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Distribution and breeding performance of a high-density Eagle Owl *Bubo bubo* population in southeast Spain

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Capsule Despite very high breeding density, no density-dependent effects on reproductive parameters were detected.

Aims To describe the distribution, abundance and breeding performance of Eagle Owls and to analyse density-dependent effects on breeding parameters.

Methods We censused a high-density population of Eagle Owls in southeast Spain between 2003 and 2010. To census the population we employed acoustic signals and searched for field signs. Breeding performance was determined by nest monitoring.

Results The population's density, productivity and fledgling rate were the highest recorded for this species. We detected a negative relationship between the laying date and productivity. Despite breeding pairs' high density, no density-dependent effects on reproductive parameters were detected.

Conclusions Our results suggest that resources in the study area (mainly the availability of Rabbits *Oryctolagus cuniculus*) and adult turnover might be responsible for this population's high density and breeding success.

Eagle Owls *Bubo bubo* are the largest strigiform in the world and are widely distributed in the Palaearctic where they are found in a wide variety of habitats from boreal coniferous, mixed and deciduous forests, to Mediterranean scrub, steppes and deserts (Mikkola 1983). Eagle Owls' breeding ecology has been the subject of several studies conducted in different western Palaearctic areas (Marchesi *et al.* 2002 and references therein). In Spain, northern populations show lower population density and productivity than southern ones, a fact which seems to relate to the availability of Rabbits *Oryctolagus cunniculus* (Donázar 1988, Martínez *et al.* 1992, Ortego & Díaz 2004). References are available about the distribution, diet and habitat selection for the region of southeast Spain (Sánchez-Zapata *et al.* 1995, Martínez & Calvo 2000, 2001, Martínez & Zuberogoitia 2001, Martínez *et al.* 2003), but there are few basic data about population size, density and breeding output and the factors affecting breeding performance (Martínez *et al.* 1992).

Previous studies of Eagle Owls conducted in southeast Spain have reported a high-density population in Alicante (100–120 pairs, approximately 2.03 pairs/100 km^2 [Martínez & Zuberogoitia 2003]) and Murcia (182–220 pairs, approximately 1.78 pairs/100 km^2 [Sánchez-Zapata *et al.* 1995]). The Sierra de Escalona (province of Alicante) has been designated as an important bird area because of the size of the Eagle Owl breeding population and its value as a temporal settlement area for Bonelli's Eagle *Aquila fasciata* and Golden Eagle *Aquila chrysaetos*.

Distribution, population size and breeding performance are key parameters for monitoring bird populations for conservation and management purposes (Newton 1979). The breeding performance of raptor populations may be influenced by extrinsic (e.g. climate, habitat and food availability) and intrinsic (e.g. population density) factors (Newton 1998).

The timing of breeding may influence reproductive parameters (Aparicio & Bonal 2002). Early breeding generally increases breeding performance, and this is usually attributed to the older age or experience of

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pairs (Viñuela 1993, Espie *et al.* 2000). However, increasing population density may lead to a density-dependent regulation of breeding performance, which is usually driven by a territorial behaviour mechanism (Rodenhouse *et al.* 1997), as previously described for different territorial raptor species (Ferrer & Donázar 1996, Carrete *et al.* 2006).

Our aims were to: (1) describe the Eagle Owl's distribution, population size and breeding performance in a high-density area of the Sierra de Escalona, which is partially devoted to the conservation of this species; and (2) analyse density-dependent effects on breeding parameters.

Figure 1. Localization of the study area. The striped section indicates the Special Protection Area of Sierra de Escalona and Dehesa de Campoamor (province of Alicante).

METHODS

Study area

The study area was located to the south of the province of Alicante, southeast Spain (38.00° N, 0.86° W; Fig. 1) and encompassed 448 km^2, including the Sierra de Escalona, part of the Natura 2000 Network, which has been recently designated as a Special Protection Area (SPA) based upon its importance for juvenile dispersal and non breeding Bonelli's Eagles and Golden Eagles, and for its high density Eagle Owl population.

The climate is semi-arid Mediterranean with low annual rainfall (300 mm) and warm mean annual temperatures (18°C). The landscape is a mosaic dominated by intensive agriculture (citrus crops and vegetables), palm trees *Phoenix dactylifera*, towns and sparse houses. Small-sized extensive crops, such as Almond *Prunus dulcis*, olive *Olea europea* and carob trees *Ceratonia siliqua*, still remain, as do remnants of natural vegetation such as Mediterranean shrubs *Pistacea lentiscus*, *Rosmarinus officinalis*, *Rhamnus lycioides*, *Chamaerops humilis*, *Thymus sp.* and pines *Pinus halepensis* and *P. pinea*. The relief is plain with low hills close to the sea (Sierra de Escalona; 300 m asl) and low rocky mountains (Sierra de Pujálvarez; 400 m asl).

Census techniques

The distribution of Eagle Owls and their breeding performance were determined over a seven-year period (2003–2010). Territories were identified using a combination of methods frequently used to study Eagle Owl populations (Penteriani *et al.* 2004). These included: (1) visiting (from October to February and from May to July) suitable areas to detect nests, pellets and feeding perches; and (2) auditory surveys at sunrise and sunset, from October to January, when the vocal activity of adults was most intense (Delgado & Penteriani 2007). Territories were considered unoccupied only after three negative adult listening sessions and the absence of any other sign of owl presence (droppings, pellets, feeding perches).

In those territories considered as occupied, we searched for nests by walking and looking at available nest substrates (caves, cliffs, steps) in a radius of 200 m of the nest used in the previous year or of the perches used by adults.

Density and nest spacing

The nearest-neighbour distance (NND) (Newton 1979) and Isolation Index (defined by $S_i = \Sigma\exp(-d_{ij})$, where S_i is the isolation of the breeding pair i and d_{ij} was the linear distance between nest i and j; range: 0–1, from more isolated to more connected; Carrete *et al.* 2006) of all the detected territories were used as density estimators (Penteriani *et al.* 2004). When territorial pairs used alternative nests during the study period, we used the barycentre, calculated as the geometric centre of the location of all the nests in that territory, to calculate density estimators (Marchesi *et al.* 2002). Regularity of nest spacing was computed by means of the G-test (Brown & Rothery 1978), calculated as the ratio between the geometric and the arithmetic means of the squared NNDs. The index ranges from 0 to 1, and values higher than 0.65 depict regular distribution. As we could not monitor all territories every year, we used the number of territories detected in 2010 ($n = 99$) when census effort was completed to calculate the density estimators. This figure can be considered a good surrogate of annual density as supported by the high inter-annual occupancy rate of territorial pairs (mean 0.94) and the apparent stability of the breeding population.

Reproductive monitoring

Each nest was visited twice in each year to assess breeding performance: (1) during the laying period (from January to April) to determine clutch size; and (2) during the nestling and fledgling period (starting when chicks were about 30–35 days old and running until June). We used the following terminology proposed by Steenhof (1987): (1) a territorial pair is a pair that occupied an area; (2) a breeding pair is a pair that laid eggs; (3) a successful pair is that which raised at least one chick to fledgling age; (4) breeding success is the percentage of successful breeding pairs; (5) clutch size is the mean number of eggs per breeding pair; (6) hatching success is the percentage of hatched eggs per eggs laid; (7) productivity is the number of fledged young per breeding pair; (8) fledgling rate is the number of fledged young per successful pair. We use productivity as an index of the quality of a nesting territory (Penteriani *et al.* 2002, Sergio & Newton 2003).

To determine the age of chicks we used differences in morphology (Penteriani *et al.* 2005) corroborated by regression of the biometry data of age-known birds. Laying date was expressed in ordinal days since 15 December and was calculated by subtracting 35 days (the average incubation period) from the hatching date, and the difference of two days between the laying date and the start of incubation (Mikkola 1983).

Data analysis

Inter-annual differences in reproductive parameters at the population level we investigated using the Kruskal–Wallis test. Generalized linear mixed models (GLMM) (McCullagh & Searle 2000) were used to relate laying date to clutch size, the number of fledglings per breeding attempt, and the number of successful pairs. To control for the possible effects of spatial and temporal pseudoreplication, we included territory and year as random effects (Carrete *et al.* 2006). To evaluate density-dependent effects on breeding performance, we employed GLMM that related laying date, clutch size and number of fledglings per breeding pair and per successful pair to NND and to the Isolation Index. Year was included as a random factor (Carrete *et al.* 2006, 2008). For all the GLMM analyses, we applied the Poisson distribution as an error function and the logarithmic function as a link.

All the analyses were conducted with the R statistical software (http://www.r-project.org) with MASS and NLME packages for the GLMM analyses. All tests were two-tailed, statistical significance was set at $\alpha \leq 0.05$, and all the means are given as ± 1 sd.

RESULTS

Density and distribution

We detected 99 different Eagle Owl territories with a mean density of 22.01 territories per 100 km^2. Mean occupation rate was 91.95% (sd = ± 17.04%; territories monitored = 87; $n = 308$ occupation records). Mean NND was 0.92 ± 0.56 km (range: 0.10–2.53 km) and nests were regularly distributed (G-statistic = 0.69).

When we focused on the SPA boundaries, nesting densities increased to 46.15 territories per 100 km^2 ($n = 48$ territories) and the mean NND dropped to 0.70 ± 0.45 km and continued to be regularly distributed (G-statistic = 0.67)

Breeding

We monitored a total of 177 breeding attempts corresponding to 68 different pairs. We recorded at least 10 cases (5.3%; $n = 187$ territorial records) in which territorial pairs did not lay eggs. Nests were located mainly in holes or caves on small cliffs (up to 2 m high; 51.3%) or on slopes and river terraces (37.9%) and rarely on large cliffs (over 2 m high; 4.5%). The remaining nests (6.3%) were situated directly on the ground, under a tree trunk or also over esparto grass *Stipa tenacissima*. During the incubation period we recorded 12 events of nest desertion. The mean laying date for the pooled data was 30 January (sd = ± 19 days; $n = 123$ nests), ranging from 19 December to 20 March; differences in mean laying date were detected between years (Fig. 2; Kruskall–Wallis test, $W_6 = 16.56$, $P < 0.01$). The annual mean values for the population reproductive parameters were: breeding success = 93.22% (sd = ± 4.46%; $n =$ 177 breeding records); hatching success = 82.76%

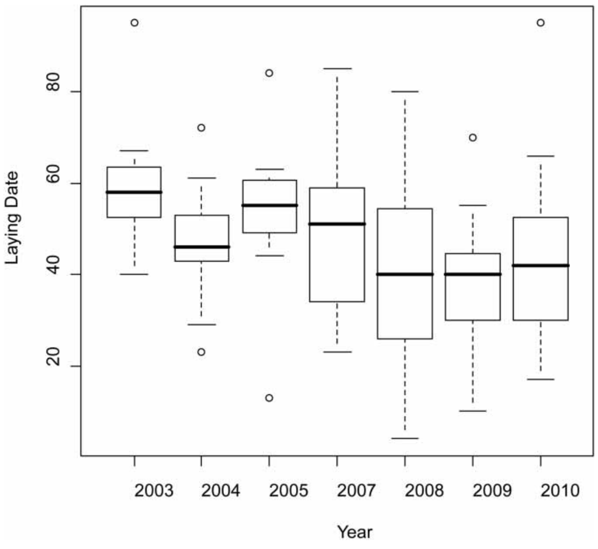

Figure 2. Box and whisker plot of the mean laying date of an Eagle Owl population in southeast Spain from 2003 to 2010. Year 2006 was eliminated because there were not enough records; days were recorded ordinally with Day 1 set at 15 December.

(sd = ± 15.42%; *n* = 41 nests); mean clutch size = 3.66 eggs/nest (sd = ± 0.66; *n* = 41 nests); productivity = 2.84 chicks per breeding pair (sd = ± 1.17; *n* = 162 nests); fledgling rate = 3.06 chicks per successful pair (sd = ± 0.82; *n* = 148 nests). No inter-annual differences were detected for any of the breeding parameters (all $P \geq 0.10$, Kruskall–Wallis test; Table 1).

Higher productivity (measured as the number of fledglings per breeding pair) was achieved by those pairs who laid eggs earlier in the breeding season (GLMM, fixed effect: laying date; random factor: territory; $P \leq 0.02$).

In spite of high local density, no density-dependent effects on breeding were detected. NND and Isolation Index did not enter any of the GLMM with laying date, clutch size or number of fledglings per breeding pair and per successful pair as dependent variables (all Ps $\geq$ 0.19).

DISCUSSION

The Eagle Owl population in the study area (southeast Spain) showed the highest breeding density ever described (see review in Marchesi *et al.* [2002]). It is higher than that described for the central and south areas of the Iberian Peninsula (Ortego & Díaz 2004, Delgado & Penteriani 2007). This population also showed a high productivity, much higher than other populations studied in the whole Palaearctic (Martínez *et al.* 1992, Penteriani *et al.* 2002, Marchesi *et al.* 2002). The high values were probably promoted by high local abundance of Rabbits (> 6 rabbits/ha [Sánchez *et al.* 2004]), and previous studies have highlighted the importance of this key species in Mediterranean environments (Delibes-Mateos *et al.* 2008), which is the primary local prey for Eagle Owls (Hiraldo *et al.* 1975, Delibes & Hiraldo 1979, Martínez *et al.* 1992, Penteriani *et al.* 2002). An ongoing study on the diet of Eagle Owls in this area has shown that Rabbit accounts for 90% of the diet by mass (Pérez-García *et al.* unpubl. data). Furthermore, Rabbit abundance has been related to high breeding performance in Eagle Owls (Donázar 1990, Penteriani *et al.* 2002, Marchesi *et al.* 2002).

High turnover rate is another factor that contributes to the high density of Eagle Owl breeding pairs. Eagle Owl populations are subject to a high mortality rate attributed to electrocution on power lines (Marchesi *et al.* 2002, Martínez *et al.* 2006, Sergio *et al.* 2004). Indeed, mortality caused by power lines is very high in the study area (Pérez-García *et al.* 2011); a total of 146 birds were found electrocuted during the study period. Such a high population turnover in other Eagle Owl populations has been related with a highly intermittent occupancy of breeding sites, and with the frequent disappearance of territorial adults, which are replaced slowly (Sergio *et al.* 2004, Ortego 2007, Schaub *et al.* 2010). However, in dense populations with high breeding success, frequent mortality of adults could create gaps in the breeding population, which could be quickly occupied by floaters. Therefore, this high replacement rate might relax territory boundaries. This effect, which leads to territorial packing, has been described for other territorial raptors such as Tawny Owls *Strix aluco* and Goshawks *Accipiter gentilis* (Hirons 1985, Selas 1997).

All the reproductive parameters in the study area were higher than those described elsewhere (Martínez *et al.* 1992, Penteriani *et al.* 2002, Marchesi *et al.* 2002), including the existence of broods of five fledglings (Pérez-García *et al.* 2010). Our data support the hypothesis that Eagle Owl populations display a clinal pattern in breeding performance throughout the distribution range, reaching maximum values in southern Spain (see the review in Marchesi *et al.* [2002]).

Early breeders showed greater productivity (Marchesi *et al.* 2002, Penteriani *et al.* 2002, Dalbeck & Heg 2006). This relationship may relate to early breeders' better physical condition (Penteriani *et al.* 2002, Dalbeck & Heg 2006), although other mechanisms

Table 1. Breeding parameters of an Eagle Owl population in southeast Spain monitored from 2003 to 2010. Data are presented as mean ± sd (number of records).

			Territorial pairs[a]					Fledged young		
Year	Monitored pairs	Occupation rate	Total	Not laid eggs	Breeding success	Clutch size	Hatching success[b]	Per territorial pair	Per successful pair	Laying date
2003	37	1.00	22	0	0.95	4.00 ± 1.41 (2)	0.73 ± 0.09 (2)	2.50 ± 1.10 (18)	2.65 ± 0.86 (17)	13 Feb ± 17.28 (7)
2004	24	1.00	17	0	1.00	3.50 ± 0.71 (2)	0.87 ± 0.18 (2)	3.31 ± 0.87 (16)	3.31 ± 0.87 (16)	30 Jan ± 13.58 (11)
2005	28	0.96	15	0	0.93	3.00 ± 0 (3)	0.67 ± 0.0 (2)	2.64 ± 1.15 (14)	2.85 ± 0.90 (13)	6 Feb ± 17.09 (11)
2006	10	0.89	8	0	1.00	–	–	2.87 ± 0.64 (8)	2.88 ± 0.64 (8)	–
2007	44	1.00	26	1	0.88	3.58 ± 0.69 (19)	0.87 ± 0.16 (19)	2.50 ± 1.18 (26)	3.18 ± 0.80 (22)	2 Feb ± 18.31 (21)
2008	43	0.91	25	2	0.96	3.67 ± 0.58 (3)	0.81 ± 0.17 (3)	2.83 ± 1.21 (24)	3.24 ± 0.77 (21)	23 Jan ± 21.48 (19)
2009	48	0.84	30	0	0.93	4.25 ± 0.50 (4)	0.76 ± 0.05 (4)	3.12 ± 1.13 (25)	3.39 ± 0.66 (23)	22 Jan ± 13.74 (24)
2010	61	0.96	42	7	0.89	3.67 ± 0.50 (9)	0.79 ± 0.19 (9)	2.04 ± 1.26 (39)	3.00 ± 0.82 (28)	26 Jan ± 17.97 (28)
Total	295	0.97	187	10	0.93	3.66 ± 0.66 (41)	0.82 ± 0.15 (41)	2.64 ± 1.32 (172)	3.09 ± 0.82 (148)	30 Jan ± 18.48 (123)

[a] Territorial pairs that have been monitored during reproduction; [b] mean percentage of eggs hatched per nest monitored.

could also intervene, for example, age/experience differences among breeders (Carrete *et al.* 2002, 2008). More experienced birds may lay early to synchronize their reproduction to the breeding cycle of their principal prey, Rabbits, whose abundance peaks in early spring and summer (Aparicio & Bonal 2002, Gonçalves *et al.* 2001). In addition, the chicks of early breeders can benefit from lower parasitism rates which are usually related to temperature (Merino & Potti 1996) and breeding density (Ortego & Espada 2007, Ortego & Cordero 2010).

We found no density-dependent effect for either the laying date or for breeding performance, and a similar result has been found for other Eagle Owl populations (Marchesi *et al.* 2002, Ortego 2007), but not all (Penteriani *et al.* 2002). Furthermore, the absence of differences in fledgling rates among territories suggests that this population does not follow the 'habitat heterogeneity hypothesis' (Ferrer & Donázar 1996). An over-abundance of prey, frequent turnovers and the effects of individual quality (or age) on breeding performance might be responsible for the absence of inter-territorial variability in our study population (Penteriani *et al.* 2002, 2004, Carrete *et al.* 2006).

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