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Breeding performance, age effects and territory occupancy in a Bonelli's Eagle *Hieraetus fasciatus* population

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Bonelli's Eagle *Hieraetus fasciatus* is one of the most endangered birds of prey in Europe. Despite mounting interest and research, several questions regarding the conservation implications of territory occupancy and site-dependent population regulation remain insufficiently explored for this species. Here, we report on a 12-year study of the territorial structure of a Bonelli's Eagle population in southeastern Spain. No signals of population decline were found in the breeding population, as mean annual productivity was stable and the presence of mixed-age pairs in the population decreased with the years. However, the average proportion of subadults occupying territories was larger than that observed in other Spanish populations. Contrary to the predictions of a despotic distribution model, we found no significant relationship between occupancy rates and breeding parameters. Our results showed significant variations in productivity attributable to differences in the quality of individuals (i.e. mixed versus adult pairs), but no variability among territories *per se* (i.e. caused by habitat heterogeneity). Moreover, coexistence with intraguild species did not have any significant effect on productivity, although the proximity of Eagle Owls *Bubo bubo* affected the occupation rate of territories. Finally, our population does not appear to experience site-dependent population regulation, as a positive relation between mean annual productivity and density was found. The threat posed by changes in land use in the study area leads us to suggest that strict protection of current territories is necessary to ensure population persistence, and we suggest that a significant population increase is only likely if new or deserted territories become available.

Keywords: ideal despotic distribution, intraguild predation, inverse density-dependence, population regulation, territory quality.

Bonelli's Eagle *Hieraetus fasciatus* is one of the most threatened raptors in Europe, with severely declining populations in most of the Mediterranean countries it inhabits. Its total population size has been estimated at 920–1100 breeding pairs (BirdLife International 2004). The species is classified as endangered in Europe due to declines of more than 50% of the original breeding population in some areas between 1970

and 1990 (Tucker & Heath 1994). As a result, Bonelli's Eagle is listed in Annex I of the EU Wild Birds Directive, and in Appendix II of the Bern Convention, Bonn Convention and CITES Convention (Heath *et al.* 2000). In Spain, which holds approximately 70% of the whole European population, the species showed a rapid decline between 1980 and 1990, mainly caused by direct persecution (e.g. shooting, poisoning), electrocution, disturbance at nest sites, competition with other species and degradation of the Mediterranean scrubland habitats where they

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mainly forage (Real & Mañosa 1997, Real *et al.* 2001, Carrete *et al.* 2002b). As a result of its endangered status (Madroño *et al.* 2004), Bonelli's Eagle has been the focus of a great deal of attention from scientists, leading to the inception of an European Action Plan (Arroyo & Ferreiro 1999), and many conservation studies have been conducted with the aim of proposing management actions for reversing the declining trends and enhancing the status of the existing populations (e.g. Ontiveros & Pleguezuelos 2000, 2003a, Real *et al.* 2001, Carrete *et al.* 2002a, Gil-Sánchez *et al.* 2004, Muñoz *et al.* 2005).

On an optimistic note, several recent studies have pointed to the stability of several local populations in Spain (Carrete *et al.* 2002a, 2005, Balbontín *et al.* 2003, Ontiveros & Pleguezuelos 2003b, López-López *et al.* 2004, Muñoz *et al.* 2005). In particular, the number of breeding pairs in the Alicante province showed a pronounced reduction during the 1980s (Rico *et al.* 1992), then a moderate decline between 1989 and 2000. Since then the population has been reported to be fairly stable (Mateache 2005). In other Mediterranean areas some authors have pointed to two warning signals, namely a decrease in productivity (Muñoz *et al.* 2005) and a decrease in the age at first breeding (Balbontín *et al.* 2003), which may indicate future negative population trends. Bonelli's Eagle is a long-lived, territorial and site-faithful species, with a mature reproduction age of about 3.5 years (Cramp & Simmons 1980). For birds with deferred maturity, an increasing recruitment of nonadult individuals to the breeding population usually reflects high rates of adult mortality (Balbontín *et al.* 2005), with negative demographic consequences (Ferrer *et al.* 2003). It has been demonstrated for several species that breeding pairs formed by at least one subadult individual are less productive than those composed only of adults (Sánchez-Zapata *et al.* 2000, Boal 2001, Balbontín *et al.* 2003). Nonetheless, the effects of age on breeding performance may be strongly influenced by variability in territory quality, as subadults usually tend to occupy low quality territories (Ferrer & Bisson 2003, Penteriani *et al.* 2003). Interspecific interactions may also influence territory quality and breeding site selection (Sergio *et al.* 2004). For instance, the adverse effects of interspecific competitive interactions may be stronger for pairs with nonadult individuals (Carrete *et al.* 2006).

The inter-relationship between the quality of the individuals (e.g. age) and the quality of territories they occupy is a widespread phenomenon associated with the ideal despotic distribution (IDD) model

[Fretwell (1972)], in which young or subordinate individuals are forced to use lower quality sites. The IDD model assumed that individuals can recognize variations in territory quality (Zimmerman *et al.* 2003), and consequently territories are chosen sequentially, with the most suitable selected first (Sutherland 1996, Newton 1998). It follows, then, that the best territories should be the most frequently occupied (Sergio & Newton 2003). Coupled with habitat heterogeneity, this despotic settlement pattern leads to site-dependent mechanisms of population regulation (Rodenhouse *et al.* 1997, Krüger & Lindström 2001). Site-dependent regulation is a density-dependent mechanism of population regulation that may arise when a pre-emptive use of sites is driven by a despotic behaviour of high quality, dominant individuals. Consequently, as population size increases, the use of progressively less suitable territories is expected to reduce the average productivity of the population (Ferrer & Donazar 1996, Krüger & Lindström 2001, Morris 2003). Obviously, this regulation mechanism has substantial consequences for the persistence of populations (McPeck *et al.* 2001) and, therefore, when implementing conservation plans, it is of special interest to discriminate between territories based on their quality, as measured, for instance, by the number of years a territory is occupied (Sergio & Newton 2003).

For Bonelli's Eagle, however, the conservation implications of these differences in territory quality have not been sufficiently explored. Many studies have gained insight into the habitat-related factors affecting breeding output (Ontiveros & Pleguezuelos 2003b, Gil-Sánchez *et al.* 2004, Ontiveros *et al.* 2005), or have modelled the selection of breeding habitats and dispersal areas (Ontiveros 1999, Balbontín 2005, López-López *et al.* 2006), but few have specifically tested some of the predictions of the IDD model and the site-dependent regulation hypotheses (Carrete *et al.* 2006). In this study we address these issues, using data from a long-term (12 years) monitored population of Bonelli's Eagle in the province of Alicante, southeastern Spain. First, we examine temporal trends in population size, productivity and the presence of nonadult individuals in the breeding population. Secondly, we discuss variations in territory quality by assessing their occupancy rates, productivities, the presence of subadults and the influence of intraguild predators and competitors. As regards this point, we specifically tested four predictions posed by the IDD model: (1) the observed occupation rate of territories should differ from a random pattern,

indicating differential use among territories, (2) the mean annual productivity of a territory should be positively related to the occupation rate of that territory, (3) low-quality territories are more frequently occupied by low-quality individuals (subadults), and (4) the occupation rate of territories should reflect their quality in terms of reducing the negative consequences of intraguild species interactions. We have assessed potential intraguild effects by examining the relationships between occupation rates and breeding parameters and the distance to the nearest Eagle Owl *Bubo bubo* nest. This owl is a top predator able to cause population effects in other raptor populations (Sergio *et al.* 2003), and largely shares habitat and main prey with Bonelli's Eagle in Spanish Mediterranean habitats (Martínez & Calvo 2000, Martínez *et al.* 2003, López-López *et al.* 2004). Although competitive or predatory interactions have not been thoroughly studied yet for both predators, there are grounds for suggesting that the smaller-sized Eagle Owl can influence the breeding output or nest distribution of the larger Bonelli's Eagle (Real & Mañosa 1990, Serrano 2000, Sergio & Newton 2003). Additionally, testing the effects of the proximity to Golden Eagles *Aquila chrysaetos* might further reveal how interspecific competition relates to territory quality (Gil-Sánchez *et al.* 2004, Carrete *et al.* 2006). This species is the main competitor of Bonelli's Eagles, and may influence the demography of its populations (Carrete *et al.* 2002b, 2005). Finally, we examined whether the population studied experienced site-dependent regulation by testing the following predictions: (5) at the population level, mean annual productivity (number of fledged young per territorial pair) should be negatively related to density, (6) the annual mean territory occupation rate should decrease as the number of territorial pairs increases, and (7) there should be a positive relationship between density and the skewness coefficient of productivity (i.e. as the number of territorial pairs increases, the form of the distribution of brood sizes becomes more left-skewed; Ferrer *et al.* 2006).

METHODS

Study area

The study was conducted in the province of Alicante (southeastern Spain), a largely mountainous territory of 5863 km² with elevations ranging from 0 to 1558 m asl. The climate varied from semi-arid

meso-Mediterranean in the south to subhumid Mediterranean in the north (Agencia del Medio Ambiente 1997). Annual rainfall ranges from 200 mm in semi-arid to 1000 mm in subhumid areas, and mean average temperature varies between 12 and 18 °C. The northern part of the province is more rugged than the southern part and is dominated by Aleppo Pine (*Pinus halepensis*) forests, scrublands, and almond and olive plantations. The south of the study area is principally covered by scrublands and agricultural fields, mainly vineyards and citrus plantations. All the coastal areas of the province suffer intense urbanization pressures.

Field work

Each year from 1989 to 2000, we checked the whole study area to assess the occupancy of Bonelli's Eagle territories. Field work was carried out between February (i.e. beginning of the reproductive period and courtship displays) and June (to check for fecundity). Each nest was visited at least twice after egg-laying, and we assessed breeding success by checking the nests just before fledging (i.e. when nestlings are approximately 50 days old, as determined by observing nestling feather growth). Differences in plumage colour allowed us to distinguish between adult and subadult birds (Parellada 1984). Following the terminology of Steenhof (1987), a territorial pair is one that occupied a given territory, a breeding pair is one which laid ≥ 1 egg, and a successful pair is one which raised ≥ 1 nestling to the fledging age (> 50 days old). Productivity was expressed both as the number of fledglings per territorial pair and as the number per successful pair (fledging rate).

Occupancy rate and territory quality

For each territory, we estimated its occupancy rate as the proportion of years that it was occupied by a pair of Eagles, regardless of whether they bred successfully or not (Zimmerman *et al.* 2003). Following Sergio and Newton (2003), territories occupied more than 60% of the years were classified as high-quality territories, whereas territories occupied less than 60% of the years were classified as low-quality territories. As further measures of quality, we also calculated the distances from each Bonelli's Eagle territory to the nearest neighbour territories of Golden Eagles and Eagle Owls. We did not consider habitat variables because previous studies, including ours, suggested little influence of the physical characteristics of the

territories on the breeding performance of different Bonelli's Eagle populations (Rico *et al.* 2001, Gil-Sánchez *et al.* 2004, Carrete *et al.* 2006). For the analyses regarding territorial occupancy rates we only considered those territories monitored for more than 6 years (> 50% of the study period).

Statistical analyses

In the absence of estimates of mortality or other demographic parameters, the population growth rate, λ , can be estimated using a log-linear regression model (Eberhardt 2002):

$$\log_e N_t = \log_e N_0 + t \log_e \lambda$$

where N_t is population size at time t and N_0 is the initial population size. We calculated the 95% confidence interval of the slope parameter to test whether the trend differed from 0 (i.e. $\lambda = 1$).

Temporal variations in response variables were analysed using generalized linear mixed models (GLMM), in which territory was considered a random effect to avoid pseudoreplication. We used a log-link function (with Poisson error distribution) for productivity parameters (number of fledglings: 0, 1, 2), and a logit-link function (with binomial error distribution) for binary variables (i.e. breeding success, presence of subadults). Differences in reproductive output between pairs with and without subadults were also tested by means of GLMM analyses, as were the effects of the distances to Golden Eagles and Eagle Owls. In addition, GLMMs provide the variance component of the random effects, which

can be interpreted as an estimate of the spatial process variation in the response variable attributable to differences between territories (Franklin *et al.* 2000). We examined these differences using the likelihood-ratio test (LRT) between the null model and the random effects model (Venables & Ripley 2002).

When appropriate, for territory-level and population-level analyses, variables were averaged across years for each territory, and across territories for each year (Sergio & Newton 2003). In these cases we used the Spearman's correlation test. Means are given \pm 1 se and statistical significance was set at $P < 0.05$. Data analyses were performed using R (R Development Core Team 2005).

RESULTS

Trends in population size and breeding performance

During the study period we monitored 212 territorial occupations and 168 breeding attempts in 24 Bonelli's Eagle territories (Table 1). The population size ranged from 15 to 23 territorial pairs, and the estimated value of λ was 0.9794 (95% CI = 0.9586, 1.0006). This estimate corresponded to a negative population trend, but was not significantly different from 0 ($\beta = -0.0209$; $P = 0.055$).

The mean annual number of fledglings per territorial pair was 1.23 ± 0.05 ($n = 12$), and the mean annual number of fledglings per successful pair was 1.59 ± 0.03 ($n = 12$). On average, $77.2 \pm 2.5\%$ of the territorial pairs reared fledglings successfully. Successful pairs of Eagles mainly produced two fledglings (59.9%),

Table 1. Main breeding parameters for the Bonelli's Eagle population studied between 1989 and 2000 in Alicante province (southeastern Spain).

Year	No. of territorial pairs	Mean no. of fledglings per territorial pair	Mean no. of fledglings per successful pair	% of mixed pairs	% of successful pairs
1989	23	1.33 \pm 0.82	1.67 \pm 0.49	36.4	80.0
1990	17	1.55 \pm 0.52	1.55 \pm 0.52	0.0	100.0
1991	19	1.33 \pm 0.82	1.67 \pm 0.49	33.3	80.0
1992	20	1.26 \pm 0.81	1.60 \pm 0.51	38.5	78.9
1993	19	1.18 \pm 0.73	1.43 \pm 0.51	20.0	82.4
1994	17	1.07 \pm 0.88	1.60 \pm 0.52	20.0	66.7
1995	16	1.31 \pm 0.87	1.75 \pm 0.45	28.6	75.0
1996	15	1.00 \pm 0.85	1.50 \pm 0.53	0.0	66.7
1997	15	1.09 \pm 0.83	1.50 \pm 0.53	0.0	72.7
1998	15	1.08 \pm 0.79	1.44 \pm 0.53	14.3	75.0
1999	17	1.14 \pm 0.86	1.60 \pm 0.52	18.2	71.4
2000	19	1.39 \pm 0.85	1.79 \pm 0.43	0.0	77.8

the remainder producing one young. Overall, breeding performance did not change during the 12 years of the study. In fact, neither the mean number of fledglings per territorial pair ($\beta = -0.0141$; $P = 0.480$), nor the mean number of fledglings raised per successful pair ($\beta = 0.0022$; $P = 0.910$), nor the proportion of successful breeding pairs ($\beta = -0.0985$; $P = 0.105$) showed a significant trend.

The presence of subadults in the population was common in our study area (mean annual percentage of individuals = $9.6 \pm 2.5\%$). Fourteen (58.3%) of the 24 breeding territories were occupied at least once by one subadult. In only two cases were both members of a pair subadult, so this type of pair cannot be analysed separately. Hereafter, we shall refer to all as 'mixed pairs'. The annual percentage of mixed pairs ranged between 0% and 38.5% (mean: 17.4 ± 4.3 ; Table 1), with a significant negative trend in this variable ($\beta = -0.1656$; $P = 0.039$).

Territory quality and IDD predictions

Most of the territories were occupied every year throughout the study period (Fig. 1). Consequently, the observed occupancy pattern clearly differed from a random pattern, providing evidence to support prediction 1 (a statistical test could not be performed due to insufficient degrees of freedom). The occupation rate of the territories did not correlate significantly with the mean number of fledged young per territorial pair ($\beta = 0.1578$; $P = 0.757$) or with the fledging rate ($\beta = 0.0399$; $P = 0.936$). The mean numbers of fledged young in low- and high-quality territories were 1.00 ($n = 3$) and 1.22 ($n = 18$),

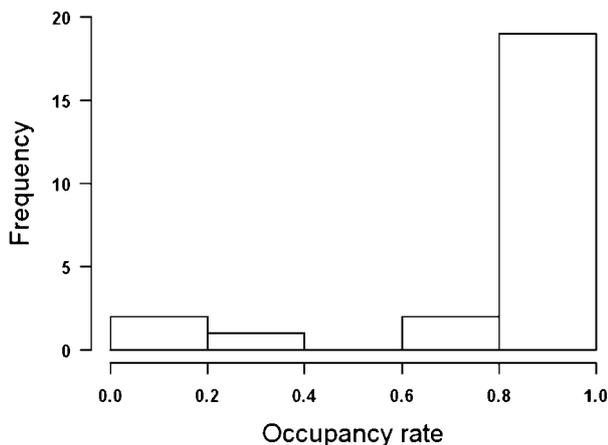


Figure 1. Histogram of territorial occupancy rates, estimated as the proportion of years that a given territory was occupied.

respectively, and the mean fledging rates were 1.00 ($n = 2$) and 1.59 ($n = 18$). These results do not support prediction 2, but must be considered with caution given the low number of low-quality territories in our sample.

For adult and mixed pairs, the mean numbers of fledglings per territorial pair were 1.44 ± 0.08 ($n = 80$) and 0.50 ± 0.14 ($n = 20$), respectively, and the mean fledging rates were 1.67 ± 0.06 ($n = 69$) and 1.11 ± 0.11 ($n = 9$). While controlling for territory (as a random effect), the differences between adult and mixed pairs were significant for the first parameter ($F_{1,77} = 11.05$; $P = 0.001$) but not for the second ($F_{1,57} = 1.54$, $P = 0.219$). These results indicate that age effects could be significant *per se* rather than through variability in territory quality. The likelihood of finding a mixed pair in a given territory correlated negatively with its occupancy rate, but the trend was not significant ($\beta = -1.4720$; $P = 0.193$), so prediction 3 was not supported. In addition, the proportion of mixed pairs correlated positively with population density ($r_s = 0.62$; $P = 0.002$; $n = 12$), but not with mean annual productivity ($r_s = 0.16$; $P = 0.602$; $n = 12$).

The occupation rate of territories only partially reflected their quality in terms of competitive interactions and mortality risk. We detected a significant positive correlation between the distances to the nearest Eagle Owl territory and territorial occupancy rates ($r_s = 0.45$; $P = 0.040$; $n = 21$), but the relationship between the distance to the nearest Golden Eagle territory and the occupancy rate was not significant ($r_s = 0.29$; $P = 0.207$; $n = 21$). Furthermore, productivity was not correlated with the proximity of competitors, even when only mixed pairs are considered (Table 2). Therefore, prediction 4 was only partially supported.

Overall, the likelihood-ratio test for random effects (territory) on reproductive output was not significant (LRT = 0.58; $P = 0.445$), thus providing little evidence of heterogeneity among territories.

Site-dependent population regulation

Contrary to what might be expected under a site-dependent regulation scenario, mean annual productivity (number of fledglings per territorial pair) showed inverse density dependence (correlation between productivity and number of occupied territories: $r_s = 0.60$; $P = 0.037$; $n = 12$; Fig. 2). Moreover, the annual mean territory occupation rate did not correlate significantly with density ($r_s = -0.12$; $P = 0.708$; $n = 12$) and a significant negative relationship

Table 2. Results of GLMMs performed to examine the influence of the distance to the nearest neighbour territories of Eagle Owl and Golden Eagle on the breeding performance of Bonelli's Eagle pairs. The analyses labelled as 'territories with subadults' included only the breeding attempts of mixed pairs.

	No. of fledglings per territorial pair		No. of fledglings per successful pair	
All territories	β	<i>P</i>	β	<i>P</i>
Eagle Owl	-0.0409	0.376	-0.0104	0.815
Golden Eagle	0.0103	0.713	0.0021	0.930
Territories with subadults	β	<i>P</i>	β	<i>P</i>
Eagle Owl	0.0104	0.940	0.1038	0.522
Golden Eagle	0.0676	0.509	-0.0103	0.922

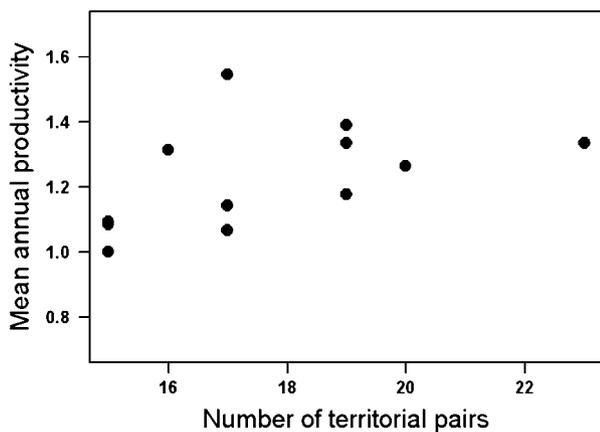


Figure 2. Relationship between density (number of territorial pairs) and mean annual productivity (average number of fledglings per territorial pair). (Spearman rank correlation: $r_s = 0.60$, $P = 0.037$).

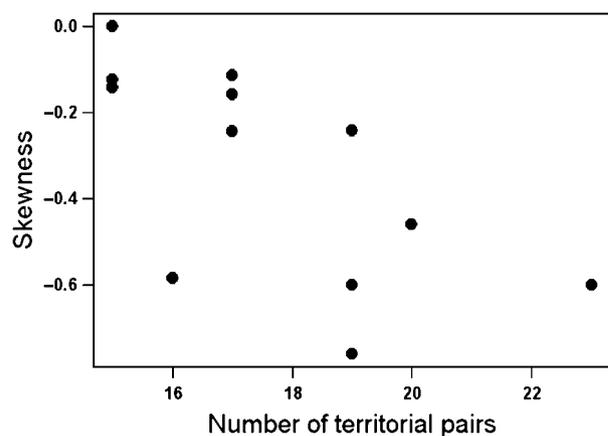


Figure 3. Relationship between density (number of territorial pairs) and skewness (Spearman rank correlation: $r_s = -0.80$, $P = 0.002$).

between density and skewness was observed ($r_s = -0.71$; $P = 0.023$; Fig. 3). This result indicates that, as density increased, the form of the distribution of brood sizes became more right-skewed (i.e. more pairs were successful). Predictions 5–7 were thus not supported.

DISCUSSION

Population trends

The number of Bonelli's Eagle breeding pairs in Alicante showed a slight decrease between 1989 and 2000, after experiencing a more pronounced reduction in previous decades (Rico *et al.* 1992). Although the estimated population growth rate did not differ significantly from 1, the result of the tests was close to the limits of statistical significance, which suggests that any findings regarding the population trend

should be treated with caution. However, current estimates of population size (not included in our analyses) give values of 21–22 pairs (Mateache 2005), which implies no decline.

Overall, breeding performance was similar to that estimated in other southern Spanish populations (Balbontín *et al.* 2003, Carrete *et al.* 2006) and none of the breeding performance variables analysed showed significant temporal variations throughout the study period. Furthermore, contrary to other studies (e.g. Balbontín *et al.* 2003), we found a significant negative temporal trend for the presence of subadults in the territorial pairs, although the average annual proportion of mixed pairs was notably higher than those of other populations for which information is available: Andalusia: 7.3% (Balbontín *et al.* 2003); Granada: 8.0%, Murcia: 10.0% (Carrete *et al.* 2006); Málaga: 12.1% (Gil-Sánchez *et al.* 2005). For the Spanish Imperial Eagle *Aquila adalberti* Ferrer *et al.*

(2003) proposed that a proportion of immature individuals of >0.10 can be considered a 'reliable warning signal' that anticipates population decline. Despite the negative trend in the percentage of mixed pairs observed in our Bonelli's Eagle population, the mean annual proportion of nonadult individuals (0.096) was close to that critical value. The most straightforward explanation for the occurrence of subadults in Bonelli's Eagle pairs is a decrease in the adult survival rate rather than an increase in resource availability or a decrease in the pre-adult survival rate (Balbontín *et al.* 2003, 2005, Ferrer *et al.* 2003). In fact, human persecution (e.g. direct shooting) and interactions with power lines are important causes of adult mortality in the study area (Martínez *et al.* 2001).

Territory quality, age effects and interspecific interactions

Our results suggest that territory occupancy may not be a good measure of territory quality for Bonelli's Eagle. The territory occupancy rate did not correlate significantly with productivity. In addition, most territories were regularly occupied in most years, and so only few territories could be considered low-quality. We also found little evidence of territory heterogeneity, as the test for the spatial process variation in productivity (Franklin *et al.* 2000) was not significant. Consequently, our results did not provide strong support for the predictions of the IDD model, although they must be interpreted with caution given the low proportion of low-quality territories in the study area.

Variability in breeding performance among nesting sites is frequently a consequence of a despotic distribution pattern, in which a strong relationship between habitat and individual quality is to be expected (Ferrer & Bisson 2003, Penteriani *et al.* 2003, Espie *et al.* 2004). Indeed, in our study population, age-related effects largely contributed to the variation in breeding performance (with mixed pairs producing significantly fewer young), but there was no apparent inter-relation between age and territory quality (as measured by its occupancy rate). Similar results were found by Carrete *et al.* (2006) for Golden and Bonelli's Eagles in two different areas of southern Spain. These authors concluded that inter-territory variability in breeding performance was likely to occur because of variations in the quality of the territorial individuals, rather than through habitat heterogeneity among territories. In an increasing population, new pairs formed by two young individuals

can occupy low-quality territories, thus contributing to a decrease in the average population productivity. However, the low proportion of cases in which both mates were nonadults suggests that subadult eagles recruit into the breeding population by joining adults that were already nesting before losing their mate. In that case, they might settle in good-quality territories, explaining the lack of relation between age and territory occupancy rate.

The coexistence of cliff-nesting raptors in semi-arid Mediterranean environments is largely influenced by interspecific territorial interactions (Carrete *et al.* 2002b, 2005, 2006, Gil-Sánchez *et al.* 2004). In fact, similar nesting habitat preferences are shown by Bonelli's Eagles, Golden Eagles and Eagle Owls in Mediterranean areas (Martínez & Calvo 2000, Martínez *et al.* 2003, López-López *et al.* 2004). However, as mentioned, we found that the occupation rate and the mean productivity of Bonelli's Eagle territories did not correlate significantly with the distance to the nearest Golden Eagle territory. Hence, although territorial interactions between Golden Eagles and Bonelli's Eagles are supposed to be strong (Gil-Sánchez *et al.* 2004, Carrete *et al.* 2005, 2006), the proximity of Golden Eagle pairs had no noticeable effect on the occupation rate or breeding outcome, even when only mixed pairs were considered.

On the other hand, Eagle Owl distances correlated significantly with the territory occupancy rates, but not with their productivities. As some studies have shown that the Eagle Owl frequently preys upon chicks and juvenile Bonelli's Eagles (Real & Mañosa 1990, Serrano 2000), these results suggest that Bonelli's Eagles could minimize the predation risk by avoiding occupying territories in the vicinity of Eagle Owl pairs. In this sense, the Eagle Owls may constitute a 'landscape modelling force' (Sergio & Newton 2003), influencing the spatial and temporal distribution of other intraguild raptors through predatory interactions (Sergio *et al.* 2003). Alternatively, the correlation between occupancy and distance to Owls could be caused by fine-grained differences in habitat quality not reported in previous studies (e.g. different foraging or nesting habitat within the seemingly homogeneous Mediterranean scrubland), in which case the correlation would not be caused by Owls. However, this hypothesis is unlikely because there is a substantial diet overlap between both predators in the study area, which suggests a true preference for the same foraging habitats (Rico *et al.* 1990, Martínez & Zuberogitia 2001).

Site-dependent regulation

Contrary to the predictions of site-dependent regulation theory, our Bonelli's Eagle population showed inverse density dependence, as mean annual productivity increased with the number of territorial pairs in the population. A similar inconsistency with the prediction that average productivity should decrease with increased breeding population size has been observed elsewhere in Spain for Bonelli's Eagles (Carrete *et al.* 2006). These authors found inverse density dependence in a low-density area (Murcia: ~ 0.19 pairs/100 km²), but negative density dependence in a high-density area (Granada: ~ 0.32 pairs/100 km²). Although they did not provide any explanation, it can be hypothesized that this contrasting pattern may arise because of differences in densities. However, the mean density in Alicante (~ 0.31 pairs/100 km²) was similar to that of Granada, where the Bonelli's Eagle population showed negative density dependence (Carrete *et al.* 2006), so this explanation does not appear to be satisfactory in our case. Anyway, under a scenario of low density and high adult mortality, the incorporation of nonadult individuals in the breeding population may act as a buffer mechanism that increases the persistence time of populations (Ferrer *et al.* 2004). Nevertheless, some caution is again needed when assessing our results, because the failure to meet the predictions of site-dependent regulation theory could be influenced by the low proportion of low-quality territories in our study area.

We also hypothesize that interactions between weather and prey abundance may contribute to determining the annual number of breeding pairs, so that in good years more pairs breed and more fledglings are produced (Steenhof *et al.* 1997). This pattern will also result in a more right-skewed distribution of brood sizes as the breeding population increases. Our results suggest that an increase in population size is mainly determined by the incorporation of subadult individuals (i.e. the proportion of mixed pairs augmented with population size), but as they contribute to lowering the average annual productivity, this effect is compensated by an increase in the breeding performance of adult pairs. Although Bonelli's Eagle's main prey (pigeons *Columba* spp., Rabbits *Oryctolagus cuniculus*, Red-legged Partridges *Alectoris rufa*; Rico *et al.* 1990) do not show population cycles, they are still subject to variations in numbers due to epizootics (Martínez & Zuberogoitia 2001, Martínez & Calvo 2001), habitat degradation (Ontiveros 2000)

or uncontrolled game re-stocking (Mañosa 2002). Furthermore, fecundity may vary with local weather conditions (Ontiveros 1999, Ontiveros & Pleguezuelos 2003a, Gil-Sánchez *et al.* 2004), and the species' distribution is limited by climate at a regional scale (López-López *et al.* 2006). Thus, favourable local conditions in a given year may promote territory occupation and more breeding attempts. Alternatively, adverse conditions may have the opposite effect, even hindering the detection of birds in their territories as they will not show conspicuous reproductive behaviour (Newton 1979).

Conservation implications

Most of the tests of our initial predictions did not provide positive results. In this way this study shows the difficulty of interpreting population dynamics and behaviour from the monitoring of breeding pairs without clear identification of individuals, which is particularly difficult and costly for populations of large raptors. The main challenge here is to discriminate between the quality of territories and of individuals. It is likely that, in addition to age or territorial effects, Lifetime Reproductive Success varies between individuals in this population, as in many bird populations. Therefore, it is not possible to be certain what population changes are due to environmental and demographic stochasticity, and what are due to deterministic effects in age-structured populations.

Nevertheless, under a scenario of habitat heterogeneity and site-dependent population regulation, determining which territories are of highest quality is probably the most important issue of conservation concern (McPeck *et al.* 2001, Penteriani *et al.* 2004). As these territories tend to produce most of the young every year, their disappearance will have strong negative consequences for the whole population. However, in our study area, we have failed to detect significant variability in breeding performance among territories (excluding age-related effects), which suggests that most Bonelli's Eagle territories in our study area should be of priority conservation concern. The modelling approach of Carrete *et al.* (2002b) in a neighbouring population also pointed in the same direction. These authors found that the demographic potential of this species (i.e. the equilibrium proportion of territories that would be occupied by females in a completely suitable region; Lande 1987) was 0.91. This high value (much larger, for example, than that of the Golden Eagle in the same study area: 0.69; Carrete *et al.* 2005) suggests

that, given a particular system of suitable territories, Bonelli's Eagle populations may be close to their population ceiling. Consequently, strict protection of current territories is necessary to ensure population stability, and a significant population recovery is likely to be produced only if new or deserted territories become available.

Policies favouring increments in the survival rates of territorial and nonterritorial birds are among the most important factors suggested for promoting conservation because they strongly influence the demographic potential of Bonelli's Eagle. However, efforts aimed at preventing the loss of territories through habitat degradation and matching the conservation status between traditional, occasional and abandoned sites (if the causes of desertion can be mitigated) may also improve the efficiency of management decisions. Unfortunately, prospects for the study area are not encouraging, as habitat quality has diminished dramatically over the last decade to the point of causing population declines in several predators (Martinez & Zuberogoitia 2004), and potentially habitat-degrading factors for Bonelli's Eagles have been detected. Increasing numbers of large wind farms, golf-courses and housing developments are being sited in favourable foraging habitat (Rico *et al.* 2001); the road network, which can upset foraging patterns of raptors (Bautista *et al.* 2004) and cause Bonelli's Eagles to desert territories (Ontiveros 2000), has also undergone a considerable extension, and outdoor recreation activities (i.e. 'green' tourism) are being developed within the home ranges (authors' unpubl. data).

As always, as most of the known mortality is caused by shooting or electrocution and mixed pairs are less productive than pairs formed by two adults, reducing man-induced mortality must also be taken into account by managers.

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