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Eagle Owl *Bubo bubo* proximity can lower productivity of cliff-nesting Peregrines *Falco peregrinus*

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The Eagle Owl *Bubo bubo* is conventionally regarded as an important predator of smaller diurnal birds of prey. In this study, we analysed the relationships between Peregrine productivity and the proximity to Eagle Owl nests/cliffs in a cliff-nesting Peregrine *Falco peregrinus* population across the central pre-Alps of Italy and Switzerland over three breeding seasons. There was no effect of Eagle Owls on Peregrine productivity over the whole study area, whereas in a restricted sub-area, where both species occurred at higher densities, proximity to Eagle Owl nests/cliffs and syntopic co-occurrence of the two species at a given cliff complex resulted in lower Peregrine productivity. Eagle Owl effects at the wider scale were probably masked by other ecological and/or environmental features affecting reproductive success of the Peregrine, whereas these became evident when focusing on a more restricted and homogeneous area. Thus, our study suggests that Eagle Owls may affect population dynamics of diurnal raptors via an effect on productivity.

1. Introduction

The Peregrine *Falco peregrinus* and the Eagle Owl *Bubo bubo* breed on cliffs raptors in large parts of their distribution range (Cramp 1998). In the Alpine and pre-Alpine range they show similar habitat requirements, both preferring low-elevation precipitous areas, at cliff sites located between urbanised or cultivated bottom-valleys (with greater food availability, such as medium-sized birds, hunted by both species, and small- or medium-sized mammals, which are taken exclusively by the owl), and wilder mountainsides, which offer opportunities for breeding (Marchesi *et al.* 1999, Marchesi *et al.* 2002, Bassi *et al.* 2003, Ortego & Díaz 2004, Sergio *et al.* 2004, Brambilla *et al.* in press a). Such a similarity in habitat choice may lead to competition for suitable nesting cliffs, and/or in frequent encounters at such sites. The Eagle Owl is dominant over Peregrines and is capable of taking them as prey when they are brooding or at night (Monneret 2000); moreover, it has often been reported as a frequent predator of other diurnal and nocturnal raptors (Mikkola 1976, 1983, Marchesi *et al.* 2002). In fact, several cases of direct owl predation on Peregrines have been reported (Juillard & Rebetez 1991, Juillard 1998, Monneret 2000), while the opposite has never been observed, even if the Peregrine is considered capable of killing owls caught in diurnal flight (see Ratcliffe 1993). Indeed, the Eagle Owl is regarded as the most important among the very few Peregrine predators (Monneret 2000), and this has led to the hypothesis that an increasing Eagle Owl density was to be blamed for the concomitant population decline of Peregrines in the French Jura (Monneret 2000).

Therefore, it could be hypothesized that owl presence may negatively affect Peregrine breeding output, because of direct predation on either chicks or adults, as observed for other diurnal raptors (Sergio *et al.* 2003). In this study, we analysed the relationships between Eagle Owl occurrence and Peregrine reproduction in the central pre-Alps, where the two species inhabit similar cliffs and sometimes breed syntopically on the same rocky complex. The analyses were carried out at two different levels. First, we considered a large study area, then focused our analyses on a sub-area characterised by the highest breeding densities of both species (particularly of owls). In fact, it is likely that the effects of the competitive process and of owl predation on Peregrine reproduction (if any) would emerge in areas where the two species coexist at high rather than low densities.

2. Material and methods

2.1. Study area and field surveys

The study area covers the pre-Alpine sector (i.e. the southern Alps) of the provinces of Varese, Como and Lecco (northern Italy) and of southern Canton Ticino (southern Switzerland), extending over 2100 km^2. It is delimited by major geomorphological features, such as Lake Maggiore (west), Lake Lugano and the Insubric Line (north), the highest mountains between Lecco and Bergamo (east) and the sharp transition between the pre-Alpine reliefs and the Po Plain (south). The high density sub-area extends over 700 km^2, and coincides with the southern half of the Como Lake valley, including some of its lateral valleys (see Fig. 1). This sub-area is also clearly delimited by major geomorphological features; at the eastern border, it is flanked by the highest Orobie mountains, while its western part is delimited by a wide low-elevation area (including the southern portion of the Lake Lugano basin); finally, the sub-area is characterized by homogeneous carbonatic rocks, surrounded by areas of gonfolite (south-western side) or partly metamorphic rocky outcrops (northern side). The sub-area is likely to be very suitable for both species (favourable geomorphological context, high density of profitable preys, such as pigeons and waterbirds, high availability of suitable hunting habitats, such as towns and cultivated areas; Brambilla *et al.* in press b and our unpubl. data; cf. Sergio *et al.* 2003, Sergio *et al.* 2004, Brambilla *et al.* in press a) and Peregrine productivity and density are higher in this sub-area compared to the whole study area (see below and Fig. 1); moreover, although the searching effort was constant for the whole area, almost all known Eagle Owl territories occur there (see Fig. 1). In fact, in the western portion of the area, the Eagle Owl has never been recorded as a breeding species (Guenzani & Saporetti 1988, Galeotti 1990), even in recent years (for years up to 2000, see e.g. Sergio *et al.* 2003, 'Lake Maggiore' study area; for 2003–2005, see Atlante Ornitologio Georeferenziato della Provincia di Varese 2003–2005, Gruppo Insubrico di Ornitologia, in prep.). The same applies to the northern sector, where the Eagle Owl is rare and absent from wide areas (see e.g. Sergio *et al.* 2003, 'Lake Lugano' study area). There are no clear reasons for the absence of the species from such large portions of the study area; it is possible that this gap in the distribution may be due to historical factors, such as former intensive human persecution.

For a detailed description of the study site and field procedures, see Brambilla *et al.* (2003a, in press a). Overall, 30 different territories were occupied by a Peregrine pair during the period 2002–2004 (1.43 pairs/100 km^2), but not all the territories were occupied each year. Fourteen cliffs were occupied by Eagle Owls (0.67 pairs/100 km^2). The high-density sub-area hosted 16 Peregrine (2.29 pairs/100 km^2) and 13 Eagle Owl (1.86 pairs/100 km^2) pairs. Eight out of 30 Peregrine nest sites (all in the sub-area) were in cliff complexes hosting an Eagle Owl breeding pair. Peregrine nest spacing

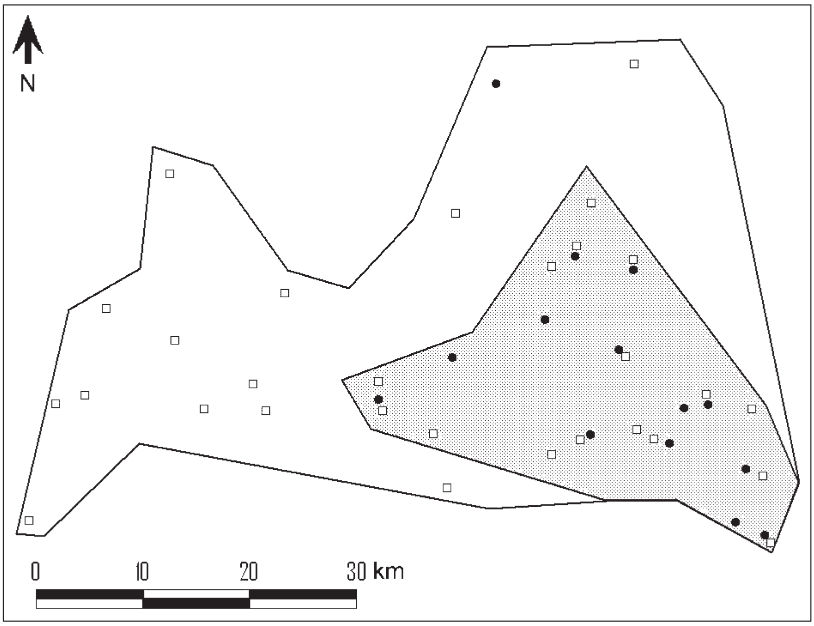

Fig. 1. Schematic map of the study area (central pre-Alps, Italy and Switzerland). The high density sub-area is highlighted (shaded area in the southern-eastern corner). Open squares represent Peregrine nests, while black dots are Eagle Owl nests/ cliffs. Detailed information is not reported because of the risk of nest robbery or disturbance to nest sites.

(evaluated through the G-statistic, see Brown and Rothery 1978, Brambilla and Rubolini 2004, Brambilla *et al.* in press a) was more uniform ($G = 0.94$ vs. $G = 0.87$) and nearest-neighbour distances were lower in the high density area compared to the whole area (4075 ± 385 (SE) m. vs. 5391 ± 609 (SE) m., respectively), and the same held true for the distance to the nearest Eagle Owl nest/cliff (2046 ± 451 (SE) m. vs. 10501 ± 2004 (SE) m., respectively). Each year between 13 and 26 Peregrine nests were surveyed to determine the number of fledged chicks. Overall, a total of 55 breeding attempts was monitored, 32 of which were by pairs nesting in the sub-area.

2.2. Analysis

To analyse the effects of the Eagle Owl on Peregrine productivity (number of young fledged per pair), we first performed an exploratory analysis by comparing the productivity of Peregrines breeding in cliff complexes occupied by the owl with that of Peregrines breeding on cliffs not occupied by the owl, by means of t-tests. Then, we related productivity to the distance from the nearest known Eagle Owl nest/cliff by means of the Pearson correlation test. For each study year, we also built two separate general linear models (GLMs) in which the response variable was productivity (a discrete, or Poisson, variable), and the predictors were Eagle Owl occurrence and distance to the nearest Eagle Owl nest/cliff, respectively. Additionally, in order to take into account the yearly variation in productivity, we calculated for each breeding season an index of relative productivity by subtracting annual means from the annual raw data (see Penteriani *et al.* 2003). By this procedure, the resulting productivity value for a given year and territory is independent of year-to-year variability (e.g. in rainy years Peregrine productivity tends to decrease, Mearns & Newton 1988), thus making values for different years comparable: negative values indicate a poorer breeding performance than the average of that year, whereas positive values indicate a better one (Penteriani *et al.* 2003).

In fact, if productivity data are pooled irrespective of the existing annual variation, the data obtained over different years may not be comparable (e.g. breeding performance was poorer in 2004 with respect to previous years; see Table 1). We thus tested for variation in the relative productivity according to Eagle Owl occurrence and proximity by means of two separate linear mixed models (LMMs) in which the dependent variable was the

Table 1. Yearly productivity (mean ± SE) of Peregrine pairs breeding in syntopic (Eagle Owl present) or non-syntopic (Eagle Owl absent) conditions with the Eagle Owl over the whole study area. The relative productivity of Peregrine pairs coexisting or not with Eagle Owls at the same cliff complex is also reported (see Methods for details of calculations); sample size (n) refers to the number of breeding attempts.

Year	Eagle Owl	n	Productivity	t	P
2002	absent	19	1.21 ± 0.34	0.15	0.569
	present	7	0.86 ± 0.40		
2003	absent	8	1.62 ± 0.46	1.11	0.290
	present	5	0.80 ± 0.58		
2004	absent	11	0.73 ± 0.38	0.20	0.844
	present	5	0.60 ± 0.40		
Total	absent	38	1.16 ± 0.22	1.17	0.249
	present	17	0.77 ± 0.25		
Relative productivity	absent	38	0.12 ± 0.22	1.10	0.276
	present	17	–0.28 ± 0.25		

relative productivity, and the predictors were Eagle Owl occurrence or distance to the nearest known Eagle Owl nest/cliff, respectively; breeding territory was entered as a random factor to control for non-independence of breeding data from the same territory. The analyses were performed separately for the entire study area and the high-density area. However, due to the reduced sample size (32 breeding attempts), the analyses for the high-density area refer only to the relative productivity. LMM and GLM analyses were performed by means of the R software (packages MASS and nlme). Linear mixed models were fitted by means of the maximum likelihood method (Venables & Ripley 2002). The significance of random effect terms in mixed models was assessed by means of a likelihood-ratio test comparing the model fit with and without the random effect, according to Pinheiro & Bates (2000) and Venables & Ripley (2002). Means and parameter estimates are reported together with their standard errors.

Over the whole study area, Peregrine productivity was negatively affected by the co-occurrence of ravens (*Corvus corax*) and sport climbing activities at breeding cliffs during the 2002 breeding season (see Brambilla *et al.* 2004). Unfortunately, we could not include these two variables in the analyses of the Eagle Owl effect because it was not possible to collect detailed data on climbing activities and raven occurrence at Peregrine cliffs during the 2003–2004 breeding seasons; however, in 2002, the occurrence of ravens and climbers did not differ between sites occupied by the Peregrine alone and sites hosting simultaneously Peregrines and Eagle Owls, both at the regional and at the local scale ($P \geq 0.3$; details not shown). Therefore, the occurrence of ravens and human climbers should not bias our analyses concerning the effects of owl occurrence/proximity on Peregrine productivity.

3. Results

The exploratory analysis showed that, in the whole study area, productivity varied among breeding seasons, and was always higher for pairs not coexisting with Eagle Owls (Table 1). However, the differences were far from significant (Table 1), and no relationship was detected in the correlation tests (either considering individual study years or total productivity; all $P > 0.4$). Consistently, the GLM analysis did not reveal any significant effect of Eagle Owl occurrence ($P > 0.6$) or proximity ($P > 0.4$) on the number of fledged young per pair during each study season (details not shown). The LMM analysis carried out on relative productivity values further confirmed the lack of Eagle Owl effects (both for syntopic occurrence and distance to the nearest owl territory) on Peregrine reproduc-

Table 2. Linear mixed model analyses of the effects of Eagle Owl syntopic co-occurrence (0 = Eagle Owl absent from Peregrine nesting cliff; 1 = co-occurrence of Peregrine and Eagle Owl territories on the same cliff; see Methods for details) and proximity (distance of Peregrine nest sites from Eagle Owl territories) on the relative productivity of Peregrine pairs for a) the whole study area and b) the high-density sub-area. The variance accounted for by the random effect was 51.0% and 51.5% in the two models for the whole study area, and 43.8% in both models for the high-density sub-area.

	Syntopic co-occurrence			Proximity		
a) *Whole study area*						
Fixed effects	Estimate (SE)	$F_{1,26}$	P	Estimate (SE)	$F_{1,26}$	P
Eagle Owl	–0.48 (0.48)	1.02	0.322	-2.84×10^{-6} (2.08×10^{-5})	0.02	0.893
intercept	0.14 (0.25)			0.04 (0.30)		
Random effect	SD (95% c.i.)	χ^2_1	P	SD (95% c.i.)	χ^2_1	P
territory	0.89 (0.57–1.38)	8.50	0.003	0.91 (0.58–1.41)	8.16	0.004
residual	0.88 (0.67–1.15)			0.88 (0.67–1.16)		
b) *High-density sub-area*						
Fixed effects	Estimate (SE)	$F_{1,13}$	P	Estimate (SE)	$F_{1,13}$	P
Eagle Owl	–1.25 (0.50)	6.32	0.026	3.45×10^{-4} (1.52×10^{-4})	5.16	0.041
intercept	0.04 (0.30)			–0.41 (0.40)		
Random effect	SD (95% c.i.)	χ^2_1	P	SD (95% c.i.)	χ^2_1	P
territory	0.73 (0.40–1.33)	4.48	0.034	0.74 (0.40–1.38)	4.22	0.040
residual	0.83 (0.59–1.14)			0.84 (0.60–1.17)		

tion over the entire study area (all $P > 0.3$) (Table 2).

However, a different pattern emerged in the high-density sub-area: Peregrine relative productivity was significantly lower for pairs coexisting with Eagle Owls compared to other pairs (-0.28 ± 0.25 vs. 0.94 ± 0.32, $n = 32$, $t = 3.04$, $P = 0.005$), and was positively related to the distance from the nearest known Eagle Owl nest/cliff ($r = 0.47$, $n = 32$, $P = 0.007$). Consistently, the LMM analyses showed that both owl proximity and syntopic co-occurrence of Peregrines and owls are associated with lower values of Peregrine relative productivity (Table 2).

4. Discussion

In this study, we analysed the effects of owl occurrence on the productivity of a cliff nesting Peregrine population in the central pre-Alps of Italy and Switzerland. We found that Eagle Owl occurrence at Peregrine cliffs and proximity to Peregrine nest sites were both associated with lower Peregrine productivity in a portion of the study area where the two species occurred at high densities. However, over the whole study area, the effects of Eagle Owl on productivity completely disappeared. Thus, these results highlight the importance of the relative density of model species in studies focusing on interspecific interactions.

When considering the sub-area in which both species breed at high densities, owl occurrence and proximity resulted in a significant decrease of Peregrine productivity, suggesting that competitive processes could be acting. For instance, Eagle Owls may prey more frequently on Peregrine chicks or nearly-fledged young, as reported elsewhere (Monneret 2000). Alternatively, the observed reduced productivity of pairs nesting close to owls may be mediated by variation in individual quality of Peregrine pairs: inexperienced (and thus probably low-quality) individuals may settle at suboptimal sites, such as cliff complexes hosting or near to Eagle Owl nests/cliffs, resulting in a lower breeding output of pairs breeding in such conditions. However, the overall productivity in the sub-area is rather high compared to the whole study area (see below and Brambilla *et al.* in press b), and it is therefore reasonable to argue that the observed effects are mainly due to direct predation exerted by the owl on Peregrine nestlings and/or fledglings. Our results show a remarkable similarity to the negative effect of owl proximity on black kite *Milvus migrans* productivity (Sergio *et al.* 2003). In fact, Sergio *et al*. (2003) clearly showed that the mean number of young fledged in kite territories increased significantly with the distance to the nearest Eagle Owl nest over three study areas.

In addition, it should be noted that the eight cliff complexes where the two species coexisted were characterized by a greater horizontal length with respect to sites occupied by the Peregrine alone (1,397 ± 274 for sites of syntopy vs. 708 ± 145 m for cliffs hosting only Peregrines; $t = -2.37$, $P = 0.025$; see also Brambilla *et al.* in press a), and that, at two small cliff complexes (one measuring 199 m in length, height 170 m; the other measuring 182 m, height 80 m), Eagle Owl settlement coincided with Peregrine disappearance from the site. These observations suggest that the Peregrine may coexist with the Eagle Owl only at the largest cliff complexes. The presence of Eagle Owl breeding pairs at other middle-sized or small cliff sites in the study area (our unpubl. data), in nearby areas (Bassi *et al.* 2003), and in other Alpine and pre-Alpine regions (Marchesi *et al.* 2002) indicates that the observed differences in cliff length were not due to owl habitat preferences.

The lack of apparent effects at the wider scale is perhaps not surprising, because the high-density sub-area represents a more favourable sector for the Peregrine, despite the higher Eagle Owl density: in fact, the relative productivity of Peregrines is higher in the sub-area compared to the pairs breeding outside, probably because of a greater availability of suitable nest sites, a higher abundance of profitable prey and favourable climatic conditions (lower rainfall) (Brambilla *et al.* in press b). Therefore, Eagle Owl effects at the regional scale are probably masked by other relevant environmental features, while they become evident when focusing on a more restricted and homogeneous area with higher owl density.

In conclusion, our study suggests that Peregrines may pay a cost for breeding close to Eagle Owls in terms of reduced productivity, likely resulting from increased predation on chicks/ fledglings. In the study area, both Peregrines and Eagle Owls appear to be increasing (Brambilla *et al.* 2003b, our unpubl. data): if the positive trend of their populations continues, coexistence problems are likely to become more severe in future years, and it would be interesting to analyse the spatial variation in patterns of Peregrine settlement in relation to settlement of Eagle Owl pairs. At present, Eagle Owl predation on Peregrines does not seem to threaten the Peregrine population, since the productivity (average value = 1.04 young/pair/year; see also Brambilla *et al.* 2003a) is within the range of values recorded for other areas (Rizzolli *et al.* 2005 and references therein), and the population appears to be increasing (see also above). Finally, our results further highlight the importance of considering interspecific interactions in studies of raptor ecology (Brambilla *et al.* 2004, Sergio *et al.* 2004, Vrezec & Tome 2004), and suggest that Eagle Owls may potentially negatively impact the population dynamics of sympatric diurnal raptors (Sergio *et al.* 2003).

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Huuhkajan (*Bubo bubo*) läheisyys saattaa alentaa kallioilla pesivien muuttohaukkojen (*Falco peregrinus*) pesinnän tuottavuutta

Huuhkajaa pidetään tavallisesti pienempien päiväpetolintujen merkittävänä saalistajana. Tutkimme muuttohaukan pesinnän tuottavuuden suhdetta huuhkajan pesien läheisyyteen Italian ja Sveitsin Alpeilla kolmen lisääntymiskauden ajan. Huuhkajan läheisyys ei vaikuttanut muuttohaukkojen tuottavuuteen, kun tarkasteltiin koko tutkimusaluetta. Sen sijaan huuhkajan läheisyys alueilla, joilla molemmat lajit esiintyivät tiheämmin, johti alentuneeseen pesinnän tuottavuuteen muuttohaukoilla. Huuhkajan vaikutukset laajemmassa mittakaavassa hävisivät luultavasti ympäristötekijöiden aiheuttamien vaikutusten taakse. Tutkimuksemme osoittaa, että huuhkajat voivat vaikuttaa päiväpetolintujen populaatiodynamiikkaan vaikuttamalla pesinnän tuottavuuteen.

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