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Physical, environmental and human factors influencing productivity in Bonelli's eagle *Hieraaetus fasciatus* in Granada (SE Spain)

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Abstract. We analysed the productivity of the Bonelli's eagle *Hieraaetus fasciatus* in relation to 26 variables that account for physiography, level of human presence, land-use, climate, laying date, and nest orientation, in the province of Granada (SE Spain), where a stable population exhibits the maximum productivity value for the species in Europe. Productivity positively correlated with cliff availability within territories and closeness of nest site to SE orientation. Cliff availability permitted some pairs to choose the best nest site orientation, thereby favouring high productivity. Nests in the preferred orientation (SE) had 35% higher productivity than those towards non-preferred orientations. Higher productivity in the best orientation nests might be related to warmer conditions. High productivity in the study area could offset the main problem for Bonelli's eagle conservation in Europe, that is, the high preadult and adult mortality. Actions required to ensure the recovery of neighbouring populations must focus on the preservation of high cliff availability and the diminution of preadult mortality in southeastern Spain. This would favour restocking of the decreased northern populations by the juvenile dispersion.

Introduction

Many factors can be involved in the breeding success of raptors, such as ecological differences between regions, habitats or territories (Gargett 1977; Watson et al. 1992; Donázar et al. 1993), and the influence of weather, parasites, and diseases (Collias and Collias 1984). The selection of a proper nest site is vital in the productivity of birds, because it determines the environment to which adults, eggs, and altricial chicks will be exposed during critical periods; therefore, birds tend to place their nest in the most favourable habitat (Skutch 1976; O'Connor 1984; Viñuela and Sunyer 1992).

The Bonelli's eagle is an accipitrid that in the western Palearctic is confined to the Mediterranean area, generally in fairly warm and dry regions (Cramp and Simmons 1980). The size of the European population is estimated at 938–1039 breeding pairs, 80% being in Spain (Real et al. 1996). This eagle is an endangered European species, with populations markedly declining in recent years (Rocamora 1994); in Spain, for example, 116 breeding pairs (15–17% of the population) disappeared during 1980–1990 (Arroyo et al. 1995). Consequently, this eagle has been classified as vulnerable in Spain (according to IUCN categories; Blanco and González 1992), and high-priority conservation measures have been urged (De Juana 1992).

Scarce prey availability has been cited as a possible cause of the low breeding success of Bonelli's eagle in some areas (Cheylan 1981; Real 1987). Notwithstanding, in southeastern Spain (the study area for the present analysis), where prey availability has been exactly measured, the distribution and productivity of the Bonelli's eagle was not affected by the availability of its main prey (Ontiveros and Pleguezuelos 2000). Nevertheless, there is no information about whether factors such as human presence and habitat characteristics influence productivity. This information is important, because in Spain Bonelli's eagle nests most frequently on cliffs and only rarely in trees (Arroyo et al. 1995), so nesting sites might be a limiting resource. Moreover, the altitude distribution of the species (below 1500 m a.s.l.) causes its territory to overlap frequently with human-populated areas (Cheylan 1981; Parellada et al. 1984; Ontiveros 1999). Nest orientation affecting reproductive success has been shown in very few cases (Austin 1974, 1976; Viñuela and Sunyer 1992), and never for Bonelli's eagle, even though the distribution of this raptor is clearly limited by temperature (Cramp and Simmons 1980), and nest orientation may influence the temperature at the nest (Collias and Collias 1984).

The present study analyses the productivity of Bonelli's eagle in relation to variables of topography, human presence, land-use, climate, and the preferred nest orientation. Laying date is also considered as a possible factor influencing productivity of the raptor (Cheylan 1981; Viñuela and Sunyer 1992). Our results are intended to provide new information on the reproductive biology of Bonelli's eagle in an area where the species maintains a relatively healthy population, a circumstance not common, since most of the studies on this species are carried out in areas where the populations are crashing. This information is essential to design conservation strategies for this raptor, and management recommendations are provided here.

Study area and methods

The Bonelli's eagle population studied is located in the province of Granada, southeastern Spain (36°50′–38°10′ N; 2°20′–4°30′ W). The region is largely mountainous, with the greatest altitude range of the Iberian Peninsula (0–3482 m a.s.l.), though the study area spans altitudes from 500 to 1490 m a.s.l. The climate is typically Mediterranean, with average minimum temperatures of 0.5–6.5 °C in winter (January), average maximum temperatures of 28.0–34.5 °C in summer (July), and annual rainfall averaging 325–850 mm (30-year standard meteorological average; CMA 1997). The vegetation is composed of evergreen oak *Quercus ilex* trees and scrub, and some species of pines *Pinus* spp. Cereal farms and tree plantations exist on plains and in valleys.

Productivity and laying date

Reproductive data of Bonelli's eagle in the study area were available for 22 territorial pairs monitored for eight years (1994–2001). To avoid problems of pseudoreplication, productivity was defined as the number of fledglings raised by

Table 1. Variables used to characterise nest site and territory of Bonelli's eagle.

Nesting site

Altitude: altitude of the nest above sea level (m).

Height cliff: nesting-cliff height (m).

Slope: inclination of the slope at the base of the nesting cliff (°).

Orientation: deviation of nest orientation from the preferred mean nest orientation of the whole population (120.6°).

Relief: topographic irregularity index. Total number of 20-m contour lines cut by two lines equivalent to 2 km designated on the map (scale 1:50000), in directions N–S and E–W, and that crossed on the location of the nesting cliff.

Nearest neighbour: distance between the nest and the closest nest of the nearest neighbour pair (km).

Cliff availability: number of squares (1 km^2) with suitable cliffs for nesting in each territory. A cliff was considered suitable for the nesting of Bonelli's eagle when there were cavities or ledges, located below 1500 m (altitudinal limit of the Spanish population; Arroyo et al. 1995), higher than 20 m, and farther than 500 m to an urban centre (minimal distances found for the population here studied).

Human presence

Distance village: distance from nest to the nearest urban centre (m).

Distance paved road: distance from nest to the nearest paved road (m).

Distance unpaved road: distance from nest to the nearest unpaved road passable by vehicle (m).

Distance inhabited building: distance from nest to the nearest inhabited building (m).

Distance cultivation: distance from nest to the nearest field under cultivation (m).

Kilometres paved road: km of paved roads in a 2000 m radius from the nest.

Kilometres unpaved road: km of unpaved roads in a 2000 m radius from the nest.

Height paved road: altitudinal difference between the nest and the closest paved road, measured at the point where the road was closest to the nest (m).

Electric power lines: km of high-tension electric power lines in the territory.

Inhabitants: total number of human inhabitants in the territory.

Land-use

Forest: km^2 of the territory covered by forests.

Scrubland: km^2 of the territory covered by natural vegetation under 2.5 m in height.

Orchard: km^2 of the territory covered by orchards.

Cultivated cereal: km^2 of the territory covered by cereal cultivation.

Meteorology

Rainfall: annual rainfall average (mm).

Temperature: average annual temperature.

Maximum temperature: average maximum temperature for the hottest month (July).

Minimum temperature: average minimum temperature for the coldest month (January).

Others

Laying date: average laying date; days from January 1 that clutch occurred (see Methods for more details).

territorial pair per number of years monitored, including reproductive failures and not laying pairs. This is the most meaningful measure of the reproductive health of a raptor population, because it would be incorrect to exclude from the analysis pairs not laying eggs (Brown 1974; Steenhof and Kochert 1982). A chick was considered as fledged when it reached at least 60 days of age (Real and Mañosa 1997). Laying dates were estimated from nestling age when possible, the latter based on the feather-growth method of Torres et al. (1981), which has an error of ±5 days. To the age of each nestling, we added 39 days (mean incubation period for the species; Arroyo et al. 1995) to estimate the laying date for each clutch, obtaining a mean laying date for each pair during the study period. The pattern of feather growth was determined by observing nestlings at a distance by telescope.

Nest site and territory characterisation

Many pairs of Bonelli's eagle changed nests during the study period, but within short distances and often between nests located on the same cliff. Nevertheless, when pairs changed to a different nesting cliff during the study period (two pairs), we considered the new situation as a new reproductive event.

We measured different variables (Table 1) and related them to productivity. The independent variables were chosen among those usually measured in studies on the breeding success of raptors (Howell et al. 1978; Donázar et al. 1993). In pairs which used different nests on the same cliff we averaged variables related to nest site and territory, calculating them from the central point of all nesting sites on the same cliff.

A previous study about nest cliff selection of the same population of Bonelli's eagle showed significant differences between orientation of the nesting cliffs and available cliffs within territories (Ontiveros 1999). This is the reason why we also included nest-site orientation in the analysis, from the data of mean nest orientation of the population calculated with circular statistics (Fisher 1995). To analyse the effect of laying date on the productivity of pairs, we related both variables distinguishing between all breeding attempts, those located in a preferred orientation, and those in non-preferred orientations (Figure 1).

We considered the same territory shape and size for each pair, i.e. circular and with a radius equal to half the average distance between nests of neighbouring pairs in a cumpled population (5.0 ± 1.2 km [mean ± SD]; n = 32), based on previous data for this area (Ontiveros 1999).

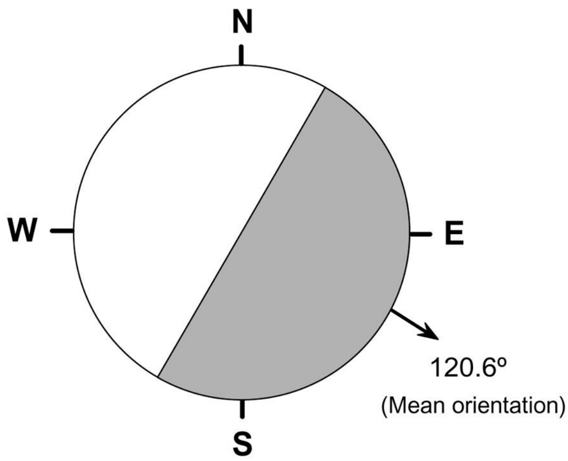

Figure 1. Mean nest orientation of Bonelli's eagle in the study area. The shaded area indicates the 'preferred' nest orientation of the population used in the analysis of the productivity.

Nesting-cliff characteristics and human-pressure variables were measured on 1:50 000 topographic maps prepared by the Spanish Army Cartographic Service, and 1:50 000 land-use maps of the Spanish Ministry of Agriculture. Variables related with nesting-cliff physiography were measured with an altimeter (VZ Performance; precision ± 1 m), theodolite (Pentax PTH 20; precision ±10″), and clinometer (Suunto MC-1D; precision ± 2°). The nest orientation was determined, by compass, to the nearest 5°. We also used the reports of Junta de Andalucía on the human population census of 1994 (IEA (Instituto Estadístico de Andalucía) 1995) and climatic variables from the weather stations closest to each pair (CMA (Consejería de Medio Ambiente) 1997). Two variables (distance paved road and inhabitants) were log-transformed to meet normality and homogeneity of variance requirements.

For the statistical analysis, we first made a linear correlation between the average productivity of each pair and the variables described in Table 1. Second, we made a global correlation among the independent variables to find out redundancy between variables, and to eliminate some of them, due to the relatively high number of independent variables and relatively low number of cases (Edwards 1985). Then, we performed a stepwise forward and backward multiple regression analysis with α = 0.05, which is not only predictive, but also serves to establish functional relationships between dependent and independent variables after controlling for their covariation (StatSoft Inc. 1998). The forward and backward procedures add and remove variables (respectively), one at a time, until the addition or subtraction of further variables does not significantly increase R^2 (Nicholls 1989).

Results

The laying period of Bonelli's eagle spanned from 20 January to 12 March, 14 February being the average laying date (n = 105), with low dispersion within pairs (mean range = 9.8 ± 5.1 days; n = 22). The percentage of pairs successfully raising young (at least one nestling) ranged between 66.7 and 95.0% according to year (sample size ranged between 16 and 22 pairs), and averaged 77.3% over the eight-year study period (n = 150). The average productivity was 1.34 ± 0.76 (n = 150) and there was no difference in this parameter among years (Kruskal–Wallis test: $H_{7,150}$ = 6.99; P = 0.43); there was a different productivity among pairs, either considering annual productivity as independent events (Kruskal–Wallis test: $H_{21,150}$ = 42.72; P = 0.003), or dependent events (Friedman ANOVA test: χ^2, df = 21; P = 0.034). The mean distance among nests on the same cliffs used by a pair during the study period was 38.0 ± 32.2 m.

Of the variables characterising nesting cliffs and territories, productivity was significantly correlated with cliff availability within territories and nest orientation (Table 2). The multiple regression analysis confirmed the importance of the nest site, since the variables selected by the models to explain productivity variability were also cliff availability and nest orientation in forward ($F_{2.21}$ = 8.01, R^2 = 0.43; P = 0.003) and backward analysis ($F_{2,21}$ = 7.65, R^2 = 0.42; P = 0.003). The higher the cliff abundance within territories and the closer the nest orientation towards the

Table 2. Values for variables and correlation between productivity (average number of fledglings per year) and variables characterising nest site and territory.

Variable	Mean	SD	Range	r	P
Nesting site					
Altitude	1030.4	235.5	500–1490	0.19	0.37
Cliff height	43.9	24.7	11–105	0.10	0.64
Slope	34.6	10.1	17–55	−0.13	0.54
Orientation	91.1	58.2	9.4–179.4	−0.55	0.005[a]
Relief	54.7	13.9	34–95	0.22	0.30
Nearest neighbour	9.5	2.8	5.8–14.5	−0.06	0.79
Cliff availability	6.5	2.5	2–11	0.59	0.002[a]
Human presence					
Distance village	3460.4	1927.1	500–7000	−0.09	0.68
Distance paved road	1622.7	1241.6	150–4200	−0.007	0.97
Distance unpaved road	528.9	374.6	60–1400	0.18	0.39
Distance inhabited building[b]	1000.0	765.5	300–3250	−0.23	0.29
Distance cultivation	992.7	1314.8	50–3050	−0.01	0.96
Km paved road[b]	3.5	3.7	0–10	0.002	0.99
Km unpaved road	4.9	2.5	0.5–12	−0.16	0.45
Height paved road[b]	208.6	124.7	30–450	−0.03	0.89
Electric power lines[b]	7.6	5.9	0–21	0.17	0.46
Inhabitants	2896.8	3242.0	0–11025	0.15	0.45
Land-use					
Forest	17.4	15.7	1–52	0.45	0.031
Scrubland	28.2	11.6	4–47	−0.02	0.92
Cultivated tree	12.0	8.4	0–26	0.17	0.43
Cultivated cereal[b]	4.1	6.7	0–27	−0.133	0.61
Meteorology					
Rainfall	533.1	114.9	274–843	0.27	0.20
Temperature	15.6	1.1	13.7–17.8	−0.06	0.79
Maximum temperature[b]	38.2	2.0	34.3–41.6	0.801	0.72
Minimum temperature[b]	−2.2	2.5	−5.3–4	0.140	0.53
Others					
Laying date	44.8	6.0	31.5–56.4	0.047	0.82

[a] Tests that remain significant ($P < 0.05$) after Bonferroni sequential correction (Rice 1989). [b] Variables excluded from the multiple regression analysis because of their redundancy.

preferred orientation (facing the southeast; Figure 1), the higher the productivity. Supporting previous results, we found a relationship between cliff availability and 'better' nest orientation ($r = -0.52$; $P = 0.009$); the higher the cliff availability within territories, the closer the orientation of the nest used to the mean nest orientation. Nevertheless, we failed to find a relationship between cliff availability and nest change in sequential years ($r = -0.05$; $P = 0.81$).

The analysis of nest orientation revealed a trend towards a southeastern orientation rather than a random distribution (Rayleigh test, $r = 0.18$, $P = 0.002$; mean orientation 120.6° ± 70.2°; $n = 119$; Figure 1). Nests located in preferred orientations (see Figure 1) had 35% higher productivity compared to nests in the non-preferred orientations, and produced more fledglings per successful nest (pairs with three fledglings [$N = 2$] pooled with pairs with two fledglings; $G = 21.1$, df =

Table 3. Number of fledglings raised by Bonelli's eagle in Granada, in 71 breeding attempts in nests located towards the preferred orientation, and 65 breeding attempts towards non-preferred orientations.

	Fledglings raised			Mean productivity ± SD
	0	1	2–3	
Preferred orientation	4/71 (5.6)	20/71 (28.2)	47/71 (66.2)	1.62 ± 0.63
Non-preferred orientations	12/65 (18.5)	30/65 (46.1)	23/65 (35.4)	1.20 ± 0.71

See Figure 1 for the groups of nests considered as preferred and non-preferred orientations. Percentages in brackets.

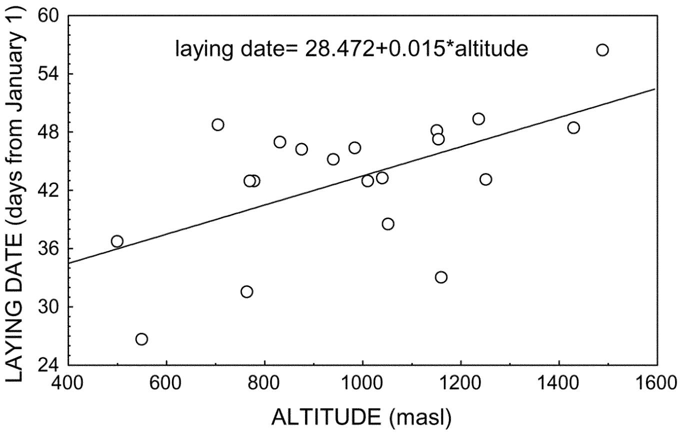

Figure 2. Laying date of Bonelli's eagle in southeastern Spain (1994–2001 period) in relation to nest altitude.

2, $P = 0.00002$; Table 3). Moreover, five out of the seven nestlings found dead in the nest during the study period were in nests located towards a non-preferred orientation.

We failed to find a relationship between laying date and productivity, either for the whole population considered (Table 2), or within the groups formed according to preferred or non-preferred nest orientation ($r < 0.21$; $P > 0.48$, in both comparisons). Laying date was directly correlated with nest altitude ($r = 0.58$, $P = 0.008$, $n = 20$; Figure 2); the higher the altitude, the later birds laid.

Discussion

According to available data, the productivity of Bonelli's eagle in the province of Granada was higher than in other European populations (1.34 compared with between 0.36 and 1.24 fledglings per pair per year; Real and Mañosa 1997). The univariate correlations, the forward and the backward multiple regression analyses, agree upon which of the independent variables are likely to be significant, which implicates reliability of the analysis (Mac Nally 2000). Productivity depended mainly on nesting-cliff availability and nest orientation, which agrees with the finding that a suitable nest cliff is the most limiting resource for this eagle in southeastern Spain (Ontiveros 1999). In the regression model these two variables explain up to 43% of the variance in productivity.

In effect, according to our results great cliff availability appears to be advantageous, since in this situation pairs could have the opportunity to choose the best nest site (i.e. nest orientation). Another possible advantage could be to shift if pairs are disturbed, displaced by another species, or if their first breeding attempt fails early (Newton 1979). Bonelli's eagle occupies low-altitude areas (Cramp and Simmons 1980), causing its territory to overlap frequently with human-populated areas, as reported elsewhere (Cheylan 1981; Arroyo et al. 1995; Ontiveros 1999). Tolerance to human proximity, the selection of the highest nesting cliff within territories (Ontiveros 1999), and the high cliff availability within some territories in the study area may explain why the different human activities had no apparent effects on productivity (Table 2).

On the other hand, a proper nest orientation is an important factor in the productivity of this Mediterranean raptor; Bonelli's eagle tends to build its nests towards a southeastern orientation. In fact, many birds choose orientations towards the east or southeast (Cannings and Threlfall 1981; Zerba and Morton 1983; Martin and Roper 1988), and the highest productivity occurred among the nests located in the preferred orientation (Viñuela and Sunyer 1992).

Protection from thermal extremes may be the most important factor in nest-site selection by medium- and large-sized raptors for which nest predation is low (Collias and Collias 1984). Nests with southeastern orientations warm early in the morning, a factor likely to be important for Bonelli's eagle, the earliest breeder among all Mediterranean eagles (Cramp and Simmons 1980). The province of Granada is rather cold in the breeding season of the eagle, and optimal nest orientation may contribute to an adequate thermal environment for the survival of the embryo or the nestlings. For some raptors, nestling deaths are more frequent in wet and cold weather because the young become soaked and chilled (Moss 1976). Therefore, the effects of cold could influence the productivity of Bonelli's eagle in the area. This would account for the finding that nests placed towards non-preferred orientations had a higher number of breeding attempts with only one nestling or none at all (Table 3).

In some raptors individuals laying near the start of the breeding season reproduce more successfully than those laying later (Newton 1979); Cheylan (1981) describe this circumstance for Bonelli's eagle in France. However, laying date had no detectable effect on productivity of Bonelli's eagle in Granada (Table 2), but rather depended upon altitude of the nests (Figure 2), a factor reflecting differences in environmental characteristics that shift with altitude (rainfall, temperature, radiation).

The southeastern Iberian Peninsula houses the most important population of Bonelli's eagle in Europe; the human presence does not condition the habitat selection of the Bonelli's eagle in the area, but the roughness of the territory does (Ontiveros 1999; Sánchez-Zapata and Calvo 1999; Rico et al. 2001). In agreement with these conclusions, our results indicate that at present, productivity is not affected by human presence in Granada, but by the availability of appropriate nest sites. Therefore, the high cliff availability in this rugged area can be the cause of the healthy population of the zone. Although cliff availability and nest orientation explain only 43% of the variance of productivity, it is an important data, because of the lack of models explaining the low productivity of other populations of this endangered raptor. Notwithstanding, this low percentage indicates the possibility of other factors influencing the productivity of Bonelli's eagle. It is possible that territory scale, variables selected for the analyses of territories, or both, are not completely adequate to describe the variation in productivity of this raptor, as occurred in other studies (Wiens 1989; Litavitis et al. 1994).

Bonelli's eagle suffer a high preadult mortality in the study area, with at least 18 preadult individuals shouted or electrocuted in the 1990–1999 period (Ontiveros 2000), although the population appears to have remained stable for the last 10 years. The study area is largely mountainous, and here Bonelli's eagle could perform changes in nesting sites when human disturbance appeared in their territories (Ontiveros 1999). The lack of alternative nesting cliffs in other less rugged regions might also preclude higher productivity of Bonelli's eagle.

Maintaining high productivity of the eagles in southeastern Spain is a important factor for the conservation of this population and, possibly, other neighbouring populations. In this way, it is necessary to maintain the high cliff availability in the distribution area of the species, avoiding road construction near nesting cliffs, abandoned in some cases because of this (Ontiveros 2000), and to decrease the high preadult mortality (Real and Mañosa 1997). These measures can contribute to the stability of the southern population, and the restocking of the northern ones through dispersion (Real and Mañosa 2001).

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