Chancellor, R. D. & B.-U. Meyburg eds. 2004
Raptors Worldwide
WWGBP/MME

Nest Occupancy Patterns of Booted Eagles *Hieraaetus pennatus* in Southeastern Spain

I. Pagán, J.E. Martínez, M. Carrete and J.F. Calvo

ABSTRACT

Between 1998 and 2002 we analysed the spatial and temporal patterns of nest occupancy of a Booted Eagle population in a forested area in the region of Murcia (southeastern Spain) and its relationship with two potentially competing species: Northern Goshawk and Common Buzzard. G tests were used to examine territorial spacing and Generalized Linear Mixed Models to model occupancy and reproductive output with respect to nearest-neighbour distances.

The spatial pattern of nest occupancy was significantly uniform during only one year, both considering the Booted Eagle separately and when considering the three species jointly. The probability of occupancy only increased significantly with increasing distances to the nearest breeding pair of any species. No relationship was found between distances and reproductive output. Estimated variance components suggest a strong influence of territorial effects on occupancy, but not on reproductive output. Temporal occupancy frequencies differ from a random distribution, indicating that some preferred nest sites are frequently occupied, while many others are scarcely used.

INTRODUCTION

Most raptor species show strong territorial behaviour (Newton 1979), a phenomenon that could be a consequence of intra- and interspecific competition for space or available resources (Tjernber 1985; Kostrezwa 1991; Gordon 1997). Usually considered as a good indicator of the existence of territoriality, the regular distribution pattern of nest sites has been explained as a mechanism for maximizing distances and thus reducing potential conflicts with other competing individuals (Penteriani 1997; Sergio & Boto 2000; Carrete *et al.* 2001). Nonetheless, the distribution pattern of a population may be constrained by other natural factors, such as habitat heterogeneity, e.g. the non-uniform distribution of potential breeding sites (Newton 1979; Watson & Rothery 1986) and trophic resources (Solonen 1993). Moreover, it has been shown that many territorial animals are attracted by other individuals, both conspecific (Stamps 1988; Danchin *et al.* 1998) and heterospecific (Mönkönen & Forsman 2002), which could lead to random or aggregated patterns of distribution.

Not all of the territories in one specific area are equally used by the individuals of a population. The analysis of occupation patterns through time usually reveals the existence of high-quality territories, frequently used, and low-quality territories, which in contrast are scarcely used or remain unoccupied (Newton & Marquiss 1976; Kostrzewa 1996). The hypothesis that relates high habitat quality to reproductive success and productivity has been proved for several species (Korpimäki 1988; Ferrer & Dónazar 1996; Donovan & Thompson 2001), although the relationship may well depend on the population size, coexistence with potential competitors and the distances to the nearest-neighbour breeding pair (Kostrzewa 1996; Krüger 2002). Furthermore, the occupancy rate and success of a territory could be a consequence of the site fidelity of experienced, high-quality individuals (Calsbeek & Sinervo 2002; Ferrer & Bisson 2003)

In this paper, we investigate the spatio-temporal pattern of territorial occupancy and breeding success of a Booted Eagle *Hieraaetus pennatus* population in southeastern Spain. This species is a medium size, tree-nesting raptor which in the study area coexists with two potential competitors: Northern Goshawk *Accipiter gentilis* and the Common Buzzard *Buteo buteo* (Sánchez-Zapata & Calvo 1999). The three species are of a similar size, exhibit strong territorial behaviour (Newton 1979) and can alternate territories in different years (Martínez 2002). While the last two species are resident in the study area, the Booted Eagle is a trans-Saharan migrant, arriving in late March and leaving in late September, a circumstance that could have a major influence on its occupation patterns.

Our objectives were: (i) to examine the patterns of spatial distribution and territory occupancy of Booted Eagles, separately and in relation to Goshawks and Buzzards; (ii) to model the probabilities of occupancy and the reproductive output with respect to nearest-neighbour distances to intra- and interspecific breeding pairs; and (iii) to analyse the differential use of territories in different years in relation to productivity.

STUDY AREA AND METHODS

The study area is located in the centre of the region of Murcia (southeastern Spain; 37°55'-38°05'N, 1°40'-1°50'W), covering about 10,000ha ranging from 550 to 1521m a.s.l. The climate is Mediterranean and the topography is characterized by rugged slopes dominated by pine forests (*Pinus halepensis*) interspersed with traditional agroecosystems (cereals, vineyards, olive and almond groves).

The investigation was conducted from 1998 to 2002. Field-work was carried out at the start of the breeding season of each species: from March to May for Booted Eagles; from February to March for Common Buzzards; and from

March to April for Northern Goshawks. Nest sites were located by searching the appropriate habitats, observing courtship and territorial flights, and using playback of taped calls. We returned annually to all known territories to determine occupancy and reproductive output. When appropriate, we intensively surveyed an area of 300m radius around each previously active nest to locate alternative nest sites. Nest locations were mapped on 1:25,000 topographic maps, recorded with a GPS unit and incorporated in a GIS (GRASS v. 5.0.2), in which nearest-neighbour distances were calculated.

To test for random spacing we estimated the G statistic, calculated as the ratio of the geometric mean to the arithmetic mean of the squared neighbour distances (Brown 1975). To account for spatial restrictions imposed by available nest sites (Watson & Rothery 1986), we conducted Monte Carlo simulations to estimate the probability that the empirical G-values were greater than expected at random (Carrete *et al.* 2001). To examine intra- and interspecific relationships, G-tests were performed for the Booted Eagle separately and for the three species jointly.

We used Generalized Linear Mixed Models (GLMMs; Serrano *et al.* 2001) to analyse the probability of territory occupancy with respect to intra- and interspecific nearest-neighbour distances. Mixed models allowed us to incorporate territories as random effects and estimate variance components for them (Franklin *et al.* 2000; McClaren *et al.* 2002). Expressed as percentages (Sokal & Rohlf 1995), variance components represent the fraction of the total variance attributable to random effects. The probability of territory occupancy and the reproductive output were modelled using a logistic and a Poisson link function respectively. Analyses were performed with the glmmPQL function, implemented in the R statistical software (URL: http://cran.r-project.org/).

Finally, we compared the observed frequencies of temporal occupancy of each territory (number of years occupied) with the expected frequencies of a random distribution (Newton & Marquiss 1976; Kostrzewa 1996). For this analysis, we excluded those territories sometimes used by Goshawks or Buzzards. The productivities of territories with different frequencies of use were compared using an ANOVA test.

RESULTS

During the study period the Booted Eagle population ranged from 21 to 29 pairs. Goshawks and Buzzards were much less common (0-2 and 6-7 pairs, respectively). Table 1 shows the results of the spatial analysis for each year. Mean nearest-neighbour distances were 1.116km for Booted Eagle and 1.053 km for all three species. G-values were less than 0.65 in all cases, and a significant pattern of regularity was obtained for only Booted Eagles in 2002, and for the three species in 2000.

GLMMs results are shown in Table 2. The probability of occupancy increased significantly with increasing nearest-neighbour distances to a breeding pair of any species. No significant relationships with distances were found when modelling reproductive output. Variance component percentages for territory were high for the occupancy models, but low for the reproductive output models.

Table 1. Territorial spacing in Booted Eagles, Common Buzzard and Northern Goshawk. NND: nearest neighbour distance (km); SD: standard deviation. *P*-values obtained after 10,000 Monte Carlo simulations.

	Booted Eagle					All species				
Year	*n*	*Mean NND (SD)*	*NND range (min-max)*	*G* [1]	*P*	*n*	*Mean NND (SD)*	*NND range (min-max)*	*G* [1]	*P*
1998	29	0.987 (0.557)	0.206-2.322	0.54	0.1007	37	0.836 (0.571)	0.153-2.322	0.43	0.0942
1999	26	1.043 (0.576)	0.206-2.432	0.55	0.0541	34	0.646 (0.432)	0.153-2.431	0.39	0.1569
2000	21	1.287 (0.710)	0.443-2.733	0.58	0.0573	29	0.779 (0.501)	0.331-2.430	0.57	0.0347
2001	23	1.116 (0.724)	0.206-3.395	0.56	0.0719	31	1.053 (0.829)	0.206-3.415	0.38	0.3263
2002	25	1.191 (0.680)	0.443-2.773	0.61	0.0286	37	0.821 (0.672)	0.254-2.733	0.37	0.2079

[1] A significant *G* value implies a regular pattern.

Table 2. Generalized linear mixed models for occupancy and reproductive output in Booted Eagles, considering territory (T) as a random effect and nearest neighbour distances (NND) as fixed effects. NND subscripts refer to Booted Eagle (B), Common Buzzard (C), and Northern Goshawk (N). NND_{CN} = min (NND_C , NND_N); NND_{BCN} = min (NND_B , NND_C , NND_N).

Model structure	*Variance component for territory* (T)	*Estimated* β_1 *(Std. Error)*	*P*
Occupancy **(logit *O*)**			
$\beta_0 + T_i + \beta_1\ NND_B$	1.8960 (77.25 %)	0.6617 (0.3376)	0.0515
$\beta_0 + T_i + \beta_1\ NND_C$	2.0061 (86.48 %)	0.3291 (0.1927)	0.0892
$\beta_0 + T_i + \beta_1\ NND_N$	2.1627 (90.13 %)	– 0.0257 (0.0609)	0.6737
$\beta_0 + T_i + \beta_1\ NND_{CN}$	1.9957 (85.59 %)	0.2793 (0.1896)	0.1423
$\beta_0 + T_i + \beta_1\ NND_{BCN}$	1.9389 (80.79 %)	0.8942 (0.3940)	0.0243
Reproductive output **($\log_e R$)**			
$\beta_0 + T_i + \beta_1\ NND_B$	0.4397 (22.72 %)	– 0.0732 (0.1518)	0.6309
$\beta_0 + T_i + \beta_1\ NND_C$	0.4328 (22.02 %)	0.0250 (0.0871)	0.7747
$\beta_0 + T_i + \beta_1\ NND_N$	0.3955 (18.78 %)	0.0119 (0.0360)	0.7422
$\beta_0 + T_i + \beta_1\ NND_{CN}$	0.4354 (22.28 %)	0.0350 (0.0849)	0.6816
$\beta_0 + T_i + \beta_1\ NND_{BCN}$	0.4315 (21.88 %)	– 0.0971 (0.1558)	0.5351

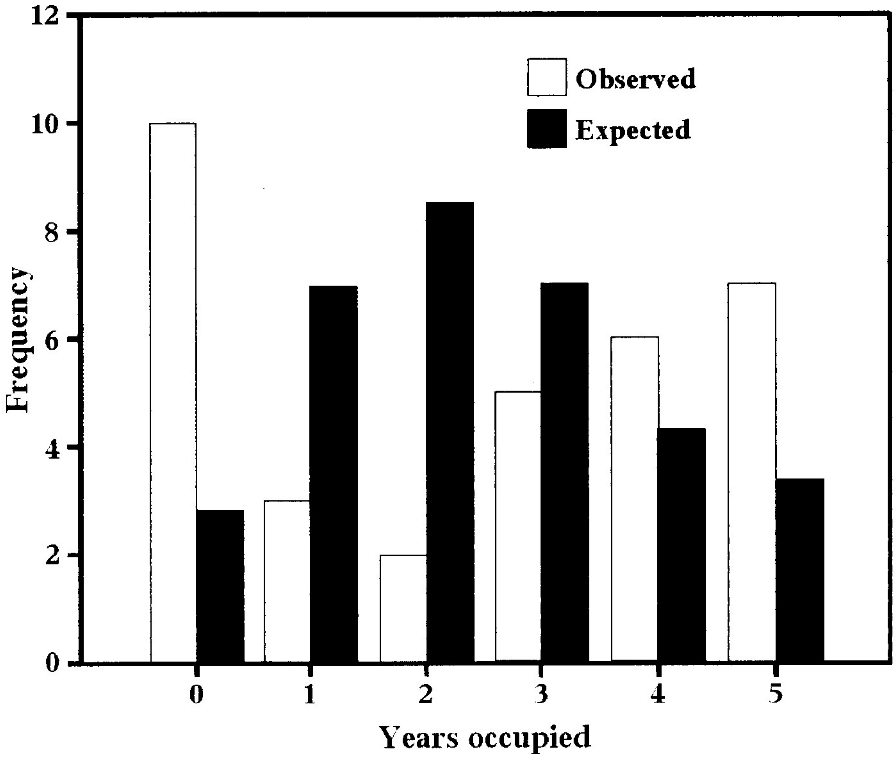
We found differences between observed and expected frequencies of occupation (χ^2 = 30.4524; P < 0.001), mainly due to the 0, 1, 2 and 5 years classes (Figure 1). A few preferred territories (with 5 years of occupancy) fledged most of the young (Table 3). Mean productivity was also higher in these high-frequency use territories, although differences are not significant ($F = 2.1923$; $P = 0.1109$; Table 3).

Table 3. Reproductive success of 33 territories of Booted Eagles during 5 consecutive years (1998-2002).

Occupancy (years)	*Number of territories*	*Number of nest-years*	*Percent successful nest-years*	*Mean productivity [1] (Std. Error)*	*Number of young fledged*
0	10	▯	▯	▯	▯
1	3	3	67 %	1.33 (0.67)	4
2	2	4	25 %	0.25 (0.25)	1
3	5	15	50 %	0.87 (0.29)	15
4	6	24	50 %	0.71 (0.12)	17
5	7	35	77 %	1.43 (0.22)	50

[1] Differences between years are non significant ($F = 2.1923$, $P = 0.1109$).

Figure 1. Observed and expected occupancy of Booted Eagle territories during 5 consecutive years ($\chi^2 = 30.45$; P < 0.001).



DISCUSSION

The patterns of spatial distribution have been widely studied in many raptor species. Most of them show a regular distribution (Newton 1979; Tjernber 1983; Kostrzewa 1991; Solonen 1993; Selas 1997; Sergio & Botto 1999; Carrete *et al.* 2001), which is commonly associated with competition for space (i.e. nest sites and territories) or resources that are linked to space (Gordon 1997). Our results show that Booted Eagles generally exhibit a non-uniform pattern of spacing, even when habitat availability constraints are considered. When analysed together with its two coexisting competitors, the above conclusion does not change substantially.

Previous studies on the ecological characteristics of the Booted Eagle in the Iberian Peninsula show that it is not a typical forest species (Sánchez-Zapata & Calvo 1999; Suárez *et al.* 2000). Moreover, its pattern of distribution in the study area could be described as a group of pairs nesting close together in a core forested area, and hunting independently in the surroundings (Martínez 2002). The migratory habits of Booted Eagles and the short time available to complete the breeding cycle may play a prominent role in the observed pattern. It has been shown for many migrant bird species that conspecific and heterospecific attraction influence the process of territory selection (Boulinier & Danchin 1997; Danchin *et al.* 1998; Mönkkönen *et al.*1999; Mönkkönen & Forsman 2001). Thus, the attraction effect of previously settled individuals could determine the non-uniform distribution of Booted Eagles which, viewed at a regional scale, may agree with the traditional aggregation hypothesis (Danchin & Wagner 1997). Despite the possible existence of this aggregation phenomenon, GLMMs revealed a significant positive relationship between the probability of occupancy and the distance to a breeding pair of any species. These findings allow us to hypothesize the existence of a trade-off between two opposing processes (attraction and interference) which could be operating at different scales.

Occupancy models also show that differences between territories are more important than intra- and interspecific relations. This importance decreases in the analysis of reproductive output where, in addition, no significant relationships with distances were observed. GLMM results and the observed distribution of temporal occupancy frequencies suggest the existence of some 'preferred' and some 'avoided' territories, a common finding in forest raptor species (Newton & Marquiss 1976; Kostrzewa 1996; Krüger & Lindström 2001). Most of the young were fledged from these preferred territories (with five years of continued occupancy) although differences in mean productivities are not significant (probably due to the small sample size). The apparent discrepancy between these results and the models of reproductive output might be explained by the exclusion from the analysis of temporal occupancy frequencies of those territories shared with other species, which might have high productivity but a reduced number of occupancies.

Site fidelity, i.e. the continued occupancy of nesting territories, is a common phenomenon observed in many raptors and other bird species, which has been related to the breeding success of the previous year (Newton 1979; Switzer 1997; Forero *et al.* 1999; Hoover 2003). In this way, habitat quality and the age and experience of breeding individuals are probably interrelated factors in the process of territory selection (Kostrzewa 1996; Ferrer & Bisson 2003) and should also be considered, together with the effects of intra- and interspecific relationships, in any attempts to explain the occupancy patterns of Booted Eagles.

ACKNOWLEDGEMENTS

We thank Ramón Ruiz, Mario León and Eloy Pérez for field assistance. This work has been funded by the University of Murcia (project no. 4964) and the Spanish Ministry of Science and Technology (project REN2002-01884).

REFERENCES

BOULINIER, T. & E. DANCHIN 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology* 11: 505-517.

BROWN, D. 1975. A test of randomness of nest spacing. *Wildfowl* 26: 102-103.

CALSBEEK, R. & B. SINERVO 2002. An experimental test of the ideal despotic distribution. *Journal of Animal Ecology* 71: 513-523.

CARRETE, M., J.A. SÁNCHEZ-ZAPATA, J.E. MARTÍNEZ, J.A. PALAZÓN & J.F. CALVO 2001. Distribución espacial del Águila Real *Aquila chrysaetos* y del Águila-azor Perdicera *Hieraaetus fasciatus* en la Región de Murcia. *Ardeola* 48: 175-182.

DANCHIN, E., T. BOULINIER & M. MASSOT 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415-2428.

DANCHIN, E. & R.H. WAGNER 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12: 342-347

DONOVAN, T.M & F.R. THOMPSON 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11: 871-882.

FERRER, M & I. BISSON 2003. Age and territory-quality effects on fecundity in the Spanish Imperial Eagle (*Aquila adalberti*). *Ibis* 120:180-186.

FERRER, M. & J.A. DONÁZAR 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77: 69-74.

FORERO, M.G., J.A. DONÁZAR, J. BLAS & F. HIRALDO 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80: 1298-1310.

FRANKLIN, A.B., D.R. ANDERSON, R.J. GUTIÉRREZ & K.P. BURNHAM 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70: 539-590.

GORDON, D.M. 1997. The population consequences of territorial behavior. *Trends in Ecology & Evolution* 12: 63-66.

HOOVER, J.P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* 84: 416-430.

KORPIMÄKI, E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's Owl. *Journal of Animal Ecology* 57: 97-108.

KOSTRZEWA, A. 1991. Interspecific interference competition in three European raptor species. *Ethology, Ecology & Evolution* 3: 127-143.

KOSTRZEWA, A. 1996. A comparative study of nest-site occupancy and breeding performance as indicators for nesting-habitat quality in three European raptor species. *Ethology Ecology & Evolution* 8: 1-18.

KRÜGER, O. 2002. Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*. *Ecography* 25: 523-532.

KRÜGER, O. & J. LINDSTRÖM 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. *Journal of Animal Ecology* 70: 173-181.

McCLAREN, E.L., P. L. KENNEDY & S. R. DEWEY 2002. Do some Northern Goshawk nest areas consistently fledge more of Murcia, Spain.

MÖNKKÖNEN, M. & J. T. FORSMAN 2002. Heterospecific attraction among forest birds: a review. *Ornithological Science* 1: young than others? *Condor* 104: 343-352.

MARTÍNEZ, J.E. 2002. Ecología del Águila Calzada (*Hieraaetus pennatus*) en ambientes mediterráneos. Ph D. Thesis. University 41-51.

MÖNKKÖNEN M., R. HÄRDLING, J. T. FORSMAN & J. TUOMI 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. *Evolutionary Ecology* 13: 91-104.

NEWTON, I. 1979. *Population Ecology of Raptors*. T. & A.D. Poyser. Berkhamsted, U.K.

NEWTON, I. & M. MARQUIS 1976. Occupancy and success of nesting territories in the European Sparrowhawk. *Raptor Research* 10: 65-71.

PENTERIANI, V. 1997. Long-term study of a goshawk breeding population on a Mediterranean mountain C (Abruzzi Apennines, Central Italy): density, breeding performance and diet. *Journal of Raptor Research* 31: 308-312.
SÁNCHEZ-ZAPATA, J. A. & J. F. CALVO 1999. Ràptor distribution in relation to landscape composition in semi-arid Mediterranean habitats. *Journal of Applied Ecology* 36: 254-262.
SELAS, V. 1997. Breeding density of Sparrowhawk *Accipiter nisus* in relation to nest site availability, hatching success and winter weather. *Ornis Fennica* 74: 121-129.
SERGIO, F. & A. BOTO 1999. Nest dispersion, diet, and breeding success of Black Kites (*Milvus migrans*) in the Italian pre-Alps. *Journal of Raptor Research* 33: 207-217.
SERRANO, D., J. L. TELLA, M.G. FORERO & J. A. DONÁZAR 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology* 70: 568-578.
SOKAL, R.R. & F.J. ROHLF 1995. *Biometry.* Freeman. New York.
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.
SUÁREZ, S., J. BALBONTÍN & M. FERRER 2000. Nesting habitat selection by booted eagles *Hieraaetus pennatus* and. implications for management *Journal of Applied Ecology* 37: 215-223.
SWITZER, P.V .1997. Past reproductive success affects future habitat selection. *Behavioural Ecology and Sociobiology* 40: 307-312.
TJERNBERG, M. 1985. Spacing of Golden Eagle *Aquila chrysaetos* nests in relation to nest site and food availability. *Ibis* 127: 250-255.
WATSON, A. & P. ROTHERY 1986. Regularity in spacing of Golden Eagle *Aquila chrysaetos* nests used within years in northeast Scotland. *Ibis* 128: 406-408.

I. Pagán, J.E. Martínez and J.F. Calvo
Departamento de Ecología e Hidrología
Universidad de Murcia
Campus de Espinardo
30100 Murcia
Spain

M. Carrete
Departamento de Biología Aplicada,
Estación Biológica de Doñana
Avda. M.ª Luisa s/n
41013 Sevilla
Spain