

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

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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 *Hieraetus 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 commu-

nities 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 *Hieraetus 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 km², 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), *Hieraetus fasciatus* (Hf), *Bubo bubo* (Bb) and *Falco peregrinus* (Fp).

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

the coordinates of the 1 km² 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*

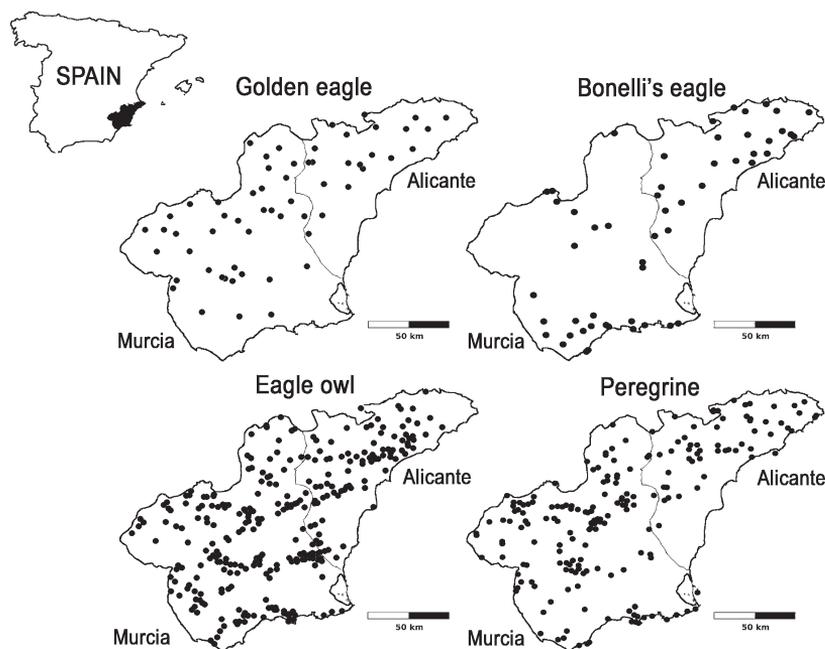


Fig. 1. Distribution of the traditional nesting sites of the four cliff-nesting raptor species in the provinces of Alicante and Murcia, SE Spain.

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
<i>Aquila chrysaetos</i> (% deviance explained = 4.62)	NND _{Ac}	0.0748	0.0207	14.95	< 0.001
	NND _{Hf}	0.0373	0.0126	9.38	0.002
<i>Hieraaetus fasciatus</i> (% deviance explained = 2.78)	NND _{Ac}	0.0689	0.0208	15.93	< 0.001
	NND _{Fp}	0.3809	0.0447	92.96	< 0.001
<i>Bubo bubo</i> (% deviance explained = 14.28)	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 (Donazar 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 (Donazar *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.

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Lajinsisäisen ja lajienvälisen kilpailun vaikutus jyrkänkeillä pesivien petolintujen ison mittakaavan levinneisyyteen

Tutkimme suuren mittakaavan jakautumista sekä lajinsisäisiä ja lajienvälisiä vuorovaikutuksia jyrkänkeillä pesivässä petolintuyhteisössä puoli-kuivalla Välimeren alueella Kaakkois-Espanjassa. Tutkittu yhteisö koostui neljästä jyrkänkeillä pesivästä huippupetolintulajista: maakotka *Aquila chrysaetos*, vuorikotka *Hieraetus 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 territori-aalisuuden säatelemiin pesienvälisiin etäisyyksiin maakotkalla, mutta vuorikotkan pesät näyttivät jonkin verran alueellisesti kasautuneemilta. 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 voimakkailla myös huuhkajan ja muuttohaukan välillä. Lajinsisäiset ja lajienväliset dominanssivaikutukset olivat suhteessa ruumiinkokoon. Huomattavaa on, että huuhkaja ei aina sopinut tähän yleistyksen; laji saattaa käyttää muita tutkittuja lajeja ravinnokseen.

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