The effect of intra- and interspecific interactions on the large-scale distribution of cliff-nesting raptors

ARTICLE *in* ORNIS FENNICA · JANUARY 2008

Impact Factor: 0.67

Ornis Fennica 85:13–21. 2008

The effect of intra- and interspecific interactions on the large-scale distribution of cliff-nesting raptors

José E. Martínez, José A. Martínez, Iñigo Zuberogoitia, Jabi Zabala, Stephen M. Redpath & José F. Calvo

Martínez, J. E. (corresponding author) & Calvo, J. F.: Departamento de Ecología e Hidrología, Universidad de Murcia, E-30100 Murcia, Spain. ecoljemt@um.es
Martínez, J.A.: C/ Juan de la Cierva 43, El Campello, E-03560 Alicante, Spain
Zuberogoitia, I.: Estudios Medioambientales Icarus s.l., Oficina Técnica, Apd. 106, E-48940 Leioa, Bizkaia. Spain
Zabala, J.: Sociedad para el Estudio de las Aves Rapaces (SEAR), C/ Kart Marx 15, 4 F, 48950 Erandio, Bizkaia, Spain
Redpath, S. M.: University of Aberdeen, School of Biological Sciences, Tillydrone Avenue, Aberdeen, AB24 2TZ, U. K.

Received 31 May 2007, revised 13 February 2008, accepted 20 March 2008

We examine the large-scale spatial distribution and the intra- and interspecific interactions in a cliff-nesting raptor community of a semi-arid Mediterranean area in southeastern Spain. The study community was composed of four top avian cliff-nesting predators: the Golden Eagle *Aquila chrysaetos*, the Bonelli's Eagle *Hieraaetus fasciatus*, the Eagle Owl *Bubo bubo* and the Peregrine *Falco peregrinus*. We tested the null hypothesis that their nest sites were distributed randomly within the study area, and built regression models as a function of the nearest neighbour distances (NNDs) among them. During a 15-year research period, we found a total of 560 traditional nest sites. Only those of *A. chrysaetos* showed regular spacing over the study area, while the distributions of the other three species did not differ significantly from random. Our modelling approach demonstrated that intraspecific NNDs were important only for the two largest species, *A. chrysaetos* and *H. fasciatus*, suggesting intraspecific territorial spacing for *A. chrysaetos*, but a certain degree of spatial aggregation for *H. fasciatus*. In addition, the models suggested competitive interactions between these species. According to the relative importance of their interspecific NNDs, *H. fasciatus* appeared to be dominant over the smaller *F. peregrinus*. Strong interspecific interactions were also suggested between *B. bubo* and *F. peregrinus*. Intra- and interspecific relationships within the community followed a general pattern of dominance related to body mass. Notable exceptions were found especially for the interspecific interactions involving *B. bubo*, which may prey upon the other species.

1. Introduction

Despite nearly eight decades of theoretical and empirical work and controversial debate, the role of interspecific competition in structuring communities remains a pervading and recurrent topic in ecological research (Abramsky *et al*. 2001, Eccard & Ylönen 2003, Hakkarainen *et al*. 2004, Morris *et al*. 2004, Zuberogoitia *et al*. 2005). Interspecific interactions among top predators have recently been shown to significantly affect the population demographics of these species (Fedriani *et al.* 1999, Caro & Stoner 2003, Sergio *et al.* 2003, Carrete *et al.* 2005, Berger & Gese 2007). Such interactions include sharing food resources and nesting sites, but also predatory relationships, such as intra-guild predation systems (Holt & Polis 1997), which may determine the competitive hierarchy among the interacting species (Hakkarainen & Korpimäki 1996, Krüger 2002, Sergio *et al.* 2003).

Many of these studies on competition have been conducted on birds of prey, for which effective competition for available nest sites is usually determined by territorial behaviour, providing an opportunity to conduct studies on the role of interactions in natural communities (Krüger *et al.* 2002, Hakkarainen *et al.* 2004). Although interspecific territoriality is a common spacing mechanism that reflects interspecific competition (Kostrzewa 1991, Robinson & Terborgh 1995), the influence of intraspecific interactions may also determine the selection of breeding habitat in multi-species assemblages. For example, Katzner *et al.* (2003) suggested that the coexistence of four large eagles in north-central Kazakhstan was primarily determined by intraspecific nest spacing, and that interspecific effects appeared to be secondary. The relative importance of both inter- and intraspecific interactions, however, may depend on the species in question (Solonen 1993).

Large cliff-nesting raptors in the Mediterranean region have received considerable attention due to conservation concerns (Carrete *et al.* 2002a, Martínez *et al.* 2003, Muñoz *et al.* 2005). Increased mortality, such as that resulting from direct human persecution (Balbontín *et al.* 2005), can lead to a gradual disappearance of territorial pairs and to changes in the spatial distribution and population sizes of the species, perhaps locally causing the substitution of one species by another (Fernández & Insausti 1986, Carrete *et al.* 2002b). Interspecific competition may produce analogous results, because the occupation of a territory by an invading species may reduce the quality of the habitat for the first settler and limit the reproductive outcome of the other species (Hakkarainen *et al.* 2004). Studies on single species or on pairs of species suggest that underlying intra- and interspecific competition may strongly shape the raptor community (Martínez *et al.* 1994, Serrano 2000, Sergio *et al.* 2004, Gil-Sánchez *et al.* 2004). To our knowledge, however, no such study has been undertaken. The term "community" is used here as a synonymy for "assemblage", and refers to the populations of a group of species that occur together in space and time (Begon *et al.* 1996).

We examined the large-scale spatial distribution and competitive interactions of cliff-nesting raptors in semiarid south-eastern Spain. Our study community consisted of the top avian cliff-nesting predators of this Mediterranean area: Golden Eagle *Aquila chrysaetos*, Bonelli's Eagle *Hieraaetus fasciatus*, Eagle Owl *Bubo bubo* and Peregrine *Falco peregrinus*. Our aim was to evaluate the relative significance of factors affecting the spacing of raptors by analysing the spatial distribution of nesting sites, and by constructing models as a function of the nearest neighbour distance among the nests. Our null hypothesis was that the nesting sites should be distributed randomly and independently within the study area. We made two predictions: (1) at both intra- and interspecific levels, the four species should space their nesting sites regularly to reduce interactions, and (2) if the results of the spatial analysis suggest interspecific competitive interactions, smaller species should avoid larger ones by maximizing the distance between their respective territories. Body size is an important predictor of the superior species in most cases of interspecific conflict (Palomares & Caro 1999, McDonald *et al.* 2007). Thus, by assuming that dominance hierarchies among species are mainly based on body mass (Fedriani *et al.* 2000, French & Smith 2005, García & Arroyo 2002, 2005), we expected the following order of dominance: *A. chrysaetos* > *H. fasciatus* > *B. bubo* > *F. peregrinus*. In accordance with this order, we also expected intraspecific interactions to be relatively more important than interspecific interactions in determining territory settlement of the most dominant species.

2. Material and methods

2.1. Study area and study species

We studied the cliff-nesting raptor community within an area of 17,180 km^2, comprising the provinces of Alicante and Murcia, south-eastern

Spain (37°23'–38°52'N, 0°14'E–3° 03'W). The community was composed of four species of conservation concern: Golden Eagle *A. chrysaetos* (body mass male 2,840–4,450 g, female 3,630–6,665 g; Cramp & Simmons 1980, del Hoyo *et al*. 1994), Bonelli's Eagle *H. fasciatus* (body mass male 1,500–2,160 g, female 2,000–2,500 g; Ferguson-Lees & Christie 2001, del Hoyo *et al*. 1994), Eagle Owl *B. bubo* (body mass male 1,220–1,770 g, female 1,750–2,390 g; Martínez *et al*. 2002) and Peregrine *F. peregrinus* (body mass male 400–650 g; female 700–1,000 g; Ferguson-Lees & Christie 2001). All species are resident in the study region and show similar habitat preferences at territory and landscape scales (Carrete *et al*. 2000, 2005, Martínez & Calvo 2000, Martínez *et al*. 2003). Typical nesting areas are mountainous, covered by Mediterranean scrubland and forests, and surrounded by a matrix of agricultural fields, and various urban areas.

2.2. Fieldwork

Between 1990 and 2004, we surveyed the study area to locate suitable cliffs and gather information on the distribution of nesting sites of the focal species. Following Solonen (1993), the term "nesting site" refers to a cliff known to have been occupied during the study period. We used three field procedures to establish the presence of nesting sites (Martínez *et al*. 2003, Carrete *et al*. 2005): (1) survey of active nests, (2) regular observations of individuals displaying territorial behaviour or calling in the vicinity of a cliff, and (3) location of deserted breeding territories as determined by the presence of old nests. Most nesting sites contained more than one nest of a given species, although in many cases we were not able to find nests, especially for *B. bubo*. Hence, with the help of topographic maps, each nesting site was assigned to a unique 1 km × 1 km Universal Transverse Mercator (UTM) grid square.

Fieldwork was carried out each year between January and July but, because of logistical constraints, not all areas and species were monitored each year. The studied species are long-lived so that the distribution of nests can be considered relatively constant throughout the study period (although some nests appeared or disappeared with time). Indeed the populations of the four species remained roughly stable throughout the study period (authors' unpublished data). Consequently, the large-scale distribution of the nesting sites, presented here, represents a refined parsimonious collation of all the surveys completed over the 15-year period (Solonen 1993, Jenkins & van Zyl 2005).

2.3. Data analysis

The study of inter- and intraspecific interactions was conducted using two complementary methods. Firstly, we measured the nearest neighbour distances (NNDs) among the nesting sites of each species and computed the G index (Brown 1975), which is the geometric mean of the squares of the NNDs divided by the corresponding arithmetic mean. Under a random spatial distribution of available sites, G values higher than 0.65 indicate a regular distribution pattern. However, since the spatial distribution of suitable cliffs in the study area might constrain the spacing distances among nesting places, we carried out four Monte Carlo simulation tests to estimate if the observed G values were greater than those drawn from a random distribution (Watson & Rothery 1986). For each species we ran 999 simulations, in which the G values were calculated after randomly locating their nesting sites within all the suitable cliffs, including those occupied by another species (Carrete *et al*. 2001). We then compared the observed G value with those obtained from the simulation and established the statistical significance of the difference. Values of $p < 0.05$ correspond with high G values and indicate regular spacing.

Secondly, we used Generalized Linear Models (GLM) to analyze the distribution of the four species as a function of the NNDs to conspecific and heterospecific pairs. For each species, the holder of a nesting site was the response variable, coded in binary form (1/0). Consequently, we used GLMs with a logit link function and binomial errors (logistic regressions). The four explanatory variables considered were the distances from a given nesting site to the nearest neighbour nesting sites of *A. chrysaetos* (NNDAc), *H. fasciatus* (NNDHf), *B. bubo* (NNDBb) and *F. peregrinus* (NNDFp). These distances were measured using

Table 1. Mean nearest neighbour distances (NND, in km) and observed G values for the four raptor species studied; *p* is the probability that the *G* value was larger than expected from a random distribution. NND values (columns 2–5; SE in parentheses) refer to *Aquila chrysaetos* (Ac), *Hieraaetus fasciatus* (Hf), *Bubo bubo* (Bb) and *Falco peregrinus* (Fp).

Species	Ac	Hf	Bb	Fp	*G*	*p*
A. chrysaetos	9.5 (± 0.6)	12.8 (± 1.1)	2.3 (± 0.4)	2.9 (± 0.3)	0.60	0.001
H. fasciatus	8.6 (± 0.6)	8.4 (± 0.7)	2.6 (± 0.4)	2.8 (± 0.3)	0.45	0.294
B. bubo	6.4 (± 0.6)	10.1 (± 1.1)	3.4 (± 0.3)	3.7 (± 0.4)	0.39	0.163
F. peregrinus	6.7 (± 0.8)	11.5 (± 1.2)	3.0 (± 0.5)	4.3 (± 0.4)	0.41	0.069

the coordinates of the 1 km^2 UTM cells. When nesting sites were shared by two or more species, NND values between those species were considered equal to 0.

We followed a forward stepwise procedure, testing the statistical significance of each explanatory variable (*F*-tests) and retaining those that contributed to the largest change in deviance from the null model until all the variables with a significant effect at $p < 0.05$ had been included in the model. To avoid pseudoreplication, each nesting place was included only once in the analysis. All analyses were performed using the R statistical package (R Development Core Team 2005).

3. Results

We found a total of 560 nesting sites in the study area, of which 67 were occupied by *A. chrysaetos*, 54 by *H. fasciatus*, 308 by *B. bubo* and 207 by *F. peregrinus* (Fig. 1). Seventy of these nesting sites were shared by two species, and only three by three species. Table 1 shows the estimated mean NNDs and G values for the four species. As expected from their relative densities, each species tended to be further apart from the less abundant ones. The only exception was *H. fasciatus*, for which the mean intraspecific NND was lower than the mean distance to the nearest neighbour nesting site of the more abundant *A. chrysaetos*. The observed G values indicated that only *A. chrysaetos*

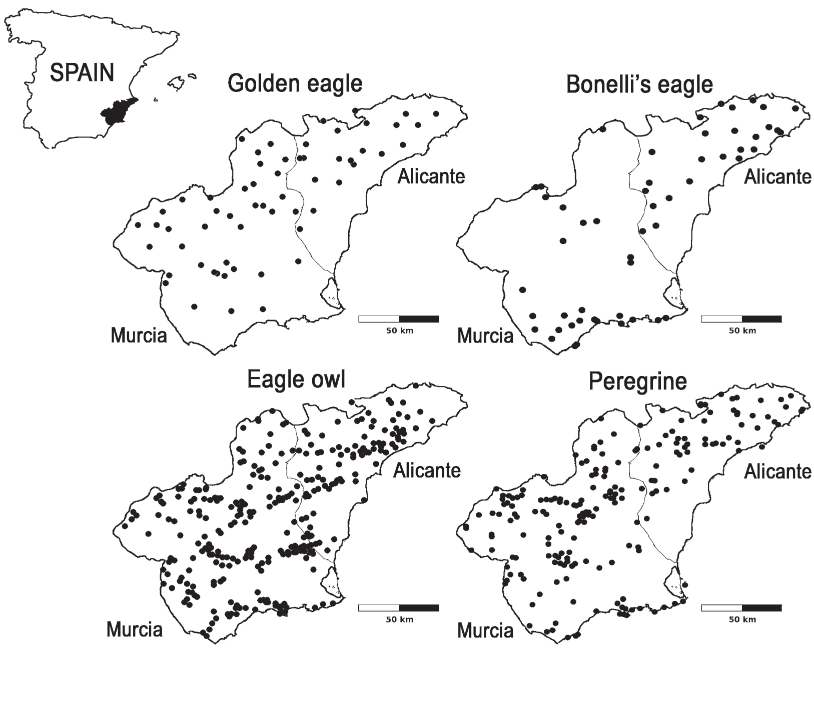

Fig. 1. Distribution of the traditional nesting sites of the four cliff-nesting raptor species in the provinces of Alicante and Murcia, SE Spain.

Table 2. Logistic regression models for the four raptor species studied, using nearest neighbour distance (NND, in km) as an explanatory variable. NND subscripts refer to *Aquila chrysaetos* (Ac), *Hieraaetus fasciatus* (Hf), *Bubo bubo* (Bb) and *Falco peregrinus* (Fp).

Species	Term	Coefficient	SE	*F*	*p*
Aquila chrysaetos (% deviance explained = 4.62)	NND_{Ac}	0.0748	0.0207	14.95	< 0.001
	NND_{Hf}	0.0373	0.0126	9.38	0.002
Hieraaetus fasciatus (% deviance explained = 2.78)	NND_{Ac}	0.0689	0.0208	15.93	< 0.001
Bubo bubo (% deviance explained = 14.28)	NND_{Fp}	0.3809	0.0447	92.96	< 0.001
Falco peregrinus (% deviance explained = 12.13)	NND_{Bb}	0.3627	0.0529	67.68	< 0.001
	NND_{Hf}	0.0314	0.0101	7.37	0.007

exhibits regular spacing throughout the study area, while the distribution of the other three species did not significantly differ from random.

Table 2 shows the final models for each of the species considered. In general, intraspecific interactions were less important than interspecific ones. Among the interspecific NNDs, the order of relative importance generally followed the expected order based on a function of body mass.

The best explanatory variable for *A. chrysaetos* was the nearest neighbour distance to the site occupied by the nearest conspecific, while the second best explanatory variable was the nearest neighbour distance to the area occupied by *H. fasciatus*. The variable with the greatest statistical significance in the probability of occurrence of *H. fasciatus* was the nearest neighbour distance to the site occupied by *A. chrysaetos*.

The best explanatory variables in the model for *F. peregrinus* was the distance to the nearest site occupied by *B. bubo* and *H. fasciatus* (in this order of significance). In contrast, for *B. bubo* the distance to the nearest site traditionally occupied by *F. peregrinus* was the most important variable.

4. Discussion

4.1. Spatial distribution of cliff-nesting raptors

Territorial behaviour is an expression of competition for available space or resources (Gordon 1997), which usually determines agonistic interactions between individuals of the same or different species (García & Arroyo 2002, Margalida & Bertrán 2005). For many birds of prey, territories seem to be regularly spaced due to the intra- and interspecific territoriality (Solonen 1993), a circumstance that can be interpreted as being a strategy towards minimising energy expenditure and time allocated to territorial defence and foraging (Donázar 1988). In our study area, *A. chrysaetos* was the only species that showed a G value significantly higher than expected from a random distribution of nesting sites. This result is consistent with other studies conducted in different areas throughout the Palaearctic and is commonly explained as being a consequence of underlying intraspecific competition (Tjernberg 1985, Watson 1997, Pedrini & Sergio 2001, Carrete *et al*. 2001). For the smaller *H. fasciatus*, *B. bubo* and *F. peregrinus*, our results indicate that in the long-term, the distribution of their nesting sites in our study area was not regular. The observed G values for these species were lower than those found for many raptors in other study areas (Solonen 1993), including *B. bubo, F. peregrinus* and *H. fasciatus* (Penteriani *et al*. 2002, Balbontín *et al*. 2003, López-López *et al*. 2004, Rizzolli *et al*. 2005, Brambilla *et al*. 2006a, Wightman & Fuller 2006). The reason for this aggregation pattern is unclear, as the G index does not allow definitive conclusions on factors determining the spatial distribution (López-López *et al*. 2004). We suggest that, in our study area, the aggregation pattern may be explained by a combination of factors acting synergically: (1) the heterogeneous distribution of resources, such as the availability of prey and nesting sites (Village 1983, Bogliani *et al*. 1994); (2) the spatial scale used in the study (Campbell 1992, Bevers & Flather 1999); (3) conspecific attraction that might support, for example, the search for a mate (Stamps 1988, Martínez *et al*. 2003, Seamans

& Gutiérrez 2006) and (4) non-natural mortality caused by man, for example, illegal hunting, electrocution or collision with electricity cables or pylons (Carrete *et al*. 2001, López-López *et al*. 2004).

4.2. GLM and competitive interactions

Our modelling approach suggests that interspecific interactions play an important role in determining the spatial distribution of nesting sites. According to the dominance hierarchy hypothesis, Golden Eagle is the only species for which intraspecific effects appear as the most important in the models (Table 2). Adult Golden Eagles have large, seldom overlapping home ranges, which suggests that their boundaries are aggressively defended from conspecifics (Donázar *et al*. 1989, Marzluff *et al*. 1997, Pedrini & Sergio 2001). For this species, however, the distance to the nearest nesting *H. fasciatus* was also included in the best models with a high relative importance, indicating strong interspecific territorial interactions between these species (Gil-Sánchez *et al*. 2004, Carrete *et al*. 2006). Accordingly, the final model for Bonelli's Eagle had the distance to the nearest nesting *A. chrysaetos* the most important variable in explaining the spatial distribution of this species. Perhaps the vicinity of Golden Eagles affects the probability for an occupied territory, and the reproductive success, of Bonelli's Eagles (Parellada *et al*. 1996, Carrete *et al*. 2002b, Gil-Sánchez *et al*. 2004). This possible effect may also be an important obstacle for the recolonisation of abandoned territories (Fernández & Insausti 1986, Carrete *et al*. 2005).

The best explanatory variable for the spatial distribution of *F. peregrinus* nests was the distance to the nearest nest of *B. bubo*, which is in agreement with the dominance hierarchy hypothesis. Among the four species, these two had the highest densities, select similar landscapes (Sánchez-Zapata *et al*. 1996) and have similar habitat requirements, usually favouring semi-arid landscapes with large steep cliffs (Martínez & Calvo 2000, Martínez *et al*. 2003, Ortego & Díaz 2004). Intuitively, such a tendency might result in strong interspecific competitive interactions. Eagle Owls can exert an important predatory pressure on Peregrines (Gainzarain *et al*. 2002, Brambilla *et al*. 2006b), which in turn may respond to the risk of predation by avoiding the area occupied by the owl, a tactic that could promote territory desertion (Hakkarainen & Korpimäki 1996, Sergio *et al.* 2004). The modelling of *B. bubo*, however, showed a strong reciprocal spatial relationship with *F. peregrinus*, which is biologically difficult to explain because, to date, *F. peregrinus* has not been documented to prey upon *B. bubo*.

Meanwhile, *H. fasciatus* appeared to be dominant over *F. peregrinus*, a finding in agreement with previous studies that have reported active displacements of Peregrines from the breeding territories of Bonelli's Eagles (Gil-Sánchez 1999), and predation (Martínez *et al.* 1994). Similarly, Peregrines have been shown to avoid the vicinity of Golden Eagles (Gainzarain *et al.* 2000, Sergio *et al.* 2004). In our study area, however, the competitive interaction with Golden Eagles appeared to be of little importance for *B. bubo* and *F. peregrinus*.

4.3. Conclusions

The long-term perspective of this study overcomes the difficulties involved in carrying out complete annual censuses of large populations in large areas, and the distributional irregularities caused by the establishment of occasional breeding territories, or by short-term changes or gaps in territory locations (Solonen 1993, Jenkins & van Zyl 2005).

Recognizing that several factors that can influence the distribution of cliff-nesting raptors, a growing number of studies point to the importance of interspecific effects in determining habitat selection (Krüger 2002, Sergio *et al.* 2003, 2004, Hakkarainen *et al.* 2004). Our results support this assertion and suggest that intra- and interspecific relationships within the community follow a general pattern of dominance related to body mass.

Acknowledgements. This study was supported by several projects on the ecology and conservation of raptors in the provinces of Alicante and Murcia, and benefited from the fieldwork and collaborative research of many colleagues and students, to whom we are greatly indebted. Paqui Carreño elaborated the maps and Mario Leon provided additional data on Eagle Owl populations. We also thank Beatriz Arroyo, Javier Balbontín and Joaquín Ortego for their helpful comments on earlier versions of the manuscript.

Lajinsisäisen ja lajienvälisen kilpailun vaikutus jyrkänteillä pesivien petolintujen ison mittakaavan levinneisyyteen

Tutkimme suuren mittakaavan jakautumista sekä lajinsisäisiä ja lajienvälisiä vuorovaikutuksia jyrkänteillä pesivässä petolintuyhteisössä puolikuivalla Välimeren alueella Kaakkois-Espanjassa. Tutkittu yhteisö koostui neljästä jyrkänteillä pesivästä huippupetolintulajista: maakotka *Aquila chrysaetos*, vuorikotka *Hieraaetus fasciatus*, huuhkaja *Bubo bubo* ja muuttohaukka *Falco peregrinus*.

Nollahypoteesimme oli, että lajien pesäpaikat olisivat satunnaisesti jakautuneet lähinaapuruusetäisyyden funktiona. Viidentoista tutkimusvuoden aikana löysimme kaikkiaan 560 perinteistä pesäpaikkaa. Vain maakotkan pesäpaikat olivat säännöllisesti jakautuneet tutkimusalueelle, muilla lajeilla jakautuminen oli satunnaista. Mallinnus osoitti, että lajinsisäinen pesienvälinen naapuruusetäisyys oli merkittävä vain suurimmille lajeille, maa- ja vuorikotkalle, mikä viittaa territoriaalisuuden säätelemiin pesienvälisiin etäisyyksiin maakotkalla, mutta vuorikotkan pesät näyttivät jonkin verran alueellisesti kasautuneemmilta. Lisäksi mallinnus viittasi lajienvälisen kilpailun olevan tärkeä selittäjä.

Eri lajien pesienvälisen naapuruusetäisyyden tarkastelun mukaan vuorikotka näytti olevan pienikokoisemman muuttohaukan suhteen dominoiva laji. Lajienväliset vuorovaikutukset näyttivät voimakkailta myös huuhkajan ja muuttohaukan välillä. Lajinsisäiset ja lajienväliset dominanssivaikutukset olivat suhteessa ruumiinkokoon. Huomattavaa on, että huuhkaja ei aina sopinut tähän yleistykseen; laji saattaa käyttää muita tutkittuja lajeja ravinnokseen.

References

Abramsky, Z., Rosenzweig, M. L. & Subach, A. 2001: The cost of interspecific competition in two gerbil species. — Journal of Animal Ecology 70: 561–567.

Balbontín, J., Penteriani, V. & Ferrer, M. 2003: Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's Eagle in Andalusia. — Biological Conservation 109: 417–423.

Balbontín, J., Penteriani, V. & Ferrer, M. 2005: Humans act against the natural process of breeder selection: a modern sickness for animal populations? — Biodiversity and Conservation 14: 179–186.

Begon, M., Harper, J. L. & Townsend, C. R. 1996: Ecology: individuals, populations, and communities. — Blackwell, Oxford.

Berger, K. M. & Gese, E. M. 2007: Does interference competition with wolves limit the distribution and abundance of coyotes? — Journal of Animal Ecology 76: 1075–1085.

Bevers, M. & Flather, C. H. 1999: The distribution and abundance of populations limited at multiple spatial scales. — Journal of Animal Ecology 68: 976–987.

Bogliani, G., Barbieri, F. & Tiso, E. 1994: Nest-site by the Hobby (*Falco subbuteo*) in poplar plantations in northern Italy. — Journal of Raptor Research 28: 13–18.

Brambilla, M., Rubolini, D. & Guidali, F. 2006a: Factors affecting breeding habitat selection in a cliff-nesting peregrine *Falco peregrinus* population. — Journal of Ornithology 147: 428–435.

Brambilla, M., Rubolini, D. & Guidali, F. 2006b: Eagle Owl *Bubo bubo* proximity can lower productivity of cliff-nesting peregrines *Falco peregrinus*. — Ornis Fennica 83: 20–26.

Brown, D. 1975: A test of randomness of nest spacing. — Wildfowl 26: 102–103.

Campbell, D. F. 1992: Nearest-neighbour graphical analysis of spatial pattern and a test for competition in populations of singing crickets *Teleogryllus commodus*. — Oecologia 92: 548–551.

Caro, T. M. & Stoner, C. J. 2003: The potential for interspecific competition among African carnivores. —Biological Conservation 110: 67–75.

Carrete, M., Sánchez-Zapata, J. A. & Calvo, J. F. 2000: Breeding densities and habitat attributes of Golden Eagles in Southeastern Spain. — Journal of Raptor Research 34: 48–52.

Carrete, M., Sánchez-Zapata, J. A., Martínez, J. E., Palazón, J. A. & Calvo, J. F. 2001: Distribución espacial del Águila-azor perdicera (*Hieraaetus fasciatus*) y del Águila Real (*Aquila chrysaetos*) en la Región de Murcia. — Ardeola 48: 175–182. (In Spanish with English summary)

Carrete, M., Sánchez-Zapata, M. A., Martínez, J. E. & Calvo, J. F. 2002a: Predicting the implications of conservation management: a territorial occupancy model of Bonelli's eagle in Murcia, Spain. — Oryx 36: 349–356.

Carrete, M., Sánchez-Zapata, J. A., Martínez, J. E., Sánchez, M. A. & Calvo, J. F. 2002b: Factors influencing the decline of a Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: demography, habitat or competition? — Biodiversity and Conservation 11: 975–985.

Carrete, M., Sánchez-Zapata, J. A., Calvo, J. F. & Lande, R. 2005: Demography and habitat availability in territorial occupancy of two competing species. — Oikos 108: 125–136.

Carrete, M., Sánchez-Zapata, J. A., Tella, J. L., Gil-Sánchez, J. M. & Moleón, M. 2006: Components of breeding performance in two competing species: habitat heterogeneity individual quality and density-dependence. — Oikos 112: 680–690.

Cramp, S. & Simmons, K. E. L. (eds.) 1980: The Birds of the Western Paleartic, Vol. II. Hawks to Bustards. — Oxford University Press, Oxford.

del Hoyo, J., Elliot, A. & Sargatal, J. (eds.) 1994: Handbook of the Birds of the World. Vol. 2. New World Vultures to Guineafowl. — Lynx Editions, Barcelona.

Donázar, J. A. 1988: Espaciamiento y dispersión de nidos de Búho real (*Bubo bubo*) en Navarra (Norte de la Península Ibérica). — Munibe 40: 35–38. (In Spanish with English summary)

Donázar, J. A., Ceballos, O. & Fernández, C. 1989: Factors influencing the distribution and abundance of seven cliff-nesting raptors: A multivariate study. — In Raptors in the Modern World (ed. Meyburg, B.-U. & Chancellor, R. D.): 545–552. WWGBP, Berlín.

Eccard, J. A. & Ylönen, H. 2003: Interspecific competition in small rodents: from populations to individuals. — Evolutionary Ecology 17: 423–440.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M. & York, E. C. 1999: Niche relations among three sympatric Mediterranean carnivores. — Oecologia 121: 138–148.

Fedriani, J. M., Palomares, F. & Delibes, M. 2000: Competition and intraguild predation among three sympatric carnivores. — Oecologia 125: 258–270.

Ferguson-Lees, J. & Christie, D. A. 2001: Raptors of the World. — Christopher Helm, London.

Fernández, C. & Insausti, J. A. 1986: Golden eagles take up territories abandoned by Bonelli's eagles. — Journal of Raptor Research 24: 124–125.

French, A. R. & Smith, T. B. 2005: Importance of body size in determining dominance hierarchies among diverse tropical frugivores. — Biotropica 37: 96–101.

Gainzarain, J. A., Arambarri, R. & Rodríguez, A.F. 2000: Breeding density, habitat selection and reproductive rates of the Peregrine Falcon *Falco peregrinus* in Álava (northern Spain). — Bird Study 47: 225–231.

Gainzarain, J. A., Arambarri, R. & Rodríguez, A.F. 2002: Population size and factors affecting the density of the peregrine falcon *Falco peregrinus* in Spain. — Ardeola 49: 67–74.

García, J. T. & Arroyo, B. E. 2002: Intra- and interspecific agonistic behaviour in sympatric harriers during the breeding season. — Animal Behaviour 64: 77–84.

García, J. T. & Arroyo, B. E. 2005: Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*. — Ibis 147: 144–154.

Gil-Sánchez, J. M. 1999: Solapamiento de hábitat de nidificación y coexistencia entre el Águila-azor perdicera (*Hieraaetus fasciatus*) y el Halcón peregrino (*Falco peregrinus*) en un área de simpatría. — Ardeola 46: 31–37. (In Spanish with English summary)

Gil-Sánchez, J. M., Moleón, M., Otero, M. & Bautista, J. 2004: A nine-year study of successful breeding in a Bonelli's eagle population in southeast Spain: a basis for conservation. — Biological Conservation 118: 685–694.

Gordon, D. 1997: The population consequences of territorial behavior. — Trends in Ecology and Evolution 12: 63–66.

Hakkarainen, H. & Korpimäki, E. 1996: Competitive and predatory interactions among raptors: an observational and experimental study. — Ecology 77: 1134–1142.

Hakkarainen, H., Mykrä, S., Kurki, S., Tornberg, R. & Jugell, S. 2004: Competitive interactions among raptors in boreal forests. — Oecologia 141: 420–424.

Holt, R. D. & Polis, G. A. 1997: A theoretical framework for intraguild predation. — American Naturalist 149: 745–764.

Jenkins, A. R. & van Zyl, A. J. 2005: Conservation status and community structure of cliff-nesting raptors and ravens in the Cape Peninsula, South Africa. — Ostrich 76: 175–184.

Katzner, T. E., Bragin, E. A., Knick, S. T. & Smith, A. T. 2003: Coexistence in a multispecies assemblage of eagles in Central Asia. — Condor 105: 538–551.

Kostrzewa, A. 1991: Interspecific interference competition in three European raptor species. — Ethology, Ecology and Evolution 3: 127–143.

Krüger, O. 2002: Interactions between common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*: trade-offs revealed by a field experiment. — Oikos 96: 441–452.

Krüger, O., Liversidge, R. & Lindström, J. 2002: Statistical modelling of the population dynamics of a raptor community in a semi-desert environment. — Journal of Animal Ecology 71: 603–613.

López-López, P., García-Ripollés, C., García-López, F., Aguilar, J. M. & Verdejo, J. 2004: Patrón de distribución del Águila Real *Aquila chrysaetos* y el Águila-azor Perdicera *Hieraaetus fasciatus* en la provincia de Castellón. — Ardeola 51: 269–274. (In Spanish with English summary)

Margalida, A. & Bertrán, J. 2005: Territorial defence and agonistic behaviour of breeding bearded vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. — Ethology, Ecology & Evolution 17: 51–63.

Martínez, J. A., Zuberogoitia, I. & Alonso, R. 2002: Rapaces Nocturnas. Guía para la determinación de la edad y el sexo en las estrigiformes ibéricas. — Monticola, Madrid. (In Spanish with English summary).

Martínez, J. A., Serrano, D. & Zuberogoitia, I. 2003: Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. — Ecography 26: 21–28.

Martínez, J. E. & Calvo, J. F. 2000: Selección de hábitat de nidificación por el Búho Real (*Bubo bubo*) en ambientes mediterráneos semiáridos. — Ardeola 47: 215–220. (In Spanish with English summary)

Martínez, J. E., Sánchez, M. A., Carmona, D. & Sánchez, J. A. 1994: Régime alimentaire de l'aigle de Bonelli

Hieraaetus fasciatus durant la période de l'élevage des jeunes (Murcia, Espagne). — Alauda 62: 53–58. (In French with English Summary)
Marzluff, J. M., Knick, S. T., Vekasy, M. S., Schueck, L. S. & Zarrielo, T. J. 1997: Spatial use and habitat selection of Golden Eagles in southwestern Idaho. — Auk 114: 673–678.
McDonald, R. A., O'Hara, K. O. & Morrisch, D. J. 2007: Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*). — Diversity and Distributions 13: 92–98.
Morris, R. J., Lewis, O. T. & Godfray, H. C. J. 2004: Experimental evidence for apparent competition in a tropical forest food web. — Nature 428: 310–313.
Muñoz, A. R., Real, R., Barbosa, A. M. & Vargas, J. M. 2005: Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. — Diversity and Distributions 11: 477–486.
Ortego, J. & Díaz, M. 2004: Habitat preference models for nesting eagle owls *Bubo bubo*: how much can be inferred from changes with spatial scale? — Ardeola 51: 385–394.
Palomares, F. & Caro, T. M. 1999: Interspecific killing among mammalian carnivores. — American Naturalist 153: 492–508.
Parellada, X., Borau, J. A. & Beneyto, A. 1996: El águila perdicera (*Hieraaetus fasciatus*) en Cataluña (NE de España): estatus y plan de conservación. — In Biology and Conservation of Mediterranean Raptors, 1994 (ed. Muntaner, J. & Mayol, J.): 231–237. SEO/BirdLife, Madrid. (In Spanish with English Summary)
Pedrini, P. & Sergio, F. 2001: Density, productivity, diet, and human persecution of Golden Eagles (*Aquila chrysaetos*) in the Central-Eastern Italian Alps. — Journal of Raptor Research 35: 40–48.
Penteriani, V., Gallardo, M. & Roché, 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 257: 365–372.
R Development Core Team 2005: R: A language and environment for statistical computing. — R Foundation for Statistical Computing. URL: http://www.R-project.org.
Rizzolli, F., Sergio, F., Marchesi, L. & Pedrini, P. 2005: Density, productivity, diet and population status of the Peregrine Falcon *Falco peregrinus* in the Italian Alps. — Bird Study 52: 188–192.
Robinson, S. K. & Terborgh, J. 1995: Interspecific aggression and habitat selection by Amazonian birds. — Journal of Animal Ecology 64: 1–11.
Sánchez-Zapata, J. A., Sánchez, M. A., Calvo, J. F., González, G. & Martínez, J. E. 1996: Selección de hábitat de las aves de presa en la Región de Murcia (SE de España). — In Biology and Conservation of Mediterranean Raptors, 1994 (ed. Muntaner, J. & Mayol, J.): 299–304. SEO/BirdLife, Madrid. (In Spanish with English Summary)
Seamans, M. E. & Gutiérrez, R. J. 2006: Spatial dispersion of spotted owl sites and the role of conspecific attraction on settlement patterns. — Ethology Ecology & Evolution 18: 99–111.
Sergio, F., Marchesi, L. & Pedrini, P. 2003: Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. — Journal of Animal Ecology 72: 232–245.
Sergio, F., Rizolli, F., Marchesi, L. & Pedrini, P. 2004: The importance of interspecific interactions for breeding-site selection: peregrine falcons seek proximity to raven nests. — Ecography 27: 818–826.
Serrano, D. 2000: Relationship between raptors and rabbits in the diet of eagle owls in southwestern Europe: competition removal or food stress? — Journal of Raptor Research 34: 305–310.
Solonen, T. 1993: Spacing of birds of prey in southern Finland. — Ornis Fennica 70: 129–143.
Stamps, J. A. 1988: Conspecific attraction and aggregation in territorial species. — American Naturalist 131: 329–347.
Tjernberg, M. 1985: Spacing of Golden Eagle *Aquila chrysaetos* nests in relation to nest site and food availability. — Ibis 127: 250–255.
Village, A. 1983: The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. — Journal of Animal Ecology 52: 635–645.
Watson, A. & Rothery, P. 1986: Regularity in the spacing of Golden Eagle *Aquila chrysaetos* used within years in northeast Scotland. — Ibis 128: 406–408.
Watson, J. 1997: The Golden Eagle. — T. & A. D. Poyser.
Wightman, C. S. & Fuller, M. R. 2006: Influence of habitat heterogeneity on distribution, occupancy patterns, and productivity of breeding Peregrine Falcons in central West Greenland. — Condor 108: 270–281.
Zuberogoitia, I., Martínez, J. A., Zabala, J. & Martínez, J. E. 2005: Interspecific aggression and nest-site competition in a European owl community. — Journal of Raptor Research 39: 156–159.