

A nine-year study of successful breeding in a Bonelli's eagle population in southeast Spain: a basis for conservation

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Abstract

We analyse the factors influencing breeding success in a healthy population of Bonelli's eagle (*Hieraetus fasciatus*) from south-east Spain, a raptor that has suffered a serious decline in Europe. Between 18 and 33 pairs were annually monitored during the period 1994–2002. Several factors that may affect four breeding parameters were studied, namely human presence, vegetation, relief, climatic factors, intra- and inter-specific relationships, diet, prey abundance, nest building, adult mortality and age of reproduction. A consistently high breeding success was registered during the study period (productivity = 1.43, SD = 0.11), which was probably the result of high adult survival, adequate prey availability and mild weather conditions. However, a certain vulnerability to the presence of golden eagles (*Aquila chrysaetos*) and to human disturbance was observed. One interesting result was the reduced survival of young chicks on north-facing cliffs owing to colder conditions, which may partially explain the decline of the Bonelli's eagle populations along its European distribution limits. We discuss the role of this healthy subpopulation in an Iberian meta-population context, and propose that the potential interference of golden eagles should be taken into account when designing management strategies for Bonelli's eagles. Finally, we pinpoint some conservation priorities and the importance of reducing the main causes of adult mortality (i.e. shooting and electrocution) to assure successful reproduction and survival of this species.

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1. Introduction

Bonelli's eagle (*Hieraetus fasciatus*) is a medium to large sized raptor distributed mainly in India and southern China (del Hoyo et al., 1994). A marginal sedentary population with about 1000 estimated pairs inhabits the Mediterranean area of Europe, mainly in the Iberian Peninsula (Real et al., 1996; Fig. 1). European populations have experienced a marked decline, and this raptor is considered as a vulnerable species (Rocamora, 1994). In Spain 116 pairs (15% of population) disappeared between 1980 and 1990 (Garza and Arroyo, 1996), with shooting and electrocution being the main known threats (Real et al., 2001). Some de-

clining subpopulations have very low breeding parameters (Real and Mañosa, 1997) and information about factors affecting reproduction success is therefore essential for the proper design of conservation strategies.

Thus, the European Action Plan proposed for this species includes improved understanding of the reproductive parameters, through research on the limiting factors (Birdlife International, 1999). However, studies on the breeding biology of Bonelli's eagle have usually been limited just to describing the parameters of some populations (Arroyo et al., 1995; Real and Mañosa, 1997; Gil Sánchez et al., 2000; Balbontín et al., 2003), apart from Carrete et al. (2002) and Ontiveros and Pleguezuelos (1999), who studied the influence on breeding of some habitat variables and adult mortality, and effects of prey availability, respectively.

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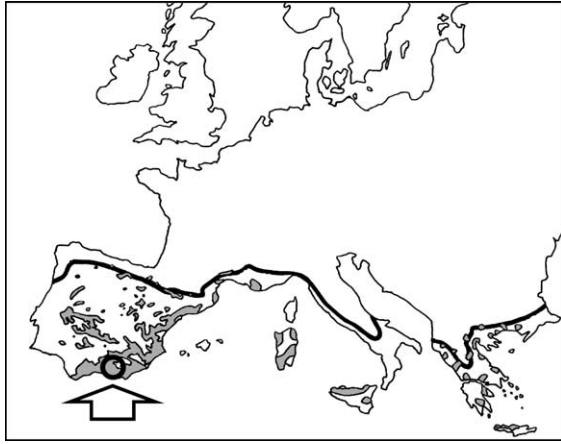


Fig. 1. Bonelli's eagle distribution in Europe (grey) and geographical location of the study area (circle). Thick line separates the Mediterranean (below) and the Eurosiberian floral regions (above). Redrawn from Real and Mañosa (1997) and Cramp and Simmons (1980).

In this paper we present the results of a study conducted in south-east Spain, on a successful breeding population of Bonelli's eagle, based on data for the period 1994–2002. Several factors that may affect reproductive parameters were studied, in order to show the optimal conditions for this threatened raptor. This may be useful information for management strategies elsewhere.

2. Methods

2.1. Study area

The study area ($\approx 9800 \text{ km}^2$) was situated in the province of Granada, south-eastern Spain (Fig. 1) ranging in altitude from 0–3482 m.a.s.l. Natural vegetation (mainly *Quercus ilex* woodlands) is much transformed, mainly by olive tree growing and cereal cultivation, with dispersed fragments of Mediterranean scrubland and pine (*Pinus halepensis*, *P. pinaster*) plantations.

2.2. Bonelli's eagle population

The Bonelli's eagle population consists of 45–50 pairs, nesting on cliffs (except one pair nesting on *P. halepensis*) within an altitude range of 200–1600 m. The population has been increasing, with five new nesting territories colonised and no abandoned territories between 1990 and 2002. Differences from previous population estimates (29–37 pairs in 1990 by Garza and Arroyo (1996); 30–37 in 1995 by Gil Sánchez et al. (1996)) were due both to better field work cover and to an actual increase of five new pairs. Breeding success is the highest known for the species, with a mean productivity of 1.4 fledglings per monitored pair (Gil Sánchez et al., 2000), whereas the maximum value cited in long-term studies was 1.24 fledglings per monitored pair (Real and Mañosa, 1997).

2.3. Breeding parameters

Between 18 and 33 pairs were annually monitored during the nine years of the study period (1994–2002; $n = 225$). Each nesting territory was visited at least twice, during February to confirm egg laying and during May to estimate fledglings (Gil Sánchez, 2000). Age was estimated from feather development (see Gil Sánchez, 2000 for details), and nestlings older than 50 days or 80% of the mean age at first flight were considered as fledglings (Real et al., 1996; Carrete et al., 2002). Nests were observed with a 20–60 \times telescope to minimize the risk of disturbance, and so data on clutch size could not be estimated. In some cases, egg losses could be recorded by telescope or by visiting the nest (one case), once a failed nest was abandoned by eagles, and some data on chick mortality were recorded during the field work. We also recorded the percent of breeding attempts (laying pairs/monitored pairs $\times 100$), percent of breeding success (successful pairs/monitored pairs $\times 100$), number of fledglings/monitored pair (or productivity) and number of fledglings/successful pair (or flight rate).

2.4. Studied factors

Twenty-seven variables describing nesting areas were studied (Table 1), related to human disturbance (variables 1–10), altitude and relief (variables 11–13), vegetation types (variables 14–25) and intra- and inter-specific relationships (variables 26 and 27). For measuring these variables we used 1:25,000 maps of the National Geographic Institute and 1:50,000 land-use maps of the Ministry of Agriculture. Vegetation data shown on 1974, 1976 and 1977 1:50,000 land-use maps of the Ministry of Agriculture were confirmed or updated by field surveys.

We explored the influence of these variables at two different scales (Sergio et al., 2003), by using two sampling circles. The first circle was 2.85 km radius around the nests, as the mean distance between the closest two pairs observed in the study area (5.7 km, Gil Sánchez et al., 1996). The second circle was 4.4 km radius around the nests, as the mean half distance between neighbouring pairs for all population (Gilmer and Stewart, 1984; González et al., 1992). These two circles are related to nest vicinity and to regional scale respectively (Sergio et al., 2003).

We considered as dependent variables the four breeding studied parameters and the coefficient of variation (CV) of each for 20 territories with seven or more monitored reproduction attempts ($n = 162$). The 27 habitat variables for each territory were considered as independent variables. We used Generalized Linear Mixed Models (GLMM) to describe the relationships between reproductive parameters and the variables measured. For productivity and flight rate (number of

Table 1

Variables describing the nesting habitat of 20 Bonelli's eagle territories. Sources: E 1:25,000 maps (N.G.I.), land use maps E 1:50,000 (Ministerio de Agricultura) and Junta de Andalucía (1992)

Variable	Mean	SD	Range
(1) Distance to nearest inhabited house (m)	980.0	802.8	300–3750
(2) Distance to nearest village (m)	3371.2	1880.2	600–7200
(3) Distance to nearest paved road (m)	2081.5	1440.4	100–6500
(4) Distance to nearest unpaved road (m)	415.0	212.8	100–750
(5) Kilometres of paved road within the 2.85 km circle	5.4	4.6	0–14
(6) Kilometres of paved road within the 4.4 km circle	13.0	9.3	0–31
(7) Kilometres of unpaved road within the 2.85 km circle	11.0	4.9	3–20
(8) Kilometres of unpaved road within the 4.4 km circle	27.0	10.6	12–47
(9) Number of humans inhabiting within the 2.85 km circle	2042.2	5573.3	0–25000
(10) Number of humans inhabiting within the 4.4 km circle	2806.5	5639.6	10–25500
(11) Altitude (m)	1035.0	266.7	550–1600
(12) Topographic irregularity index ^a within the 2.85 km circle	109.5	33.1	60–209
(13) Topographic irregularity index ^a within the 4.4 km circle	260.1	78.8	142–497
(14) Habitat variability index ^b within the 2.85 km circle	9.7	6.1	0–21
(15) Habitat variability index ^b within the 4.4 km circle	24.0	13.1	5–50
(16) Percentage of forests within the 2.85 km circle	20.0	20.3	0–60
(17) Percentage of forests within the 4.4 km circle	15.0	15.3	0–50
(18) Percentage of scrub within the 2.85 km circle	42.6	18.1	20–85
(19) Percentage of scrub within the 4.4 km circle	41.7	21.9	10–80
(20) Percentage of olive/almond trees within the 2.85 km circle	17.6	10.9	0–45
(21) Percentage of olive/almond trees within the 4.4 km circle	24.25	14.3	5–55
(22) Percentage of cereal cultivations within the 2.85 km circle	16.5	16.6	0–70
(23) Percentage of cereal cultivations within the 4.4 km circle	14.5	16.9	0–60
(24) Percentage of irrigated cultivations within the 2.85 km circle	3.4	5.9	0–25
(25) Percentage of irrigated cultivations within the 4.4 km circle	4.5	10.9	0–50
(26) Distance to nearest <i>Hieraetus fasciatus</i> pair (km)	9.02	2.79	5.7–14
(27) Distance to nearest <i>Aquila chrysaetos</i> pair (km)	9.61	6.16	3–28

^a Number of 20 m contour lines cut by two lines from the centre of the sampling circle, one line on the North–South axis and one line on the East–West axis.

^b Number of vegetation types cut by two lines from the centre of the sampling circle, one line on the North–South axis and one line on the East–West axis.

fledglings), we used the log link function and Poisson error distribution, while for the other reproductive parameters we used the identity and Normal error distributions (Breslow and Clayton, 1995). The effect of each variable was first tested separately through univariate models, by considering linear and quadratic forms. We then built multivariable models to identify the relative contribution of each variable, using a forward stepwise procedure resulting in models where only significant variables were retained. For all cases, we included “year” and “territory” as random effects to avoid pseudo-replication. A model was significant if the probability associated with its coefficients was <0.05. We used the Akaike's Information Criterion, AIC, which is usually applied to ranked alternative models (smaller AIC values corresponded with better model; Franklin et al., 2000).

Cliff orientation was studied separately as a categorical variable. Productivity and number of fledglings per successful pair were compared between pairs nesting on north (from 315° to 25°), east (from 26° to 134°), west (from 226° to 314°) and south (from 135° to 225°)-oriented cliffs. Thus, productivity and number of fledglings per successful pair were compared by Kruskal–Wallis

tests, and percentage of breeding success by χ^2 tests. In this case, nests with known causes of failure independent of orientation (as adult mortality or predation) were excluded, and therefore percentages of breeding attempts were not compared.

The influence of weather was studied at a population level, since detailed meteorological data was not available for each territory, and changes of microhabitat may be decisive for the breeding biology of Bonelli's eagles through microclimatic effects (Gil Sánchez, 2000). A weather station was situated at the geographic centre of the study area (600 m.a.s.l) and monthly rain, total rain and mean, maximum and minimum monthly temperatures were recorded. We only considered data corresponding to the breeding season of Bonelli's eagle: pre-laying in January, laying and incubation in February, incubation and hatching in March, and chick and fledgling data in March, April and May (Gil Sánchez, 2000). For the nine years of study, we used non-parametric correlations to relate the four estimates of breeding performance and their CV with annual weather variables.

This data analysis was also performed separately for territories with north-facing nests, because it is the coldest orientation, and therefore a priori the worse nest

orientation for a species from warm areas (Cramp and Simmons, 1980). To determine thermal differences related to cliff orientation, temperature was measured for three pairs of cliffs: at 850, 1250 and 1600 m altitude. Each pair included one north-facing cliff and one south-facing, both separated by <1 km. Some of these cliffs had Bonelli's eagle nests so temperature was not measured during the breeding season to avoid disturbance. However, in the study area, the November temperature is equivalent to the March temperature (Junta de Andalucía, 1992), and so temperature was recorded on 15–16 November 2002, between 1000 and 1100 h during sunny days, with a thermometer situated 10 cm from the base of cliffs.

Bonelli's eagle pellets were sampled from 1995 within the nesting areas, at the end of the breeding season to monitor the diet ($n = 1424$). The pellets were analysed individually and, following Real (1996), each species identified in one pellet was counted as one individual. To study the possible influence of feeding habits on breeding success, a Spearman correlation was performed between the annual studied breeding parameters with their respective CVs and the annual percentage in diet of rabbit (*Oryctolagus cuniculus*), red-legged partridge (*Alectoris rufa*) and pigeons (*Columba* sp.), which are the main prey.

Line transects were used to determine rabbit and partridge availability (Burnham et al., 1980; Gil Sánchez, 1998). Sampling was carried out within the radius of 4.4 km around the nests. A total of 12 territories were studied during 1997 and 11 during 2002. For each territory, a mean of 8.7 km (range = 3.45–13.175 km) were walked by one person on a mean of three line transects (range = 1–6). Censuses were carried out between 0600 and 1000 h and between 1400 and 1600 h as the main activity periods of prey. To avoid seasonal variations in prey, sampling was during March and April, at the middle of the Bonelli's eagle breeding season. Seasonal increases in prey take place in the study area during May for rabbits (Gil Sánchez et al., 1999), and during June for red-legged partridges (Gil Sánchez, 1998). Rabbit abundance was estimated using a linear regression given by Palomares et al. (2001) to obtain an estimate for samples where small numbers were observed (between 2 and 16):

Rabbit density (ind./ha) = $0.57 \times$ number of observed rabbits within 10 m of each side of the transect per km walked ($r^2 = 0.97$, $fd = 68$, $P < 0.0001$).

The possible differences in visibility among habitats were avoided by using a short distance of 10 m (Palomares et al., 2001). For red-legged partridge estimates, we used birds observed within 25 m each side of the transect because the partridges are easier to see than rabbits (Duarte and Vargas, 2001). The effect of prey availability was evaluated through an analysis of differences in prey abundance between territories with two

or three fledged chicks, vs. territories with zero or one fledged chicks, by using Mann–Whitney U-tests.

Nineteen cases of nest building previous to breeding season (July–January) were registered for 15 different pairs. Breeding parameters in these cases were compared with breeding parameters in the rest of the population by Mann–Whitney U-tests.

Following Real and Mañosa (1997), the annual territorial bird mortality was estimated from its replacement of adult birds by non-adult birds. Different plumage colour during the first four years of life (Parellada, 1984) allowed us to assess this replacement, but replacement of adult birds by other adults is undetectable by this method, so these data must be considered as a conservative estimate. Single eagles did not hold a territory for more than three months. The percentage of minimum annual adult bird mortality was related to annual breeding parameters by means of non-parametric correlation. Breeding variables for pairs with one non-adult bird were compared with breeding variables for pairs with two adult birds. The same analysis was carried out for cases of first breeding attempt of a new member of the pair.

3. Results

3.1. Breeding output and causes of failure

The annual breeding parameters are given in Table 2. Successful breeding attempts for this population of 18–33 pairs ranged from $\approx 86\%$ to 100%, breeding success from 75.0% to 94.4%, productivity (fledglings per monitored pair) from 1.17 to 1.55, and flight rate (fledglings per successful pair) from 1.57 to 1.70. In no case was there any significant inter-annual difference (Kruskall–Wallis test and ANOVA gave $P = 0.08$ – 0.43). Comparison between pairs nesting on new nests and old nests showed no significant differences in breeding parameters.

We did not register breeding attempts for 14 cases (13 different pairs), of which 11 (78.5%) were pairs with a non-adult bird ($n = 9$), or temporarily solitary adult birds ($n = 2$). Causes of whole breeding failure included: egg predation by stone marten (*Martes foina*; 1 brood), chick predation by unknown predator (1 chick), chick deaths from a swarm of bees (*Apis mellifera*) colonizing a nest (two chicks), chick death from unknown cause (1), and unknown (12 cases: broods or chicks?). In four successful breeding attempts (broods of two chicks) one of the chicks died – three suspected of trichomoniasis disease and one by mammal predation.

3.2. Influence of habitat variables

Values of the 27 independent variables are given in Table 1. Significant results of the GLIMMIX analysis

Table 2
Annual reproduction parameters and mortality

	1994	1995	1996	1997	1998	1999	2000	2001	2002	Means
Monitored pairs	18	21	19	23	27	24	28	32	33	
Percentage breeding attempts	94.44	100	89.47	87.5	96.29	91.66	85.71	100	90.90	92.78 (SD = 5.20)
Percentage breeding success	94.44	90.47	84.21	91.66	88.88	91.66	75.0	81.25	81.81	86.59 (SD = 6.37)
Total fledglings	28	32	27	34	39	37	33	45	45	
Pairs with 0 fledgling	1	2	3	3	3	2	7	6	6	
Pairs with 1 fledgling	6	6	5	7	10	8	9	7	9	
Pairs with 2 fledglings	11	13	11	12	13	13	12	19	18	
Pairs with 3 fledglings	0	0	0	1	1	1	0	0	0	
Productivity	1.55	1.52	1.42	1.47	1.44	1.54	1.17	1.40	1.36	1.43 (SD = 0.11)
Flight rate	1.64	1.68	1.68	1.70	1.62	1.68	1.57	1.73	1.66	1.66 (SD = 0.04)
Percentage adult mortality	2.17	1.85	5.66	3.38	1.63	1.44	10.90	0.00	2.63	3.29 (SD = 3.24)

were observed for all dependent variables except for breeding attempts and breeding success (Table 3). Univariate models were selected for productivity, flight rate and CV of productivity, whereas a multivariable model was selected for CV of flight rate (Table 3). Models were made with 11 independent variables related to human presence (variables 1, 7, 8, 9, 10), vegetation type (variables 17, 18, 22, 24, 25) and golden eagles (variable 27). No important results were observed by increasing the sampling circle to 4.4 km (Table 3). Pairs nesting on north-facing cliffs had significantly lower breeding success than pairs nesting on the other cliff orientations (Table 4). Statistical differences were observed between north- and south-facing cliffs for productivity (Kruskall–Wallis test, $H = 16.02$, $P = 0.001$) and for fledglings per successful pair (Kruskall–Wallis test, $H = 9.13$, $P = 0.025$), but not between other orientations (E–W;

S–W; S–E; N–E; N–W: Kruskall–Wallis test $P > 0.05$ for all cases).

3.3. Influence of weather variables

Average annual temperature had no important variation during the study period: total rainfall registered strong annual variations (Fig. 2), but showed no relationship with the annual breeding parameters. In the case of breeding attempts on north cliffs, however, a significant positive relationship was observed between number of fledglings per successful pair and mean April temperature ($R_s = 0.925$, $P < 0.01$, $n = 9$). North-facing cliffs had a mean temperature of 10 °C less than south-facing cliffs at the same altitude, and the lowest north-facing cliff registered a colder temperature than the highest south-orientated cliff (Table 5).

Table 3
Results of the GLIMMIX analysis for four dependent variables (productivity, flight rate, and their CV) in relation to 27 habitat variables

	Variable	Estimate	SD	DF	<i>t</i> value	<i>P</i>
Productivity	27 (dist Aquila)	0.015	0.007	162	2.21	*
	17 (forest 4.4 km)	0.024	0.010	161	2.39	*
	17 ² (forest 4.4 km)	–0.001	0.000	161	–2.54	*
Flight rate	27 (dist Aquila)	0.009	0.004	137	2.16	*
	17 (forest 4.4 km)	0.014	0.006	136	2.20	*
	17 ² (forest 4.4 km)	–0.000	0.000	136	–2.24	*
	25 (irrigation 4.4 km)	0.006	0.002	137	2.60	*
	10 (humans 4.4 km)	0.000	0.000	137	2.79	**
	24 (irrigation 2.85 km)	0.011	0.004	137	2.59	*
	9 (humans 2.85 km)	0.000	0.000	137	2.65	**
Productivity (CV)	1 (dist house)	6.193	1.598	16	3.88	**
	1 ² (dist house)	–0.128	0.034	16	–3.80	**
Flight rate (CV) ^a	22 (cereals 2.85 km)	–3.435	0.897	9	–3.83	**
	18 (scrub 2.85 km)	16.127	5.040	9	3.20	*
	27 (dist Aquila)	12.188	3.037	9	4.01	**
	7 (unp. roads 2.85 km)	–212.580	78.295	9	–2.72	*
	7 ² (unp. roads 2.85 km)	14.738	5.790	9	2.55	*
	22 ² (cereals 2.85 km)	–0.128	0.047	9	–2.69	*

Only significant habitat variables are shown. See Table 1 for variable abbreviations.

* $P < 0.05$.

** $P < 0.01$.

^a Multivariate model.

Table 4
Nest orientation and breeding parameters

Orientation	Productivity	Flight rate	Breeding success
North (<i>n</i> = 52)	1.46	1.65	88.46
East (<i>n</i> = 55)	1.58	1.64	98.46
South (<i>n</i> = 34)	1.82	1.82	100
West (<i>n</i> = 53)	1.54	1.60	96.22
Kruskall–Wallis/ χ^2 tests	<i>H</i> = 6.71	<i>H</i> = 4.30	χ^2 = 12.24
<i>P</i>	ns	ns	**

ns: not significant.
** *P* < 0.01.

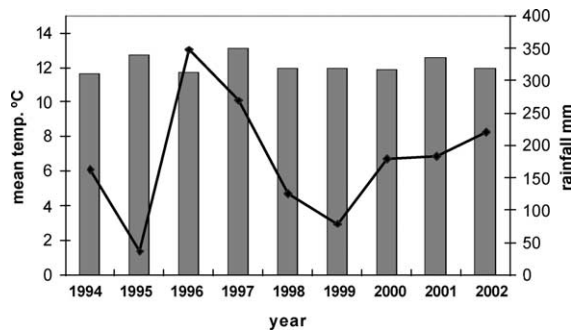


Fig. 2. Annual rainfall (line) and mean temperature during the Bonelli's eagle breeding season.

Table 5
Thermal differences between nests on north-facing cliffs and nests on south-facing cliffs

Orientation	Nest	Altitude	Temperature °C
South	Yes	850	26.0
North	No	850	16.5
South	Yes	1250	23.5
North	Yes	1250	13.0
South	Yes	1600	21.5
North	No	1600	11.2

3.4. Diet and prey availability

Diet was 65% based on rabbits and red-legged partridges. Pigeons, other mammals, other birds and lizards were secondary prey (Fig. 3). Only rabbits showed some inter-annual variation in the diet (Fig. 3), but no relationship between any prey item and breeding parameters was found by Spearman correlation analysis. No inter-annual difference in rabbit and partridge availability (from transect counts) was found, so data from 1997 and 2002 were pooled. There were no significant differences between the observed prey availability in territories with 2–3 fledglings (means: 0.19 rabbits/ha and 0.13 partridges/ha) and territories with 0–1 fledgling (means: 0.37 rabbits/ha and 0.18 partridges/ha).

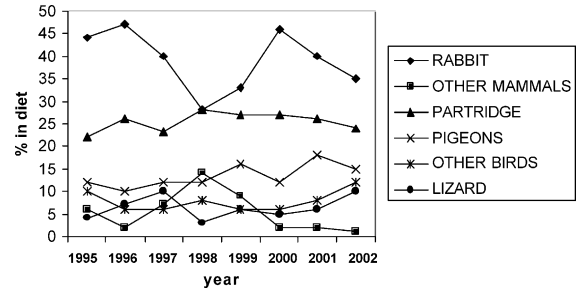


Fig. 3. Annual changes in Bonelli's eagle diet.

3.5. Adult mortality and age of territorial birds

Minimum annual adult mortality ranged from 0.00% to 10.90% (Table 2), with no inter-annual differences (Kruskall–Wallis test, *H* = 7.99, *fd* = 8, *P* = 0.43). A significant relationship of adult mortality with year was observed only in the case of breeding attempts (*R*_s = -0.84, *P* < 0.05, *n* = 9). In 12 cases of pairs with one non-adult member, the reproductive success was very low, with only 0.25 fledglings per monitored pair. Laying was not observed for 10 of these, but during the following breeding season they all showed increased success, with an average of 1.60 fledglings per monitored pair (*n* = 10).

4. Discussion

4.1. Human disturbance and land use

Known causes of egg losses or chick death had no important influence on the breeding success of the studied Bonelli's eagle population. Some variables selected by the GLMM analysis were the same as those found in a nesting habitat selection study carried out in the same area, namely distances to nearest golden eagle nest, unpaved roads, forest, scrub, cereal crops, and irrigated cultivations within the sampling circle of 2.85 km (Gil Sánchez et al., 1996). All these variables might be related to human disturbance and/or prey availability, although for the studied population, prey availability was not an important variable defining breeding biology of Bonelli's eagles. However, the observed positive effects on flight rate of percentage of irrigated cultivations was an unexpected result, which is hard to explain, since it is the habitat type with the highest human use.

4.2. Effects of golden eagles

Proximity of golden eagle pairs had been previously suggested as a negative factor for Bonelli's eagle breeding success (Parellada et al., 1996), and our GLM analyses suggest that this might affect eclosion rate and/or chick survival, but probably not breeding attempts.

Territorial interactions between both raptor species are well known, with cases of usurpation and displacement of Bonelli's eagle pairs by golden eagles (Parellada et al., 1996; Arroyo et al., 1995). Moreover, competition with golden eagles interacting with human persecution has influenced the decline of a nearby population of Bonelli's eagles in south-eastern Spain (Carrete et al., 2002).

Competition between golden and Bonelli's eagles is an expected phenomenon in Mediterranean areas of sympatry, since both are cliff-nesting raptors with a high overlap in diet preferences (Gil Sánchez et al., 1994). In our study area there is a population of 42 pairs of golden eagle (personal data), and the proximity to golden eagle nests is a negative factor for nest-site selection by Bonelli's eagles (Gil Sánchez et al., 1996). In fact, the density for both species together is as high as one pair per 106 km², and cliffs for nesting become a scarce and limiting factor. During the field work, we could see some direct interactions with a very strong aggressive response of Bonelli's eagles when golden eagles flight near the occupied nests. This behaviour was also observed by Cheylan (1981) in southeast France, and it might be common for neighbouring pairs of both species.

Consequences for breeding are related to the temporal absence of adults from the nest, which may be very important for egg viability and/or the survival of very young chicks. In our study area, egg-laying of Bonelli's eagles occurs a month earlier than golden eagles, and this may carry bad consequences for the former because golden eagles are actively defending their territory (Watson, 1997) when Bonelli's eagles are laying. We believe that competition for prey resources is probably not an important factor, since there is an optimal prey availability in the study area, and the breeding success of both species is high (present study, Gil Sánchez et al., 1994; Moleón et al., 2002).

The great tolerance of Bonelli's eagle to human presence (see Table 1) could avoid some of the potential negative influence of golden eagles competition for nest sites (Gil Sánchez, 1996), which may explain the selection by our GLMM models of the number of humans and irrigated cultivations as a variable with positive effect on the flight rate. Although human presence is usually known to have negative effects for raptors (Newton, 1979), it may paradoxically be positive for Bonelli's eagles, since golden eagles avoid areas with human presence (Gil Sánchez et al., 1994; Carrete, 2002).

4.3. Cliff orientation

Microclimatic factors might explain why nests on north-facing cliffs registered a lower breeding success because these cliffs have a lower sun exposure and a colder influence than south-facing cliffs (Table 5). This

finding was also supported by a positive relationship between mean temperature in April and the number of fledglings per successful pair in north-facing nests. Low temperatures could thus affect chick survival during the first weeks of age by increasing heat loss, as this is one of the most important factor affecting chick survival in nidicolous species (Elkins, 1983).

Hawk-eagles (*H. fasciatus*, *H. spilogaster*, *H. ayresi*, and *Spizaetus* spp.) are a raptorial group of tropical distribution that is well adapted to environments of high rainfall levels (del Hoyo et al., 1994). As a tropical raptor therefore, the effects of weather on nestling success of Bonelli's eagles would be mostly related to cold conditions affecting the survival of small chicks. This hypothesis not only agrees with the observed relationships between cliff orientation and breeding success, but also with the European distribution of the species along the Mediterranean area (the warmest Palearctic region; Fig. 1); it is also the altitude limitation for breeding, since 1600 m (present study) is the highest value observed in Europe, whereas a typical Holarctic raptor such as the golden eagle nests as high as 2500 m in the same study area.

Ontiveros (1999) has suggested that Bonelli's eagles breeding at our study area select cliffs with southern orientations because they provide more thermal lift to the eagles, thus enhancing the possibilities of soaring, which in turn would be important for reproductive success. On the contrary, we did not find such a selection for south-facing cliffs. Thermal soaring by adult eagles breeding on north-facing cliffs was often observed as these eagles could reach the thermal bubbles within a short flight to the nearest southern slope, usually located less than 100 m away.

It should be pointed out that in the studied population, even those pairs breeding on north-facing cliffs showed a high reproductive success. Local weather variations had little consequences for breeding at a population level, and therefore observed values of temperature and rainfall can be assumed to be suitable for Bonelli's eagles. A negative relationship between rainfall and breeding success was found in a relic and endangered population of Bonelli's eagle in northern Spain (Fernández et al., 1998). However, this northern population lives at the thermal tolerance limits of the species, within an area of very low prey abundance (Fernández et al., 1998), and therefore where the eagles may be more vulnerable to rain (Newton, 1979; Elkins, 1983; Gargett, 1990).

4.4. Food supply

We did not find any inter-territorial influence of prey availability on reproductive success, but it has been observed in northern Spain and France, probably because of a lower abundance of rabbits and partridges

than in southern Spain (Cheylan, 1981; Fernández et al., 1998). A previous study carried out within our study area analysed the effect of prey availability on breeding success of Bonelli's eagles, but rabbits and partridges were estimated from line transects without any truncated distance (Ontiveros and Pleguezuelos, 1999). We observed during prey censuses a great variability of scrub cover and visibility (especially for rabbits), so we believe that the methods used by that study are not appropriate, although in any case, the results were similar to ours.

4.5. *Adult mortality*

Adult mortality is one of the main factors affecting reproductive success of Bonelli's eagle populations in the East Mediterranean coast of Spain, which is related to intensive direct human persecution by hunters and competition pigeon fanciers (Real and Mañosa, 1997; Real et al., 2001; Carrete et al., 2002). In our study, adult survival reached one of the highest scores observed among the long-term studies carried out using the same estimation method and species (see Real and Mañosa, 1997). Adult mortality may be underestimated, since it was not possible to identify cases of breeding adults substituted by other adults. However, adult birds are substituted by other adults when the population is healthy (Ferrer, 1993). On the other hand, for the studied population, the annual rate of substitution was the lowest known for the species, and no problems of population dynamics have been observed during the last 10 years. Unlike some problematical regions (Real et al., 2001; Carrete et al., 2002), the Granada region has little tradition of rearing racing pigeons and this may partly explain the low adult mortality here.

4.6. *Conservation implications*

The Bonelli's eagle subpopulation of Granada may serve as an important source for some Iberian declining 'sink' subpopulations (Pulliam, 1988; Wootton and Bell, 1992; Real and Mañosa, 1997). Moreover, the great distance of young dispersal flights in the Bonelli's eagle (up to 2100 km and daily distances of 254 km; Alcántara et al., personal communication) increases the geographic range for developing a good management strategy. It is therefore priority to preserve the habitat features for the important monitored population and assure the vigilance of the breeding areas by the environmental authorities.

One applied result of this study is the list of habitat variables associated with a healthy population, which might be assumed as optimal and therefore used for comparison with areas where the Bonelli's eagle is declining. This is a key information for the conservation of the Bonelli's eagle, because it is generally scarce or non-existent for endangered species. Data from vegetation

characterization and prey abundance may be used in habitat restoration programmes, like those carried out in critical areas of the European distribution (Mure, 2003). Data from human presence may be useful when planning new roads or urban projects.

The effect of golden eagles may pose an interesting conservation problem, because it is also an endangered species. Within our study area, golden eagles do not have an important effect, since the breeding success of Bonelli's eagles is high. However, in other areas land-use manipulations to enhance Bonelli's eagle populations (like prey management), could favour golden eagles, with subsequent negative effects on the former species. It is therefore important to consider the presence and abundance of golden eagles in order to design the management strategies for declining populations of Bonelli's eagles. Thus, conservation projects that include rabbit reintroductions (Mure, 2003) may not give the expected results, because these actions may also favour golden eagles (which are more specialized on mammal predation; (Moleón et al., unpublished). The reintroduction of other prey species, such as partridges or pigeons (i.e. doves), may be more useful for the recovery of the Bonelli's eagle populations.

Variables related to weather conditions could also yield comparative results, which may aid our understanding of the biology of the species and its decline in European areas at current distribution limits (i.e. colder and more humid), as is required by the European Action Plan for the Bonelli's eagle (Birdlife International, 1999). Usually, the funds for conservation programmes are limited elsewhere so it is important to concentrate protection efforts on the more productive pairs of the population to be most effective (Pedrini and Sergio, 2002). Thus, the conservation priorities for the Bonelli's eagle should focus on the pairs nesting on south-facing cliffs and where human presence reduced interference from golden eagles.

On the other hand, survival data from breeding birds confirms the importance of controlling adult mortality by environmental authorities elsewhere (Real and Mañosa, 1997). This requires strict vigilance of the hunting areas to avoid adult mortality by shooting, and to reduce electrocution from power lines by taking appropriate measures (Ferrer and Janss, 1999).

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