest almost exclusively on cliffs (usually well protected by overhanging rock), it is likely that in Alpine areas rainfall mainly depresses owl hunting activity/efficiency (cf. Lehikoinen et al. 2009), resulting in food shortage for chicks.

In our population, territory quality appears to vary greatly among different sites, with a few pairs producing most of the fledged chicks, a pattern also observed over a much larger sample by Penteriani et al. (2004).

The wetland interspersion index has been reported as important for Eagle Owl breeding success (Sergio et al. 2004); it is probably an indirect estimate of Brown Rat *Rattus norvegicus* density, which is the most important owl prey in Alpine populations (Marchesi et al. 2002; Bionda, unpublished data) and is particularly abundant in areas rich in water habitats (Hausser 1995; Sergio et al. 2004).

The cover of urbanized areas negatively affects breeding output, as also found in a more easterly pre-Alpine area (Bassi et al. 2003). Urban areas in our study province are probably unsuitable for hunting, and their occurrence in the nest surrounding may reduce the availability of suitable foraging areas, forcing owls to hunt far from their nests, with consequent high energetic costs and long periods spent away from the nest.

Nest spacing among breeding pairs does not affect productivity in our population, possibly due to the low breeding density, consistent with Martínez et al. (2008) but in contrast to Marchesi et al. (2002), suggesting the prevalent effect of other elements of nesting sites (Penteriani et al. 2004).

This study is the first attempt to simultaneously model the effects of multiple factors of different kind (climate, habitat cover/structure, competition) on the Eagle Owl. Our findings (1) confirm the importance of the wetland network, (2) perfectly match with the low toleration of rainy days and areas reported for Eagle Owl, and (3) provide a possible mechanism for explaining the recently reported avoidance of high-rainfall sectors in a nearby area (Brambilla et al. 2010).

Our study shows a variety of different factors affecting habitat quality. Considering different types of environmental variables allows deeper insights into habitat quality determinants, and more comprehensive analyses of factors potentially affecting habitat quality, such as habitat features, interactions and climate, should be encouraged.

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